EXPLORING THE EFFECTS OF SHARED HOME RANGES ON HUMAN-WILDLIFE INTERACTIONS, PARASITE OVERLAP, AND STRESS RESPONSES IN VERVET MONKEYS (*Chlorocebus pygerythrus*) IN EAST AFRICA

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A DISSERTATION SUBMITTED TO

THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN BIOLOGY

YORK UNIVERSITY

TORONTO, ONTARIO

FEBRUARY 2025

ABSTRACT

As human populations continue to expand and encroach upon natural habitats, the boundaries between human settlements and wildlife habitats are increasingly blurred. The dynamics of human-wildlife coexistence and habitat sharing play a critical role in shaping interactions between humans and wildlife, as well as influencing the risk of anthropozoonotic disease transmission. This dissertation explores the impacts of shared home ranges on human wildlife conflicts, parasite community overlap, and stress response of a non-human primate: the vervet monkey (*Chlorocebus pygerythrus*). The dissertation begins with an overview of human-wildlife coexistence, how it affects conflicts reported by humans, as well as the overlap of parasite communities, and the stress and behavioural responses of animals in relation to parasitism. Chapter 2 compares human-wildlife conflicts (HWCs) reported at two distinct sites in Uganda and Kenya and examines the socioeconomic factors that influence villagers' responses to these conflicts and explores their perceptions of the effects of living near a research site and a conservancy. I found significant differences in the severity and frequency of HWCs reported with villagers noting both positive and negative effects of their proximity to each site. Chapter 3 explores parasite community overlap among sympatric hosts (dogs, humans, livestock, and vervet monkeys) sharing the habitat near Lake Nabugabo, Uganda, and discusses how these parasites might be transmitted. I found that dogs, humans, livestock and vervets at Lake Nabugabo harboured multiple parasite taxa, with parasite community overlap between humans and animals. Chapter 4 examines the effects of gastrointestinal parasites on vervet fecal glucocorticoid metabolites (fGC) and behaviours using a parasite removal experiment (deworming treatment and subsequent natural reinfection). I found that reinfection with parasites increased fGC levels in vervets, and there were changes in certain behaviours of vervet monkeys following deworming and reinfection but not always in the

predicted direction. Overall, this dissertation offers a comprehensive analysis of how shared habitats influence the dynamics of human-wildlife interactions and parasite overlap, as well as how wildlife responds behaviourally and physiologically to parasitism, providing valuable insights into the complex and multifaceted nature of human-wildlife coexistence.

DEDICATION

I dedicate this thesis to my grandmother, whose unfaltering belief in me has been a constant source of strength. She has stood by my side since the very beginning of my life, offering love and encouragement that have inspired me every step of the way. I also dedicate this work to my family and friends, whose unwavering support and encouragement have been my guiding light throughout this journey. Your belief in my abilities has inspired me to persevere, even during the most challenging times. The countless moments of laughter, heartfelt conversations, and unwavering presence have been invaluable to me. I am truly grateful for your love and understanding, which have provided me with the strength and motivation needed to reach this milestone.

I would also like to dedicate this work to all the pets in my life—both my own and those of friends and family—who have provided me with companionship and kept me grounded over the past five years. These furry friends have a unique way of bringing joy and comfort into everyday moments, reminding me of the importance of love and connection. Whether it was a wagging tail greeting me after a long day or the soothing presence of a purring cat, their unconditional affection has helped me navigate the ups and downs of this journey. Their playful antics and gentle companionship have offered solace and joy, making my experience not just bearable but also richly rewarding. Last but certainly not least, I would like to dedicate this thesis to the vervet monkeys of Lake Nabugabo, Uganda, whose charm and shenanigans made this journey truly worthwhile.

ACKNOWLEDGMENTS

I would like to express my heartfelt gratitude to the many individuals who have accompanied me on this journey every step of the way. Their assistance and encouragement have been instrumental in helping me reach this point.

First and foremost, I want to express my heartfelt gratitude to my supervisor, Dr. Valerie A. M. Schoof. Her unwavering faith in my abilities has been a constant source of motivation, encouraging me to push my boundaries and strive for excellence. Dr. Schoof has not only provided me with generous opportunities that have enriched my experience but also guided me with insightful feedback and mentorship. Her support has been instrumental in my personal and academic growth, allowing me to develop skills and knowledge that will serve me well in the future. I truly appreciate her commitment to my success, which has made this journey both rewarding and transformative. I would also like to thank my supervisory committee members, Dr. Suzanne E. MacDonald and Dr. Bridget J. M. Stutchbury, who always provided support, constructive criticism, and helpful comments on my writing and statistics. I acknowledge the contribution of the field team at Lake Nabugabo, Uganda for collecting data on the vervet monkeys: Matovu Ponsyano, Katwere Livingstone, Hillary Tashobya, Justine Namuyomba, and Dennis Twinomugisha for managing the team and field team at Lewa, Kenya: Vincent Karani and Kenneth Murithi as well as Lewa management team. I want to express my gratitude to my lab mates—Karin Snyder, Simon L'Allier, Justine Vermey, Melissa Martins, Angelica Drexler, Simran Prasad, Taylor Fane, Lina Rademacher, Margaux Dupuis, and Dr. Landing Badji—for being such incredible colleagues and friends. I would like to especially thank Megan Schwegel for her constant support and valuable insights on statistical analyses.

A part of this thesis project received funding from the Anne Innis Daag Research Grant from the Canadian Society of Zoologists. I would like to extend my gratitude to Dr. Daag for her generous support and to the Canadian Society of Zoologists for providing this grant. I would like to thank the York Graduate Fellowship (PU), York Graduate Scholarship (PU), York University Research Cost Fund (PU), Natural Science and Engineering Research Council of Canada (Valerie Anna Mylene Schoof, Colin A Chapman), York Research Chair Program (VAMS), New Frontiers in Research Fund (VAMS, Suzanne E MacDonald, Yuhong He), Canada Research Chair Program (CAC), Fonds Québécois de la Recherché sur la Nature et les Technologies (CAC), and National Geographic Society (CAC) for funding this various aspects of this research. Without these funds, none of this research would have been possible.

This dissertation reflects the culmination of years of hard work and dedication from many individuals and countless contributions. The firm support and encouragement I have received from them have profoundly impacted both this work and my personal growth. Their belief in me has motivated me to persevere through challenges and has enriched my academic journey in ways I will always cherish. For all of this, I am profoundly grateful and will carry their influence with me throughout my future endeavors.

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LIST OF ABBREVIATIONS

ACTH	Adreno-Cortico-Trophin Hormone
AICc	Akaike's information Criterion corrected
ANOSIM	Analysis of Similarity
ASV	Amplicon Sequence Variant
BLAST	Basic Local Alignment Search Tool
CI	Confidence Interval
COD	Community Outreach & Development
df	Degrees of Freedom
DNA	Deoxyribonucleic Acid
EIA	Enzyme Immunoassays
fGC	fecal Glucocorticoid
GLM	Generalized Linear Model
GLMMs	Generalized Linear Mixed Effects Models
HPA	Hypothalamic-Pituitary-Adrenal
HTS	High-Throughput Sequencing
HVR-IV	Hypervariable Region
HWC	Human Wildlife Conflict
HWI	Human Wildlife Interaction
HWID	Human Wildlife Interaction Diagram
ITS	Internal Transcribed Spacer
IUCN	International Union for Conservation of Nature

JC	Jukes-Cantor
K2P	Kimura 2-Parameter
K3P	Kimura 3-Parameter
LMMs	Linear Mixed Effects Models
MPSR	Maximum Parasite Species Richness
MuMIn	Multi-Model Inference
NCBI	National Center for Biotechnology Information
PCoA	Principal Coordinate Analysis
PCR	Polymerase Chain Reaction
PERMANOVA	Permutational Analysis of Variance
PVA	Polyvinyl Alcohol
qPCR	quantitative Polymerase Chain Reaction
rRNA	ribosomal Ribonucleic Acid
SD	Standard Deviation
SE	Standard Error
SSU	Small Subunit
TIM2	Tamura-Ito Model
TN	Tamura-Nei
TPI	Triosephosphate Isomerase
USGS	United States Geological Survey
VIF	Variance Inflation Factor
WHO	World Health Organization
WOAH	World Organization for Animal Health

CHAPTER 1: GENERAL INTRODUCTION

1.1 HUMAN-WILDLIFE CO-EXISTENCE

Humans and wild animals have coexisted and interacted throughout their shared history. While many interactions can cause damage or harm to humans and/or wildlife, not all are negative, yet research often focuses on such challenges and labelling them human-wildlife conflicts (Bhatia et al., 2020). Human-wildlife interactions (HWIs) range along a spectrum from positive to negative, vary in intensity from minor to severe, and differ in frequency from rare to common (Soulsbury & White, 2015). The Human-Wildlife Interaction Diagram (HWID) classifies four primary types of HWIs determined by the effects these interactions have on both the wildlife and the people directly involved (Figure 1.1) (Marchini et al., 2021): 1) human-wildlife conflict (HWC), which is harmful for both humans and wildlife - e.g., humans killing leopards as a retaliation for attacking humans and livestock (Mbise, 2021); 2) overexploitation of wildlife, which is primarily harmful to wildlife - e.g., killing of jaguars for body parts and medicinal purposes (Polisar et al., 2023); 3) nuisance wildlife, which is negative mainly for humans - e.g., rodents can be considered nuisance because of their presence (Horan & Bulte, 2001); and 4) human-wildlife coexistence, which is beneficial for both - e.g., a portion of the revenue generated from jaguar-watching tourism is used for jaguar conservation (Marchini et al., 2024). HWIs can result in various negative impacts, such as vehicle collisions, damage to property and agriculture, zoonotic diseases, and the exploitation of animals as resources; all of which can make dealing with HWIs increasingly more complex (Aguirre, 2017; IUCN, 2020; Marchini et al., 2021; Pooley et al., 2017). Recently, the concept of coexistence has received greater focus from researchers, managers, and decision-makers working to mitigate the negative effects of HWIs (Marchini et al., 2021). Due to climate change, habitat conversion, and efforts to

recover and reintroduce species, interactions between humans and wildlife are increasing, making coexistence with wildlife in multifunctional landscapes crucial (Pooley et al., 2021). This growing challenge is driven by rapid and significant changes in the physical environment and societal values due to the Anthropocene and industrialization (Vucetich et al., 2021). These changes include climate change, expanding infrastructure, urbanization, economic globalization, digital revolution, and a broader range of ethical considerations (Vucetich et al., 2021). While human-wildlife conflict and coexistence involve species that are rare and protected, common and seen as pests, heavily managed or domesticated, and are found across various ecosystems, much of the research has focused on species of conservation concern (Nyhus, 2016), creating a research gap for species of Least Concern such as vervet monkeys (*Chlorocebus pygerythrus*).

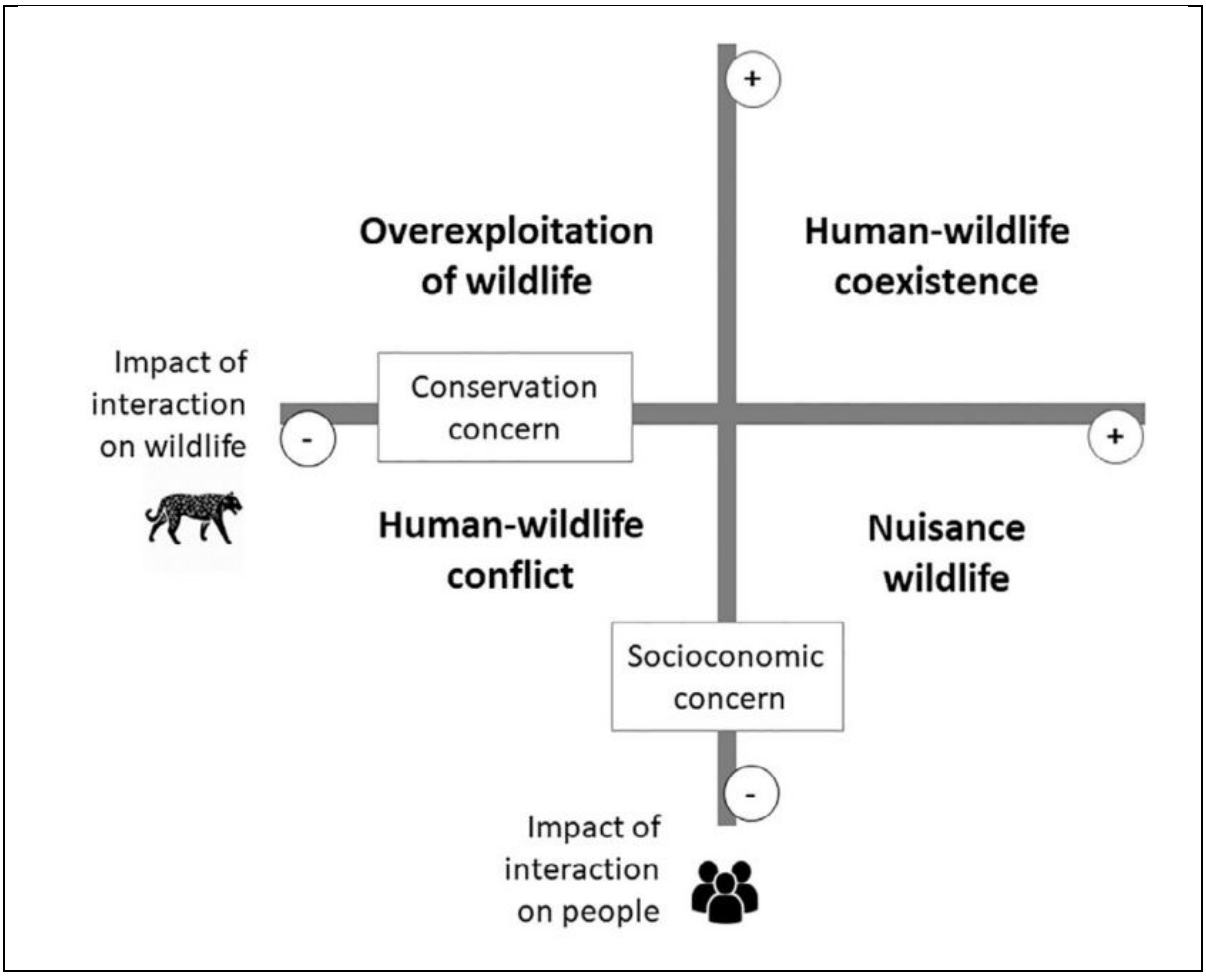

Figure 1.1: Human-Wildlife Interaction Diagram (HWID) using two axes to represent the effects of interactions—ranging from highly negative to highly positive—on both wildlife (horizontal axis) and humans (vertical axis). Source: (Marchini et al., 2024).

Research on HWIs has shown that fast-adapting synanthropic (i.e., animals that live in close proximity to people) non-domesticated species that are ecologically associated with humans can thrive in environments shared with humans. Recent studies have shown that wildlife such as vervet monkeys is equally abundant in non-protected areas as in protected ones (Choki et al., 2023; Thapa et al., 2021) (Figure 1.2). Since non-protected areas are primarily human-dominated and altered landscapes, it is essential to understand the needs of local communities, especially in regions where they hold land ownership (Burger et al., 2019; Ciuzio et al., 2013; Kamal et al., 2015; Mudappa & Shankar Raman, 2007). HWIs for synanthropic wildlife can be conceptualized as a dynamic process, starting with coexistence (where neither party experiences negative consequences) (Harris et al., 2023). Over time, some wildlife species adjust to human surroundings and lose their natural fear of humans, becoming synanthropic (Harris et al., 2023). Additionally, in recent years, human populations have grown rapidly, extending into wildlife habitats and causing more frequent interactions with species that aren't synanthropic, which in turn leads to human-wildlife conflicts (Harris et al., 2023; Thapa et al., 2024). Depending on the extent of this conflict, wildlife species may either be persecuted or tolerated. Tolerating wildlife incurs various costs for humans, such as energy, time, mental well-being, financial resources (Barua et al., 2013), and other intangible consequences such as fear and other negative emotions (Ardiantiono et al., 2021). Any shift from conflict to coexistence in HWI is shaped by factors like human responsibility (i.e., shared accountability for outcomes: Tan, 2021), equity (i.e., fair distribution of costs and benefits: McDermott et al., 2013), justice (i.e., securing livelihoods: Vucetich et al., 2018), and inclusion (i.e., unbiased participation: Jones & Solomon, 2019).

Figure 1.2: An example of synanthropic species: vervet monkeys (*Chlorocebus pygerythrus*) foraging in proximity to a chicken (*Gallus gallus domesticus*), a goat (*Capra aegagrus hircus*), and a residential building.

Studies on HWIs often examine variables such as age, gender, occupation, income, wealth, and education of local community members (Agarwala et al., 2010). These factors are known to significantly influence people's attitudes (Best & Pei, 2020; Dickman et al., 2014; Mir et al., 2015; Mkonyi et al., 2017) and behaviors toward wildlife (Zainal Abidin & Jacobs, 2019), thereby shaping the possibility for human-wildlife coexistence (Bencin et al., 2016). Understanding and addressing the attitudes and behaviors of local communities toward human-wildlife conflict (HWC) is considered essential for achieving successful human-wildlife coexistence (Basak et al., 2023). By acknowledging the diverse factors that shape how people perceive and respond to wildlife, we can better address the root causes of conflict and foster a more harmonious relationship between humans and the natural world.

1.2 PARASITE OVERLAP AND ANTHROPOZOONOSES

A key aspect of shared geographical human-wildlife overlap is the spread of parasites and diseases between wildlife and humans (Figure 1.3) (Soulsbury & White, 2015). Many wildlife species act as reservoirs for pathogens, with zoonotic and vector-borne diseases posing significant risks to the health of livestock, humans, and other wildlife (Daszak et al., 2000). Zoonotic diseases have had large impacts throughout history and remain a major global public health challenge (Conover & Vail, 2015; Jones et al., 2008). During the 400 years of the Black Death beginning in the 14th century, the plague (*Yersinia pestis*) killed approximately 50% of the population in China, 33% in Europe, and 17% in Africa (Conover & Vail, 2015). Globally, around 60% of emerging infectious diseases are zoonotic, affecting both humans and animals, with 72% of these originating from wildlife (Jones et al., 2008). Diseases can affect animal behaviour, which can escalate conflicts. Around 350 pathogens, including rabies, canine distemper, and canine parvovirus, can infect domestic dogs and endanger both wolf and wild dog

populations (Gompper, 2014; Lescureux & Linnell, 2014). In 20th century Europe, the majority of documented wolf attacks on humans were associated with rabid wolves (Linnell et al., 2002). The World Organization for Animal Health (WOAH) states that 75% of emerging diseases originate from domestic or wild animals, making them zoonotic in nature (Tazerji et al., 2022).

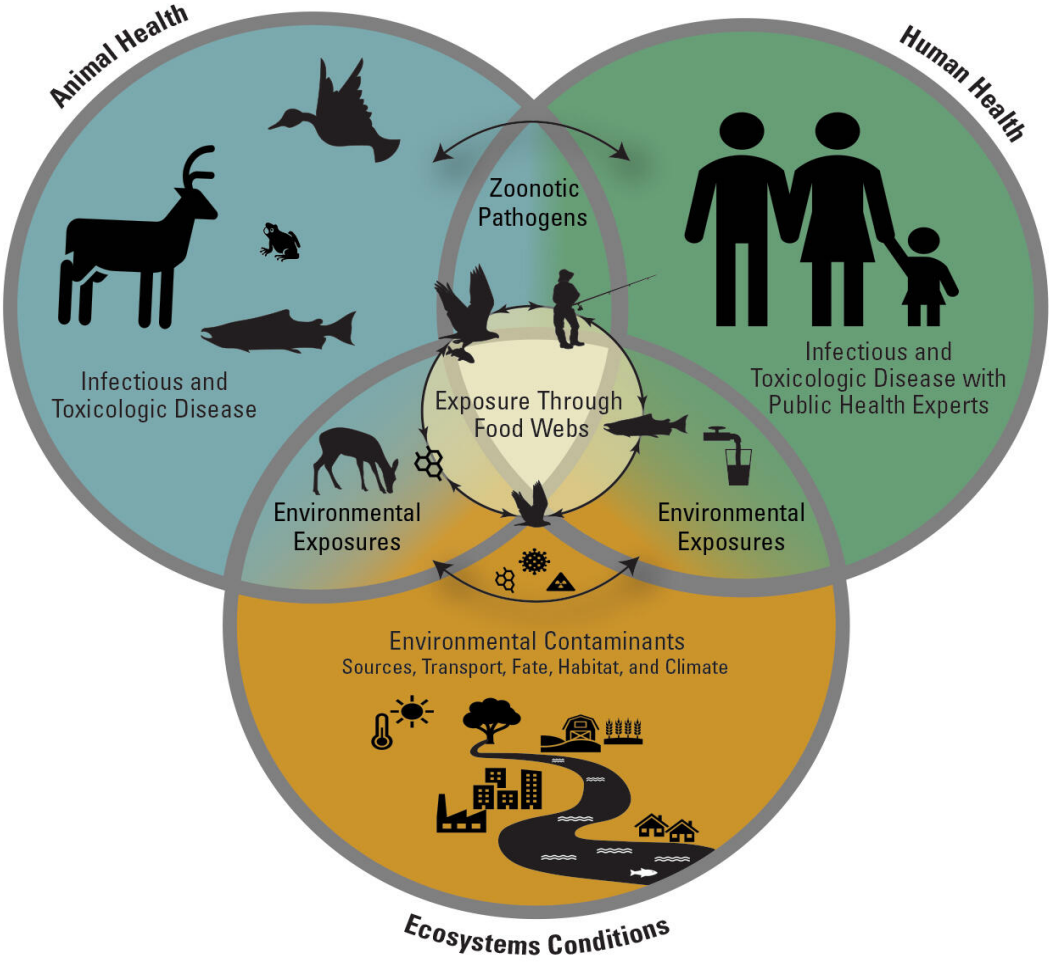

Figure 1.3: The United States Geological Survey (USGS) One Health approach showing the interconnection between people, animals, plants, and their shared environment. Source: https://www.usgs.gov/

Anthropozoonotic diseases typically occur as consequences of drivers such as anthropogenic actions (e.g., urbanization, deforestation, agricultural expansion etc.), environmental factors (e.g., drought, temperature, wind etc.), biological factors (e.g., genetic drift, reassortment etc.) and so on (El-Sayed & Kamel, 2020; Tazerji et al., 2022; WHO, 2016). A significant gap in our understanding of anthropozoonotic disease emergence is the absence of data on how wildlife parasite-sharing patterns differ between wild and domestic host species or across different biogeographical regions (Wells et al., 2018). In anthropozoonotic diseases, a key factor in the emergence of parasitic infections is the overlap of environmental factors and biological traits that facilitate the transmission of parasites between animals and humans (Wells et al., 2015, 2018; Wells & Flynn, 2022). This overlap creates opportunities for parasites to spill over from wildlife to humans, or vice versa, particularly when environmental conditions such as climate change, habitat destruction, or changes in land use bring humans and animals into closer proximity. For example, *Echinococcus multilocularis* relies on foxes and coyotes as definitive hosts, but in the past two decades, it has become a significant urban zoonosis due to various human activities (Thompson, 2013). Similarly, *Giardia* is a key example of a zoonotic parasite that is mainly found in wildlife as a result of human actions (Thompson, 2013).

While direct parasite transmission between humans and wildlife is a major concern, domestic animals living near humans can also play a significant role as hosts for wildlife parasites (Wells et al., 2018). In addition to the environmental context, host characteristics, such as phylogenetic relationships and habitat overlap, are important for assessing the likelihood that hosts will share the same parasite species through a mechanism called ecological fitting (Streicker et al., 2010; Wells et al., 2015). Ecological fitting is the process by which organisms establish themselves and thrive in new environments, exploit new resources, or form new

relationships with other species, based on the traits they possess when they encounter these novel conditions (Agosta & Klemens, 2008). Understanding parasite dynamics at these interfaces is crucial for human and animal health, species conservation, and the development of effective strategies for parasite prevention and control (Daszak et al., 2000; Deem et al., 2001; Ferber, 2000; Nunn & Altizer, 2006).

1.3 STRESS RESPONSE

Parasites can trigger acute and/or chronic stress responses in some animals that are crucial for their survival (Seguel et al., 2019). The animal stress response involves a range of behavioral and physiological mechanisms designed to help cope with challenges, including social, behavioral, chemical, and physiological stressors (Baker et al., 2013; MacDougall-Shackleton et al., 2019). A temporary increase in glucocorticoids (GCs) is a key physiological mechanism that vertebrates use to respond to stressful environmental or social stressors (Romeo et al., 2020). However, stressors and parasitism share a reciprocal relationship (Figure 1.4), which suggests that parasite infection can be both a trigger and a result of the stress response (Beldomenico & Begon, 2016). Parasites that harm their hosts function as physiological stressors, triggering the release of GCs. On the other hand, elevated GCs from previous stressors may enhance parasite infection through neuroimmunomodulation (Defolie et al., 2019). While the positive correlation between GCs and parasites may be due to hypothalamic-pituitary-adrenal (HPA) axis in response to parasite-imposed energetic stress (Coop & Kyriazakis, 1999), it is unclear whether the relationship is influenced by the resulting immunosuppression, the host stress response itself, or both (Foerster et al., 2015; Muehlenbein, 2006). On the other hand, negative relationships between GCs and parasites have also been documented in several studies (Cizauskas et al., 2015; Ehrström et al., 2005; Hufschmid et al., 2013; Morales-Montor et al., 2003) and could result from chronic stress

induced HPA axis dysfunction (Hufschmid et al., 2013), which could lead to immunosuppression (Beasley et al., 2010) and ultimately to low GC levels and increased susceptibility to parasites (Defolie et al., 2019). The nature of the relationship between GCs and parasites is also influenced by host tolerance to the infection, intensity of the effects caused by the parasites on host energy reserves, and types of responses that parasites stimulate in a host's immune-endocrine system (Goldstein et al., 2005; Monello et al., 2010).

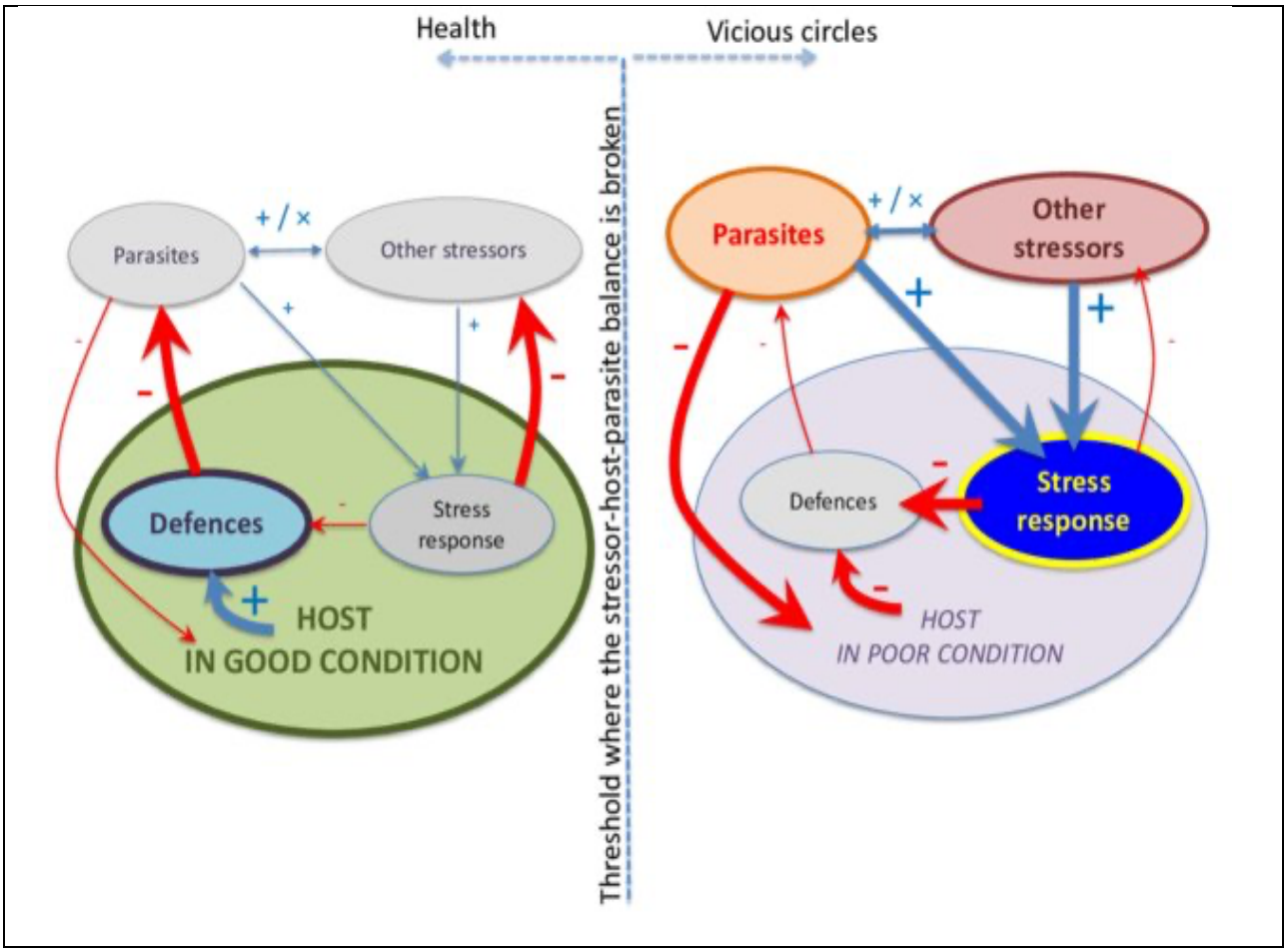

Figure 1.4: Balanced and unbalanced stressor-host-parasite interactions. Source: *(Beldomenico & Begon, 2016)*

Similarly, parasite infections can also change vertebrate behavior in ways not tied to a specific disease, known as "sickness behaviors", which are a set of changes in an animal's behavior in response to infection; these may include reduced activity, exploration, social interactions, and food or water intake, as well as altered grooming and pain sensitivity (Lopes et al., 2021). Sickness behavior was traditionally seen as a passive response to energy diversion for immune defense, but the prevailing view now is it as an adaptive strategy that enhances disease resistance and recovery (Johnson, 2002). Sickness behaviors are also often linked to increased sleepiness, longer sleep, and difficulties with learning and memory (Dantzer, 2001; Dantzer et al., 2008; Lopes et al., 2021). Sickness behaviors have been observed across a wide range of mammalian species, extending beyond just domesticated or laboratory animals, and have been documented in both controlled and natural environments, highlighting their broad relevance in animal biology. For example, sickness behaviors have been noted in guinea pigs (*Cavia porcellus*; Hennessy et al., 2004), Siberian hamsters (*Phodopus sungorus*; Prendergast et al., 2008), vampire bats (*Desmodus rotundus*; Stockmaier et al., 2018), degus (*Octodon degus*; Ramirez-Otarola et al., 2019), humans (Lasselin et al., 2018; Sandiego et al., 2015; Schedlowski et al., 2014; Shattuck & Muehlenbein, 2015), and non-human primates like red colobus monkeys (*Procolobus rufomitratus*; Ghai et al., 2015) and rhesus macaques (*Macaca mulatta*; Friedman et al., 1996). These species exhibit common sickness behaviors, such as anorexia, reduced nest building (Prendergast et al., 2008), decreased activity (Ramirez-Otarola et al., 2019; Stockmaier et al., 2018) and allogrooming (Stockmaier et al., 2018), and increased somnolence (Friedman et al., 1996) and resting (Ghai et al., 2015). Additionally, sickness behaviors are often accompanied by an increased sensitivity to pain and temperature, changes in social dynamics, and disruptions in normal cognitive functions such as learning and memory (Dantzer, 2001). These responses are thought to be adaptive mechanisms that help the

body conserve resources and prioritize recovery (Dantzer & Kelley, 2007). However, while many sickness behaviors are shared across species, the specific symptoms and the degree to which they manifest can vary depending on the species and the nature of the infection (Lopes et al., 2021). For instance, certain species may show more pronounced social withdrawal or grooming reductions, while others may have more marked changes in feeding behaviors.

1.4: CURRENT WORK: ASSESSING THE IMPACT OF OVERLAPPING HOME RANGES ON HUMAN-WILDLIFE INTERACTIONS, PARASITE TRANSMISSION, AND STRESS RESPONSES IN VERVET MONKEYS IN EAST AFRICA

One of the aims of this dissertation was to compare reports of human-wildlife conflicts (HWC) at two distinct sites in East Africa: a Ugandan village in a non-protected area and a Kenyan village near a protected area using a survey methodology (Chapter 2). In the same chapter, I also examine whether socioeconomic factors influenced human responses to HWC at both sites, as well as the perceptions and attitudes of community members about the impact of living close to a research site and a conservancy. The findings indicated that there were differences in both the severity and frequency of HWCs reported between the two sites, with more frequent but less severe conflicts being reported near the protected area compared to the non-protected area. I also found that larger cultivated areas were associated with a higher number of reported HWCs, while individuals with secondary education tended to report less severe HWCs. While I found community support for research/conservation in both areas, several challenges were reported, which highlights the need for tailored, site-specific management strategies to effectively address local HWIs.

Building on the effects of shared human-wildlife home ranges and resources in Chapter 2, in Chapter 3 I explored parasitism among sympatric hosts—humans, vervet monkeys, livestock, and dogs—coexisting along the shores of Lake Nabugabo, Uganda. Vervet monkeys (*Chlorocebus*

pygerythrus) are distributed across East Africa, from Ethiopia and Somalia to South Africa (Kingdon et al., 2008). The members of *Chlorocebus* stand out from other catarrhines for their ability to thrive in much drier environments, occupying a wide range of habitats, including forest-grassland mosaics, miombo woodlands, open woodlands, and arid savannas (Cheney & Seyfarth, 1987; Isbell et al., 1990; Kingdon et al., 2008; Struhsaker, 1967; Turner et al., 2019). In addition to relatively undisturbed areas (Baldellou & Adan, 1998; Struhsaker, 1967), vervet monkeys are also found in habitats with secondary vegetation (Chapman, 1985; Foord et al., 1994), fragmented landscapes (Baranga et al., 2013), agricultural zones (Saj et al., 1999), as well as rural (Legesse & Erko, 2004a) and urban areas (Albert et al., 2014; Kingdon et al., 2008). Their ability to thrive in human-modified environments, unlike most other primates, is likely linked to their behavioral adaptability. For instance, vervets are highly flexible in their diet, capable of foraging outside of arboreal refuges, adjusting group sizes, and even reducing the intensity of their alarm calls to evade predators (Albert et al., 2014; Chapman et al., 2016). In agricultural regions, vervets are considered pests because they frequently forage on crops, including beans, peas, young tobacco plants, vegetables, fruit, and grains (Cancelliere et al., 2018; Chapman et al., 2016). Vervet monkeys provide an ideal model for studying the risks of interspecific parasite transmission in human-altered environments due to their high adaptability as omnivorous primates. They are capable of tolerating anthropogenic disturbances and utilize both terrestrial and arboreal habitats (Turner et al., 2019). Thus, vervet monkeys in a human-modified landscape are an ideal study system for examining the overlap of parasite communities among sympatric vervet monkeys, humans, livestock and dogs, as well as the effects of gastrointestinal parasites in stress response (in terms of glucocorticoid metabolites secretions and sickness behaviours).

For Chapter 3, I collected fecal samples from dogs, humans, livestock (cows, pigs and goats) and vervet monkeys to examine gastrointestinal parasite overlap among these potential hosts. I assessed which species of order strongylids, genera *Strongyloides*, *Cryptosporidium*, *Giardia*, *Encephalitozoon*, and *Enterocytozoon* are genetically shared among these four host categories. The findings indicated 25 unique parasite taxa with dogs harbouring 17 parasite taxa, livestock harbouring 15 parasite taxa, vervet monkeys harbouring 10 parasite taxa, and humans harbouring nine parasite taxa with a significant difference in the parasitic infection rate (i.e. presence of at least one parasite in the fecal sample) between vervet monkeys (89%), humans (24%), dogs (40%), and livestock (48%). I did not find any *Strongyloides* infections in humans, and only limited overlap between vervets and other hosts (i.e., dog, pig). Among protists, I found that *Cryptosporidium andersoni* occurred in both dogs and cows. Although I did not find evidence of human-animal overlap for *Cryptosporidium*, there is the potential for anthropozoonotic disease transmission given that *C. ubiquitum* has previously been found in humans. The results also indicated parasite community overlap (*Giardia intestinalis* and *Enterocytozoon bieneusi*) between humans and animals, which may be evidence of past anthropozoonotic disease transmission.

In Chapter 4, I investigated the stress response to gastrointestinal parasites in vervet monkeys at Lake Nabugabo, Uganda, by analyzing fecal glucocorticoid (fGC) metabolite levels and behavioral changes using a parasite removal experiment. The findings showed that there was no significant change in mean fGC after deworming, but there was an increase following natural reinfection (Upadhayay et al., 2025). I also found that there was no change in feeding behavior across the study phases; however, movement, grooming, and resting behaviors varied between the post-deworming and late reinfection phases, though not always in the expected direction (Upadhayay et al., 2025). Although behavioral changes varied between study phases, these

changes cannot be definitively attributed to parasitism, as other seasonal factors may also be influencing them, though I did not find seasonal variation in these behaviours in a non-experimental year. However, the increase in fGC following reinfection supports the idea that parasitism imposes a cost on hosts.

Taken together, this dissertation provides valuable insights into human-wildlife conflict (HWC) and parasitism dynamics in East Africa, highlighting the complex interplay between human activities, wildlife behavior, and ecological health. These findings align closely with the One Health approach, which emphasizes the interconnectedness of human, animal, and environmental health (Figure 1.3). By investigating how people and wildlife—particularly vervet monkeys—interact in shared, human-modified landscapes, this work contributes to a more holistic understanding of how ecological disturbance, health risks, and conservation challenges are deeply intertwined. This dissertation broadly aims to explore the multifaceted dynamics of human-wildlife coexistence in East Africa, focusing on the ecological, social, and health-related implications of shared landscapes. Through an interdisciplinary lens that draws from conservation science, public health, and animal behavior, I examine the reciprocal impacts of human and wildlife presence. Specifically, this includes comparative analyses of human-wildlife conflict at two East African sites (Chapter 2), molecular screening and coproscopic identification of gastrointestinal parasites in sympatric host species (Chapter 3), and experimental assessments of parasite-induced stress responses in wild primates (Chapter 4). Together, these studies underscore the importance of integrated, context-specific strategies that not only address conservation goals, but also enhance human well-being and reduce zoonotic risk. Ultimately, the findings advocate for a One Health-oriented approach to managing human-wildlife interfaces—

one that is socially equitable, ecologically sustainable, and responsive to the realities of shared environments.

ETHICS APPROVAL

All research received clearance from York University (ACC-2016-7W, ACC-2020-06; HPRC-E2019-191), McGill University (ACC-5041), and relevant authorities in Uganda (UWA EC 361 and COD-96-05; MAKSHSREC-2022-297; MAKSS REC 03.19.273; SVAR_IACUC/125-2022; UNCST 267, NS349ES, NS563) and Kenya (ISERC/05/19; KH IERC-02718/0057/2019; NACOSTI/P/21/3425).

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CHAPTER 2: IMPACTS OF SHARED HOME RANGE ON HUMAN-WILDLIFE CONFLICTS

Upadhayay P, MacDonald SE, Schoof VAM. In revision. Impacts of shared home range on human-wildlife conflicts. *African Journal of Ecology* (28 Jan 2025).

Chapter Summary

Human-wildlife conflicts (HWC) are increasing in human-modified landscapes. We examined HWCs in Bbaale village adjacent to the Nabugabo Research Site (Uganda) and Manyangalo village near the Lewa-Borana Conservancy (Kenya) by surveying 73 households in Bbaale and 50 households in Manyangalo. We examined the socioeconomic factors influencing responses to HWC and assessed community perceptions of the benefits and drawbacks of living near a research site or conservancy. HWC were reported as more severe at Nabugabo but more frequent near Lewa. Bbaale respondents employed diverse management strategies, while Manyangalo respondents relied mainly on noisemaking. Larger cultivable areas correlated with more reported HWC, and individuals with secondary education reported less severe HWC. Despite these differences, most respondents in both villages had positive views toward the research site and conservancy, which may indicate community support for conservation. These findings highlight the need for site-specific management strategies.

Keywords: co-existence, conservation, human-wildlife interactions, mitigation

2.1 INTRODUCTION

The rapid growth of human activities since the Anthropocene has severely affected natural habitats, threatened global biodiversity, and placed > 44,000 species at risk of extinction due to habitat loss, degradation, and fragmentation (IUCN Redlist, 2024; Yang et al., 2024). Human-wildlife conflict (HWC), an issue of high concern for conservation, refers to a negative impact of the needs, goals, or behaviours of humans on wildlife and vice-versa (IUCN, 2023). HWCs have been documented globally throughout history (Lamarque et al., 2008), and pose a significant threat to wildlife populations worldwide (Ladan, 2014). HWCs arise from competition over resources, leading to human concerns about crop damage, livestock predation, property loss, disease, safety risks, and well-being, while also negatively impacting wildlife through mortality, poaching,

behavioural disruptions, invasive species introduction, and population decline or extinction (Mukeka et al., 2019; Thirgood et al., 2009; Treves et al., 2006). The frequency and severity of HWCs have increased in recent times (Manfredo, 2008).

HWC is a complex issue with no single solution. Effective management requires a combination of strategies that consider animal needs as well as human socioeconomic and cultural factors (Blackwell et al., 2016; Li et al., 2023). Although the incidents of HWC occur all over the world, they are not uniformly distributed (Mekonen, 2020): the spatial and temporal patterns of HWC are influenced by human attitudes towards wildlife (Dickman et al., 2013), human activities and behaviours (Penteriani et al., 2016), wildlife adaptation and exploitation of anthropogenic resources (Kumar et al., 2019), and climate-induced shifts in biotic distributions (Pecl et al., 2017). For example, people tend to report fewer instances of HWC in developed regions where there is less competition for limited resources (Engeman & Sterner, 2002; Tzilkowski et al., 2002), whereas people in developing regions rich in biodiversity such as south and south-east Asia tend to report more HWC (Madhusudan & Karanth, 2002). Socio-economic factors such as age, gender, education level, and economic status influence people's values, religious beliefs, attitudes, and socialization, which in turn affect how they perceive the world, interpret information, and make decisions (Castleman et al., 2019). Additionally, an understanding of animal behaviour and awareness of the risks posed by wildlife have also been linked to human responses (Marchini & Macdonald, 2012).

The impacts of protected areas or conservancies on local economies have been extensively discussed in the literature (Adams & Hutton, 2007; Roe, 2008). While the global benefits of biodiversity and ecosystem services are widely acknowledged (Balmford et al., 2002), the costs associated with conservancies may disproportionately affect local communities (Clements et al.,

2014) because their effects on people's livelihoods, which can influence their attitudes toward conservation (Abukari & Mwalyosi, 2018; Bragagnolo et al., 2016). It is crucial to understand not only the requirements of individual wildlife species, but also the broader cultural and economic factors that significantly influence conservation (Baillie et al., 2004). There is a growing acknowledgment that the loss or preservation of biodiversity hinges on local actions, making it vital to understand the viewpoints of local communities for sustainable wildlife management programs (Pratt et al., 2004).

This study attempts to answer the questions related to incidences of HWC reported in two different sites: Bbaale village on the shores of Lake Nabugabo, Uganda, and Manyangalo village near Lewa-Borana Conservancy, Kenya (see below), socioeconomic factors influencing the responses to HWC at both sites, and perceptions of community members regarding the positive and negative effects of living in close proximity to a research site and a conservancy, respectively.

Research Question 1: What is the extent of HWC in Nabugabo and Lewa? Given that Bbaale is situated on the shores of a lake surrounded by diverse habitats such as wetlands, grasslands, patches of swamp forest, and degraded forests and Manyangalo is a village near a conservancy with a higher concentration of larger predators, I anticipated a greater occurrence of reports of HWC, as well as more frequent and severe reports of HWC in Lewa compared to Nabugabo. Answers to this question help us to assess the current state of perceived HWC in two communities affected by HWC. For this research question, my specific questions were:

a. Is there a site difference in reported HWC between Nabugabo and Lewa?
b. Which animals are involved in HWC at Nabugabo and Lewa?
c. What type of conflicts are these animals reported to be involved in and what is the reported severity of the conflicts?

d. Is there temporal variation in when HWC are reported to occur? Does this differ between sites?
e. What are the most common reasons given by community members to explain the occurrence HWC?
f. What are the most commonly used methods to mitigate costs imposed by wildlife?

Research Question 2: How do social and economic factors influence the responses to wildlife conflict at Nabugabo and Lewa? For this research question, my specific question was how do respondents' age, gender, education level, land used for cultivation, distance between the cultivable land and the households, and number of sources of income and site influence their responses to:

a. the number of types of conflicts reported.
b. severity of conflicts reported.
c. frequency of conflicts reported.

Research Question 3: What are the perceived negative effects and benefits from the Nabugabo Research Site and Lewa-Borana Conservancy? Answers to this question may be useful in developing mitigation strategies that minimize the perceived costs of HWC. For this research question, my specific questions were:

a. What are the local perceptions on i) negative effects and ii) benefits of living close to the research site and conservancy on the household and/or community and their ranks?
b. What do local people see as an option(s) to improve community-researcher/site relations and conservation efforts?

2.2 METHODS

2.2.1 Study Sites

The study was conducted in Bbaale village adjacent to the Nabugabo Research Site on the shores of Lake Nabugabo, Uganda (herein Nabugabo) (0.21˚S, 31.52˚E; Chapman et al. 2016a) and Manyangalo village adjacent to Lewa-Borana Conservancy in Kenya (herein Lewa) (0.20°N, 37.42°E; Dupuis-Desormeaux et al. 2023). Lake Nabugabo is mostly surrounded by wetlands, grasslands, and patches of swamp forest, and consists of farmers' fields, degraded forests, and a few buildings on the west side of the lake (Chapman et al., 2016). The Nabugabo Research Site hosts long-term research on monkeys, fish, and local ecology. At Lewa, the landscape consists of savannah grasslands with patches of Northern Acacia-Commiphora bushlands and thickets (Dupuis-Desormeaux et al., 2023) and a network of roads, villages, agricultural lands, and pastures (Davidson et al., 2019). Agricultural activities along the Lewa border encompass a spectrum, ranging from sizable commercial farms to community farming on smaller plots involving cultivation of subsistence crops like maize, carrots, onions, and wheat (Dupuis-Desormeaux et al., 2023).

2.2.2 Survey methods

The survey method combined with a semi-structured interview format (Connelly et al., 2012) was used to interview haphazardly selected households at Nabugabo in 2019 and Lewa in 2022. The survey (Appendix A1) was modified from a survey previously used in the communitites near Lewa-Borana Conservancy, Kenya (Dupuis-Desormeaux et al., 2023) and modified with questions from surveys around Kibale National Park, Uganda (MacKenzie et al., 2017). The survey was conducted by a female local community member at Nabugabo and two male local community members at Lewa with the help of community liasions, who were trained before the data collection. Survey questions fell into three broad categories: 1) household demographics (e.g., age, gender,

education level, livelihood(s), land ownership, residency length), 2) experiences with wildlife (e.g., observed wildlife, experienced HWC, severity and frequency of HWC, methods used to guard against wildlife), and 3) perceptions (i.e., risks and benefits) towards the Nabugabo Research Site and Lewa-Borana Conservancy. Research assistants and community liaison staff explained the purpose of the study, and obtained consent. Participants were interviewed in English, Luganda (Uganda), or Kiswahili (Kenya) based on their preference, and were offered a small honorarium.

2.2.3 Statistics

We analysed respondents' answers to HWC questions at Nabugabo and Lewa using Chi-square to compare percentages for types, severity, frequency, perceived causes, mitigation methods, and local perceptions of the research site or conservancy. We categorized the negative effects and their ranks (e.g., Rank 1 being the most important, and Rank 2 being the second most important) reported by the respondents as negative effects from the researchers, negative effects from the animals, and no negative effects (Appendix A2).

We used ordinal logistic regression to test for the influence of socioeconomic factors (i.e., respondents' age, gender, education level, acres of cultivable land, distance between households and cultivable land, number of sources of income, and site (Appendix A3) on types, severity, and frequency of reported HWCs (Appendix A4). For each model, we used the 'dredge' function in the MuMIN package (Barton, 2023) to identify the "top" model(s) within Δ7 AICc (Burnham et al., 2011). When multiple top models were identified, we conducted model averaging and calculated 95% confidence intervals for each predictor variable (Buckland et al., 1997; Burnham et al., 2011). Because there were few data points "moderately severe" and "less severe" HWC, we combined them into the single category "low severity". Models were checked for multicollinearity

among predictor variables (VIF < 5) (James et al., 2017). All analyses were conducted in R statistical software RStudio, version 4.0.3 (R Core Team, 2021).

2.3 RESULTS

We collected responses from a total of 123 respondents from Nabugabo (N = 73) and Lewa (N = 50) to the questions regarding the number of types, severity, and frequency of HWC. For the second research question, we used a subset of the data including 115 responses [Nabugabo: (N = 68) and Lewa: (N = 47)] after excluding the respondents for whom socioeconomic information was incomplete.

2.3.1 HWC between Nabugabo and Lewa

People at Lewa reported lower severity ($\chi^2 = 19.98$, $p < 0.05$) but higher frequency ($\chi^2 = 37.29$, $p < 0.05$) of HWC than at Nabugabo. There were also significantly more reports of HWC at Nabugabo than Lewa in terms of crop foraging ($\chi^2 = 211.33$, $p < 0.05$), destruction of food stores ($\chi^2 = 12.54$, $p < 0.05$), scaring livestock ($\chi^2 = 95.42$, $p < 0.05$), and threatening of people ($\chi^2 = 48.89$, $p < 0.05$). At Nabugabo, most of the respondents reported HWC with birds of prey, rats, and vervet monkeys as the most severe while HWC with colobus monkeys, redtail monkeys, small antelope, small birds, snakes, and wild dogs were reported as not severe (Figure 2.1). Very few respondents reported HWC with wildlife as moderately severe or least severe (Figure 2.1). At Lewa, most respondents reported HWC with baboons and vervet monkeys as the most severe, whereas HWC with birds of prey, rats, and snakes were reported as moderately severe. Additionally, HWC with small antelope and small birds were reported as the least severe, while HWC with elephants, hyenas, lions, and wild dogs were reported as not severe (Figure 2.1).

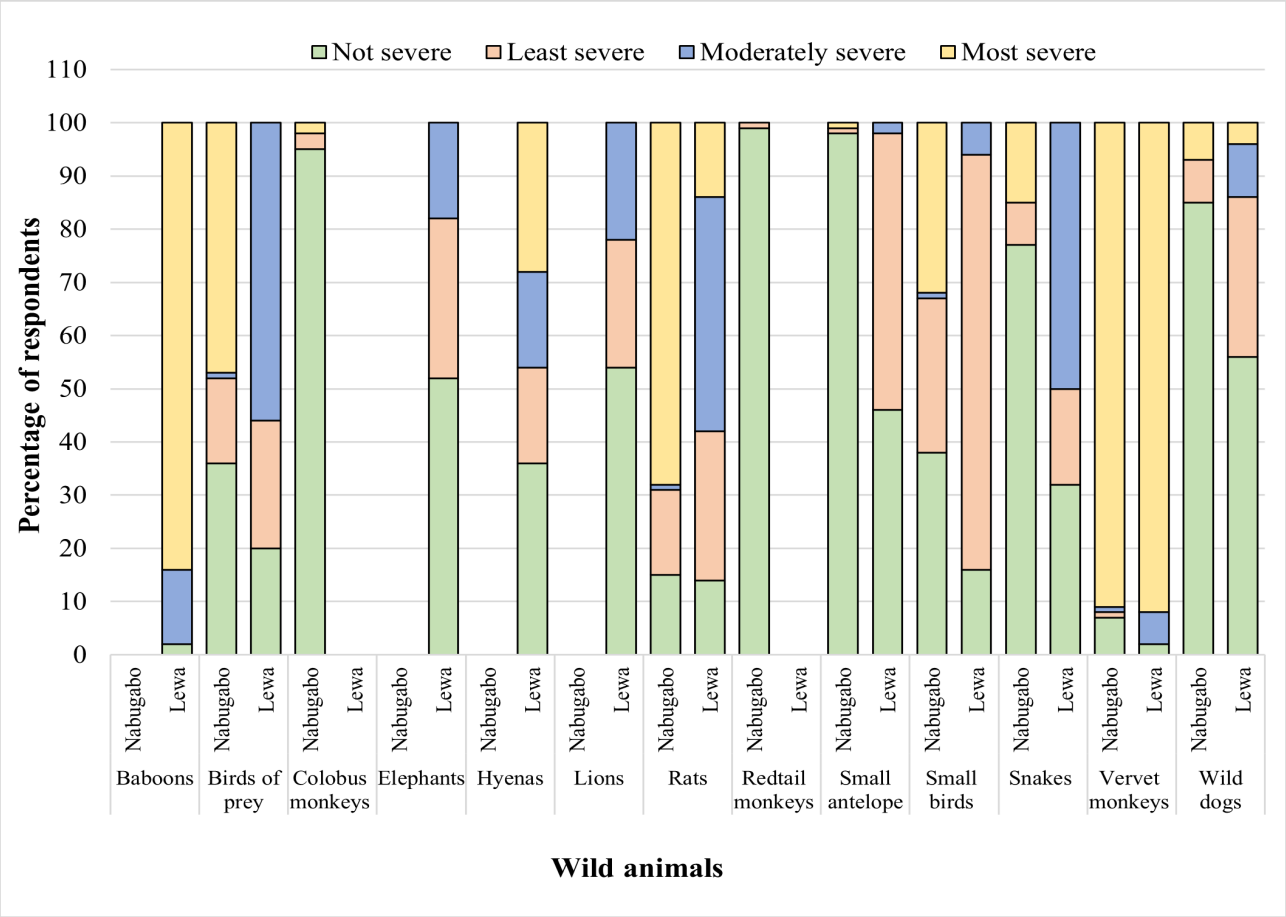

Figure 2.1: Percentages of respondents who reported severity (A) and frequency (B) of conflicts by wildlife at Nabugabo (N = 73) and Lewa (N = 50).

The frequency of HWCs reported at Nabugabo and Lewa differed significantly between sites by time of the day ($\chi^2 = 45.24$, $p < 0.05$) and month ($\chi^2 = 94.01$, $p < 0.05$). While most of the respondents at Nabugabo and Lewa reported HWC in the morning, afternoon, and evening, only respondents at Lewa reported HWC at night. At Nabugabo, there was a bimodal distribution in the seasonal timing reported HWC frequency, peaking in March-April and again in August-October, while at Lewa, HWC were reported to be most frequent from July to November (Figure 2.2).

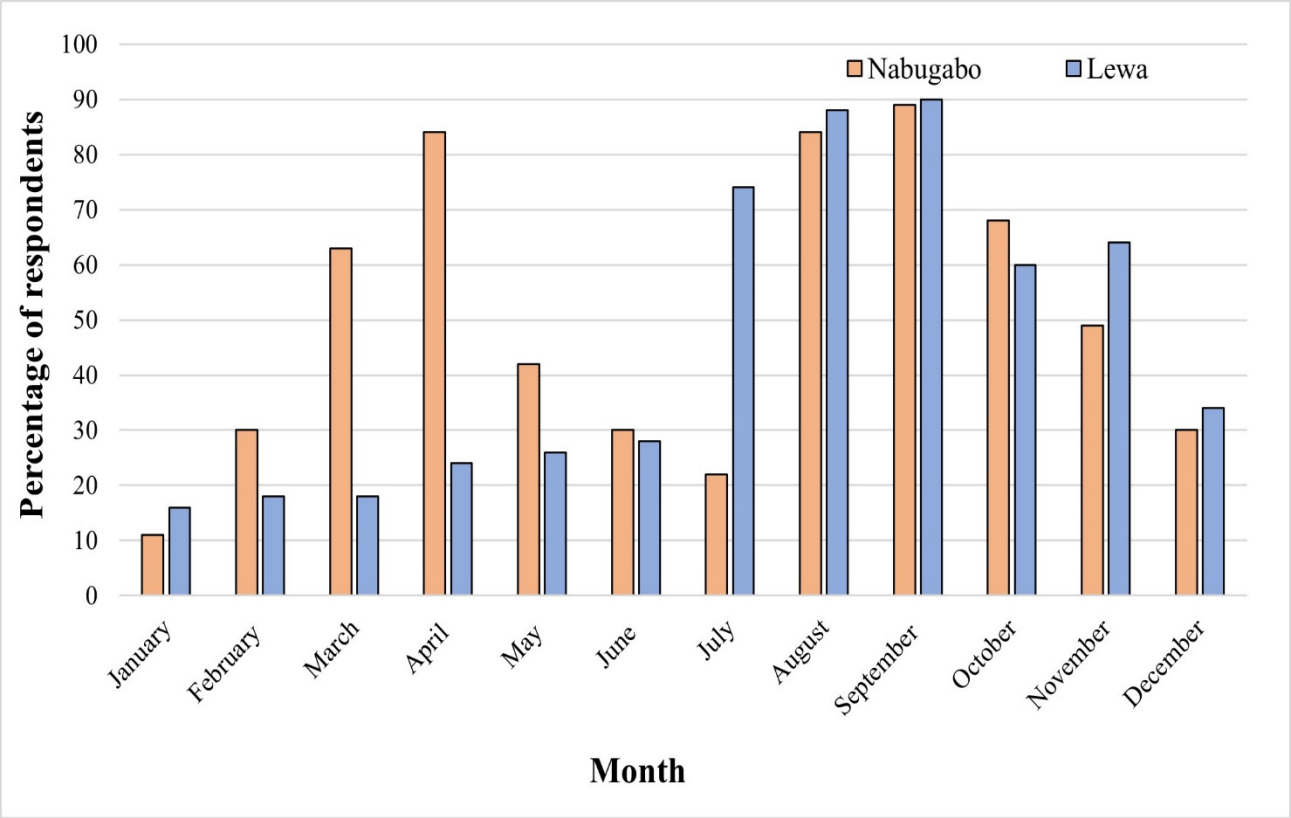

Figure 2.2: Percentage of respondents who reported frequency of conflict with wild animals during different months within the last one year in Bbaale village, Uganda (N = 73) and in Manyangalo village near Lewa Borana Conservancy, Kenya (N = 50).

There was a significant difference in response to when local HWC started ($\chi^2 = 58.69$, $p < 0.05$) and the causes of HWC ($\chi^2 = 57.63$, $p < 0.05$). Most of the people at Lewa stated HWCs started about 6-10 years ago, while most people at Nabugabo reported uncertainty about the beginning of the HWC. At both Nabugabo and Lewa, respondents commonly attributed HWC to factors like insufficient food in animal habitats, growing animal populations, and expanding human settlements, with additional respondents from Nabugabo indicating the presence of researchers in the area and other causes (such as the proximity of forests to their gardens) (Figure 2.3).

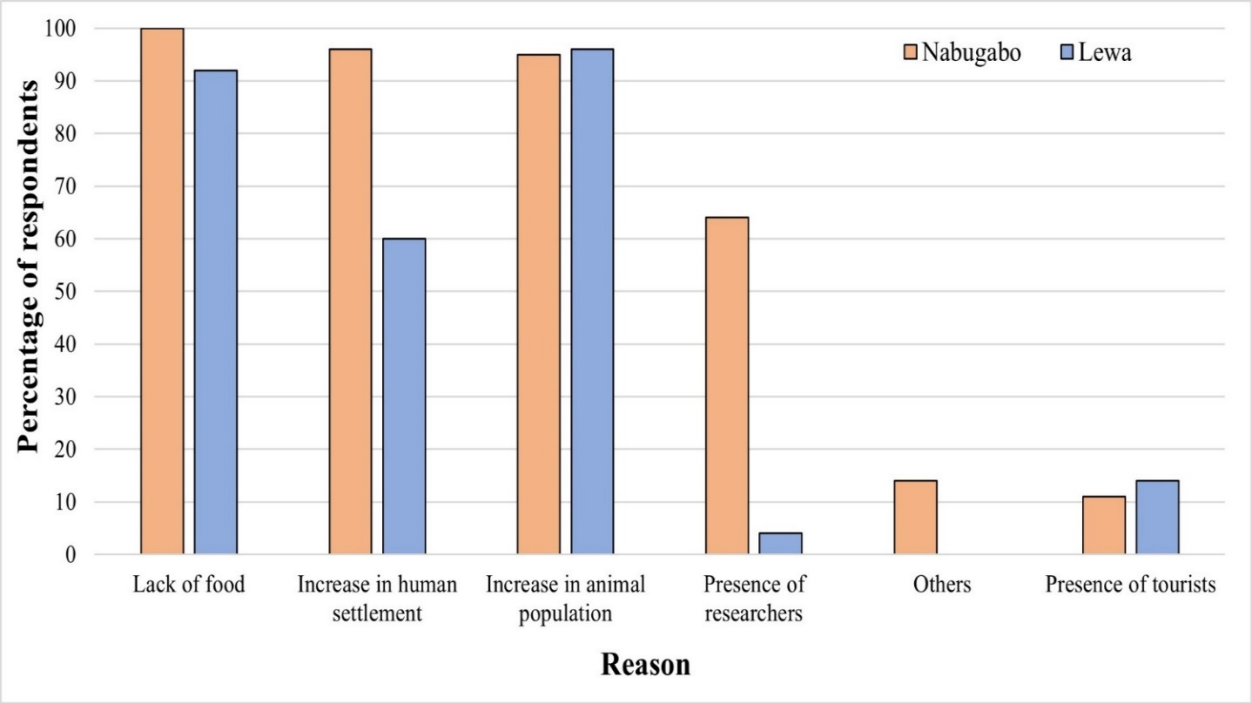

Figure 2.3: Percentage of respondents who reported different reasons for the wildlife conflicts in Bbaale village, Lake Nabugabo, Uganda (N = 73) and Manyangalo village, near Lewa-Borana Conservancy, Kenya (N = 50).

While there was a significant difference in the mitigation strategies used to guard against wildlife between Nabugabo and Lewa ($\chi^2 = 84.34$, $p < 0.05$), shouting was the most commonly reported method for deterring wildlife from crop foraging at both Nabugabo and Lewa. At Nabugabo, respondents frequently mentioned strategies like banging tins, using dogs and scarecrows, and less commonly reported strategies including fencing, poisoning, trapping and killing, trapping and releasing, and lighting bonfires; these latter methods were not used or used less frequently at Lewa (Figure 2.4).

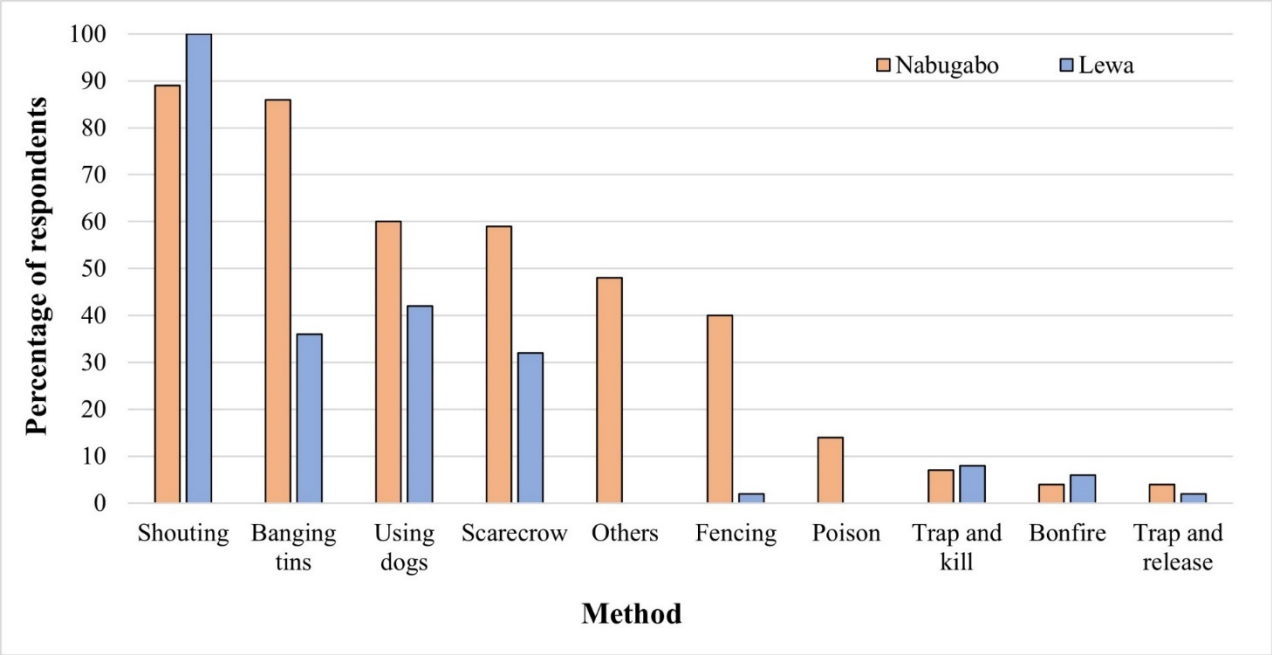

Figure 2.4: Percentage of respondents who reported different types of methods used to guard against the wildlife in Bbaale village, Lake Nabugabo, Uganda (N = 73), and in Manyangalo village in Lewa-Borana Conservancy, Kenya (N = 50).

2.3.2 Socio-economic factors influencing responses to HWC

Of the 115 survey respondents at Nabugabo and Lewa for whom we had socioeconomic data, 26% reported only one type of HWC, 18% reported two types of HWC, 21% reported three types of HWC, and 35% reported four types of HWC. The model selection procedure identified 44 models within ΔAICc < 7. Model averaging indicated that amount of cultivable land was a significant predictor of the number of types of HWC reported, with the odds ratio indicating the respondents who cultivated > 1000 acres reporting significantly higher number of HWC than those who cultivated < 100 acres.

In terms of HWC severity, 80% reported high severity, 14.8% reported low severity, and 5.2% said they were unsure. The model selection procedure identified 12 models within ΔAICc < 7. Model averaging showed that education and site were significant predictors of reported HWC severity, with the odds ratio of the respondents reporting high severity who attended or completed secondary level was lower than the respondents who did not attend any schooling. Furthermore, the odds ratio of the Nabugabo respondents reporting high severity was greater than for the Lewa respondents.

With regard to HWC frequency, 65.2% reported that HWC occurred more than once per day, 13% reported once per day, 6.1% reported two-three times per week, 12.2% reported once per week, and 3.5% (N = 4) reported once per month. The model selection procedure identified 36 models within ΔAICc < 7. Model averaging indicated that site was the only significant predictor of the frequency of HWC reported by the respondents, with the odds ratio of the Nabugabo respondents reporting high frequency of HWC being less than that of the Lewa respondents.

2.3.3 Perception of people towards the Nabugabo Research Site and Lewa-Borana Conservancy

Among the 24 respondents at Nabugabo who reported Rank 1 negative effects, more respondents attributed these effects to the researchers (71%) than to the monkeys (29%), while this was split evenly among the four respondents who reported Rank 2 negative effects. When asked to rank the benefits from the Nabugabo Research Site, among the 71 respondents who reported Rank 1 benefits, the majority (83%) reported job opportunities, while only a small number mentioned financial aid to villagers, school activities, infrastructure development, and similar aspects (Figure 2.5A). Among the 51 respondents who reported Rank 2 benefits, some reported help for villagers (31%) and knowledge about research (24%) while a few highlighted job opportunities, infrastructure improvements, organized activities, and enhanced tourist attractions (Figure 2.5A). In terms of ideas to improve the relationship between community and researchers at Nabugabo, the majority of the respondents (49%) suggested more job opportunities, followed by researchers taking initiatives to stop monkeys from crop foraging or looking after *"their"* monkeys (33%), improving communication with the villagers (30%), providing more healthcare to the community members (25%), providing financial help to the villagers (11%), providing financial compensation for damage caused by the monkeys (8%), and < 5% suggesting other solutions.

At Lewa, among the 50 respondents who reported Rank 1 negative effects, most (84%) attributed these effects to wildlife, while a smaller number (16%) pointed to the conservancy and researchers as the causes of HWC. Among the 22 respondents who reported Rank 2 negative effects, 59% attributed them to the researchers, while 41% pointed to the monkeys. When asked to rank the benefits from the Lewa-Borana Conservancy, the majority of the respondents (62%)

reported benefits from the water projects as Rank 1, while very few respondents reported education programs, security, job opportunities etc. (Figure 2.5B). Among the 48 respondents who reported Rank 2 benefits, some mentioned security (48%) and education programs (28%), while a few highlighted other benefits such as water projects, job opportunities, emergency responses, and healthcare (Figure 2.5B). In terms of ideas to improve the relationship between the community and conservancy, 30% of respondents suggested preventing wildlife from entering community farms and destroying crops (e.g., better fencing), 26% suggested that researchers should fulfil their promises and help the community, and 20% of respondents suggested food donation should be provided during droughts. Additionally, 14% suggested financial compensation for any damage caused by the wildlife, 14% suggested finding markets for the local produce, 10% suggested that the results of the survey should be made available to the community, only 6% suggested that more job opportunities should be made available, made other suggestions, or did not respond.

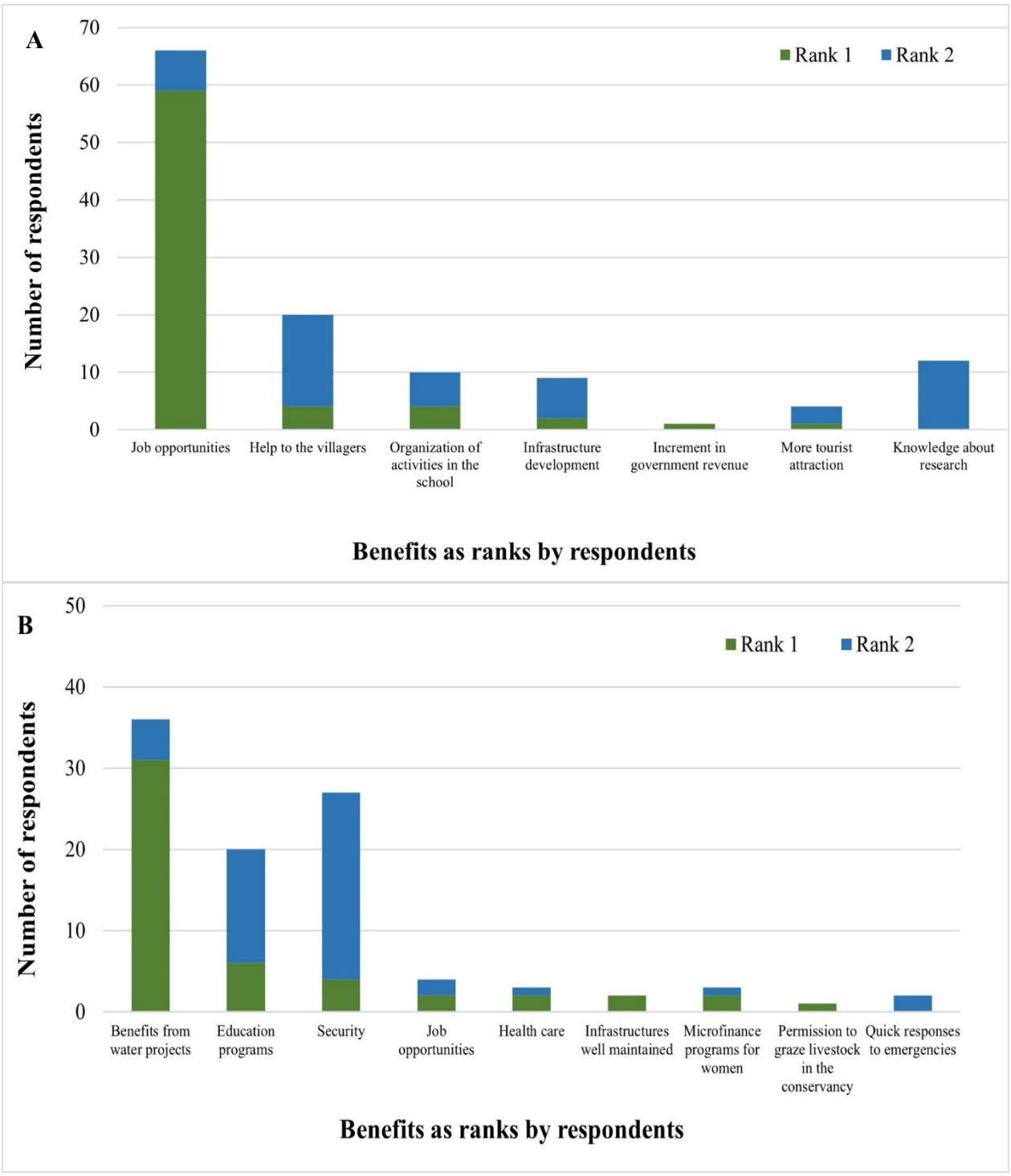

Figure 2.5: Number of respondents who ranked the benefits from the (A) Nabugabo Fish & Research Project on the shores of Lake Nabugabo, Uganda and (B) the Lewa-Borana Conservancy in and around Lewa-Borana Conservancy, Kenya.

2.4 DISCUSSION

2.4.1 HWC in East African villages located near research and conservancy sites

We found that more animal species were observed in the village near the Lewa-Borana Conservancy in Kenya than in the village adjacent to the Nabugabo Research Site, Uganda; thus, it is not surprising that a higher number of species were reported foraging on crops at Lewa. However, respondents at both sites frequently cited non-human primates (herein primates) as involved in crop foraging and food store destruction. In addition to primates, other wild animals were also reported to be involved in crop foraging and destruction of food store at both Nabugabo and Lewa. HWC at both sites may have been prompted by cultivations such as cassava (*Manihot* sp.), beans, sweet potatoes (*Ibomoea* sp.), maize (*Zea mays*), bananas (*Musa* sp.) at Nabugabo and onions (*Allium* sp.), maize, beans, and potatoes (*Solanum* spp.) at Lewa (data not shown). This is consistent with research in Rwanda, where wild animals foraged on crops such as maize and potatoes (Mc Guinness & Taylor, 2014) and in Ethiopia's Bale Mountains, where species like baboons and warthogs fed on wheat, barley, and legumes (Mekonen, 2020). While it has been hypothesized that crop foraging may occur because of nutritional benefits, one study at Nabugabo found no difference in proteins, lipid, or fibre content between wild and crop foods, indicating instead that crop foraging may simply confer an accessibility benefit (Cancelliere et al. 2018).

More animal species reportedly scared livestock and threatened people at Lewa than at Nabugabo, likely due to the higher number of terrestrial predators like lions, hyenas, and wild dogs at Lewa, compared to Nabugabo, where only wild dogs were reported as threats. Major predators like leopards and hyenas have been reported to affect livestock in and around several protected areas (Demeke & Afework, 2013; Mekonen, 2020; Messmer, 2009), including near the Lewa-Borana Conservancy where leopards, hyenas, jackals, and elephants were reported to be most commonly involved in encroachments (Dupuis-Desormeaux et al., 2023). In addition to the greater

variety of wildlife, the type of wildlife present at each site may be important, as large herbivores and carnivores need extensive home ranges and substantial food resources (Owen-Smith, 1988; Sukumar, 1990), which may lead them to venture into human-occupied areas, especially during food shortages.

People at Lewa reported experiencing HWC during the day and night, whereas HWC were reported only during the day at Nabugabo. The animal species involved in HWC—except for rats—are primarily diurnal. This may explain why respondents at both sites reporting HWC during daytime hours. That said, a meta-analysis revealed that large mammals often become more active at night due to human disruption (Gaynor et al., 2018), increasing nighttime activity by as much as 68% when humans are present. Given that Lewa has more large mammals and predators than Nabugabo, this trend may explain the occurrence of nighttime HWC at Lewa.

The finding that across the year, HWC is bimodally distributed at Nabugabo but unimodally at Lewa suggests that seasonality significantly affects the timing and frequency of these conflicts (Long et al., 2020). Our results may be linked to rainfall patterns influencing planting (Bedane et al., 2022), growing, and harvesting, with rainfall also potentially influencing wild animals' crop foraging behaviour since it may be affected by the seasonal availability of naturally occurring food (Seiler & Robbins, 2016). For example, Naha et al. (2019) found that human-elephant conflicts in North Bengal were more frequent during the rainy season, coinciding with key crop harvests. Increased HWC during dry seasons at Lewa may result from food scarcity in the natural habitat during peak HWC months of July-September (Hockings et al., 2009; McLennan & Hill, 2010). This is supported by Ibrahim et al. (2023) who reported higher crop foraging by hamadryas baboons during the dry season in Borena-Sayint National Park, Ethiopia.

Interestingly, the availability of wild foods does not appear to influence crop foraging behaviour of vervet monkeys at Lake Nabugabo (Cancelliere et al. 2018, Schwegel et al. 2023).

That more than half of respondents at Nabugabo and Lewa cited insufficient food, rising animal populations, and increasing human settlement as primary causes of HWC aligns with global trends (Amaja et al., 2016; Mekonen, 2020). Similar factors, including human settlement and agricultural expansion, have been noted across several African countries (Ladan, 2014; Makindi et al., 2014; Mekonen, 2020). At both sites, crop farming was the main income source (data not shown). While few at Nabugabo raise livestock, many at Lewa do, suggesting that agricultural expansion into wildlife habitats may heighten HWC.

The use of diverse strategies to manage HWC, such as shouting, using dogs and scarecrows, reflects the reported severity of HWC at Nabugabo. In contrast, Lewa's reliance primarily on shouting indicates a less varied approach, which may reflect the frequent but less severe HWC being perceived as a nuisance more than a serious problem. The practices at Nabugabo are consistent with broader regional strategies for mitigating HWC, aligning with methods observed in other East African countries (Mekonen, 2020; Musyoki, 2014).

2.4.2 Socio-economic factors influencing responses to HWC

Crop foraging is a major source of HWC globally, as many people rely on subsistence agriculture (Hill, 2002). In our study, individuals with larger cultivated areas were more likely to report higher HWC, though our findings contrast with others who found no significant link between landholding size and reported losses due to HWCs (Bhushal et al., 2024). Larger land areas may offer more opportunities for wildlife to access unguarded crops and could support a wider variety of crops that attract wildlife. Our findings also indicated that respondents with secondary education reported experiencing less severe HWC than those with no formal schooling,

though the difference was smal. Nonetheless, higher education levels have been previously correlated with reduced risk perception and more positive attitudes (Hanisch-Kirkbride et al., 2013; Kimmig et al., 2020). Additionally, less educated individuals may be more likely to see wildlife for its tangible benefits, while those with higher education tend to have a broader appreciation of wildlife (Manfredo et al., 2003). As noted above, respondents at Nabugabo reported higher severity of HWC compared to those at Lewa, but experienced HWC less frequently. This difference may be due to Lewa's proximity to a conservancy, which are protected areas that typically have organized HWCs mitigation and management strategies (Baral & Heinen, 2007; Sharma et al., 2019). Additionally, perceptions of HWC can be influenced by infrequent but intense incidents or hearsay, which may not reflect actual HWC-associated losses (Naughton-Treves & Treves, 2009).

2.4.3 Perception of people towards the Nabugabo Research Site and Lewa-Borana Conservancy

At both Nabugabo and Lewa, most respondents expressed positive feelings toward the research site and conservancy, with few showing dislike or neutrality. This aligns with studies from various regions that found local communities generally hold positive attitudes toward protected areas (Myanmar: Allendorf et al. 2006; Nepal: Allendorf 2007; Cameroon: Bauer 2003; Kibale, Uganda: MacKenzie et al. 2017; Ethiopia: (Munaw, 2023). These positive attitudes may stem from recognizing conservation benefits and effective management (T. Allendorf et al., 2006).

When negative views were expressed by respondents, they disliked the Nabugabo Research Site due to perceived negative effects from researchers and monkeys. They felt the researchers should manage the monkeys, which they believed were becoming bolder and damaging crops. Additionally, many blamed the site for the increasing monkey population, which was perceived as

contributing to crop destruction. At both Nabugabo and Lewa, some expressed dissatisfaction with researchers' treatment and unfulfilled promises. For example, at Lewa, most people cited poor communication from researchers and insufficient job opportunities as major drawbacks, along with wildlife-related issues like crop damage and threats to livestock. Our findings emphasize the need for clear communication with community members and caution against overpromising.

Perhaps not surprisingly, when asked how to improve relations between the community and researchers, many respondents at both sites suggested increasing job opportunities. At Nabugabo, respondents also highlighted the need for improved communication, sharing research findings, and healthcare. Since the respondents who reported negative effects of the research site viewed monkeys as the researchers' responsibility, they proposed financial compensation for damages caused by the monkeys. Similarly, at Lewa, respondents suggest that community-researcher and conservation efforts could be improved by finding ways to prevent wildlife from entering farms and providing financial compensation for wildlife-related damages. Lewa already had extensive fencing to exclude elephants from human-occupied areas, but this does not prevent smaller animals from entering crop fields. Additional suggestions included fulfilling promises to the community, providing food donations during droughts, and recommended sharing survey results with community members to keep them informed.

2.5 CONCLUSION

This study contributes to the limited literature comparing HWC in a non-protected area (Nabugabo) and a protected area (Lewa). It reveals that Lewa has low severity but high frequency of HWC, while Nabugabo shows the opposite pattern, suggesting the need for tailored management strategies. Socioeconomic factors also appear to influence perceptions of HWC. Effective management should address these elements to meet the unique needs of each community. Additionally, the overall positive attitudes toward the research site and conservancy may indicate

community support for conservation efforts, creating a favourable environment for initiatives that promote human-wildlife coexistence.

2.6 CONTRIBUTIONS STATEMENT

VAMS and SEM designed the study and methodologies; PU refined the research questions, analysed the data, wrote and edited the manuscript; VAMS and SEM revised and edited the manuscript.

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CHAPTER 3: OVERLAP IN PARASITE COMMUNITIES AMONG VERVET MONKEYS, HUMANS, LIVESTOCK AND DOGS AT LAKE NABUGABO, UGANDA

Chapter Summary

Overlap in wildlife habitat and human settlements can facilitate the transmission of anthropozoonotic parasites. We examined parasitism in sympatric hosts, including vervet monkeys (N=75), humans (N=25 household latrines), dogs (N=25), and livestock (N_{cows}=9, N_{goats}=7, N_{pigs}=9) in the human-modified landscape at Lake Nabugabo, Uganda. We used sedimentation technique for coproscopic analysis, and molecular techniques for the identification of *Strongyloides*, strongylid nematodes and protists. We identified 25 unique parasite taxa with dogs harbouring 17 parasite taxa, livestock harbouring 15 parasite taxa, vervet monkeys harbouring 10 parasite taxa, and humans harbouring nine parasite taxa. The coproscopic analysis of fecal samples showed that there was a significant difference in the parasitic infection rate between vervet monkeys (89%), humans (24%), dogs (40%), and livestock (48%). General taxonomic assignment of 157 Amplicon Sequence Variants (ASVs) indicated that the studied host species harbour at least seven known genera of strongylid nematodes, with *Ancylostoma*, *Murshidia* and *Oesophagostomum* being the most prevalent. We did not find any *Strongyloides* infections in humans, and only limited overlap between vervets and other hosts (i.e., dog, pig). Among protists, we identified species-specific *Cryptosporidium* taxa in dogs, goats, and pigs, and *C. andersoni* was found in both dogs (4%) and cows (8%). *Giardia intestinalis* assemblage A was found in vervets (1.3%), humans (12%), and dogs (16%), *Enterocytozoon bieneusi* occurred in humans (12%), and *Encephalitozoon intestinalis* occurred in vervets only (4%). Our results indicate overlap of *G. intestinalis* between humans and animals. Although we did not find evidence of human-animal overlap for *Cryptosporidium*, there is the potential for anthropozoonotic disease transmission given that *C. ubiquitum* has previously been found in humans.

3.1 INTRODUCTION

It is estimated that over 60% of human infectious diseases are zoonotic in origin (Taylor et al., 2001). However, the majority of disease control programmes focus on humans only (Morse et al., 2012), following single-pathogen single-host epidemiological theory (Antonovics, 2017). In recent decades, several disease outbreaks have been caused by pathogens that can persist and infect multiple host species (Murray et al., 1999). For instance, the populations of African wild dogs (*Lycaon pictus*) in the Serengeti region, Tanzania and the Masai Mara, Kenya (Alexander et al., 1993; Gascoyne et al., 1993) and Ethiopian wolves (*Canis simensis*) in the Bale region, Ethiopia (Laurenson et al., 1998; Sillero-Zubiri, 1996) were reported to have been affected by the *Rabies lyssavirus* transmitted by domestic dogs (*Canis lupus* f. *familiaris*). Similarly, human *Measles morbillivirus* and *Influenza* virus have been reported to have been transmitted to chimpanzee (*Pan troglodytes*) and mountain gorilla (*Gorilla beringei beringei*) populations (Wallis & Lee, 1999). Various factors have been reported as causes of emerging diseases, such as pathogen characteristics like mutation, recombination, genetic drift, host characteristics such as age, sex, immunosuppression, host population characteristics such as population size, behaviour, and movement, and ecological factors such as changes in agriculture and urbanization (Cleaveland et al., 2001; Morris & Potter, 1997; Morse, 1995; Schrag & Wiener, 1995). In the last few decades, there has been an increase in the interaction and exposure among humans, livestock, and wildlife due to increased intrusion by humans into wildlife habitat, which has led to transmission and evolution of pathogens, and the emergence of infectious diseases (Cleaveland et al., 2001; Cole & Viney, 2018; Jones et al., 2008).

Studies on parasite epidemiology have traditionally focused on factors related to individual hosts such as host behaviour (Cote & Poulin, 1995), host morphology (Ezenwa & Jolles, 2008), and host genetics (Kloch et al., 2010; Luikart et al., 2008; Rijks et al., 2008) or interactions between

a single host species and parasite such as habitat structure and ecology (Chapman et al., 2006a, 2006b). However, recently it has become clearer that parasites exist within a network of complex relationships involving multiple hosts (Belden & Harris, 2007), and thus it is important to understand the dynamics of parasite transmission and impact on individual disease risk and health conditions (Farrell et al., 2013; Johnson et al., 2013; Longdon et al., 2011). When several host species share the same habitat, it provides a pathway for contact and transmission of gastrointestinal parasites (Obanda et al., 2019). However, both intrinsic (host immune response, physiology etc.) and extrinsic (rainfall, temperature, etc.) factors contribute to determining whether a parasite eventually establishes itself into a particular host species or population (Duffy et al., 2007; Turner & Elena, 2000). It is likely that some parasite species that are prevalent or dominant in one host species might not be able to establish themselves in another host species despite sharing the same habitat and resources (Obanda et al., 2019).

Human activities such as deforestation, urbanization, or changes in land use have resulted in the close proximity and increase of interactions between humans and animals (Esposito et al., 2023). Animals such as birds, bats, rodents, pigs, cows, camels, primates, and insects such as mosquitoes, ticks, and fleas are known to be a link between disease and humans, thereby leading to the emergence of diseases (Cavallero et al., 2021; White & Razgour, 2020). Human interference in wildlife habitat can influence parasite infection in wild hosts by reducing natural food availability and compromising host nutrition (Chapman et al., 2006; Hussain et al., 2013a), transmission through domestic animals (Chomitz, 2007), agricultural expansion and wildlife-livestock exposure (Holechek et al., 2017), and sharing common resources such as water sources (Lane-deGraaf et al., 2014; R. C. A. Thompson, 2013).

Human and non-human primates (primates hereafter) share a close phylogenetic relationship, which may facilitate the exchange of several parasite taxa between them (Gillespie & Chapman, 2006; Tomley & Shirley, 2009; Wolfe et al., 1998). Previous research has shown that expanding human settlements into wildlife habitats and forest fragmentation have led to increased transmission of parasites in several primate species (redtail guenons *Cercopithecus ascanius*: (Gillespie et al., 2005), red colobus *Piliocolobus tephrosceles*: (Gillespie & Chapman, 2008), indris *Indri indri*: (Junge et al., 2011), lion-tailed macaques *Macaca silenus*: (Hussain et al., 2013) and chimpanzees *Pan troglodytes verus*: (Sá et al., 2013; Zommers et al., 2013)) and in humans such as Simian Immunodeficiency Virus (Heeney et al., 2006), and Herpes B virus *Macacine Herpesvirus 1* (Vasireddi & Hilliard, 2012). However, the relationships among hosts, parasites, and habitat remain intricate and multifaceted despite the increasing awareness that habitat alterations influence host-parasite dynamics (Acevedo-Whitehouse & Duffus, 2009; Daszak et al., 2000). Contrary to studies that show increase in parasitism with the increase in anthropogenic impact, there are several studies that show no differences in parasitism based on habitat characteristics (ectoparasite species richness: (Wright et al., 2009); nematode prevalence: (Hodder & Chapman, 2012); parasite species richness and prevalence: (Young et al., 2013)) and there are studies that show lower parasite infections in primate populations living close to habitats disturbed by human encroachment (Altizer et al., 2007; Lane et al., 2011; Wenz et al., 2010).

3.1.1 Strongylid nematodes

Strongylid nematodes include a vast diversity of gastrointestinal parasites, commonly known as hookworms and lungworms (Brooker et al., 2004; Lichtenfels et al., 2008; Van Wyk et al., 2004), infecting numerous mammalian taxa (Ilík et al., 2023). These nematodes are found mainly in gastrointestinal and pulmonary tracts feeding on blood and tissues of hosts for several

years (Červená et al., 2017; Delano et al., 2002; A. M. Zajac, 2006). Although these nematodes do not cause mortality, their severe infections can cause inflammatory reactions, lesions, weight loss, anemia, and malnutrition (Delano et al., 2002). Since strongylid nematodes infect a wide range of mammals, including humans and primates, they are of zoonotic potential in the areas where humans and primates live in close proximity and share habitat and resources (Ghai et al., 2014; Hasegawa et al., 2014, 2017; Ota et al., 2015). For example, *Oesophagostomum* spp. have been reported from humans and great apes in Eastern Africa (Cibot et al., 2015; Ghai et al., 2014) and Tibetan pigs in China (Li et al., 2017). Similarly, *Necator americanus* has been reported from gorillas (*Gorilla gorilla gorilla*) and humans in Gabon (Hasegawa et al., 2017) as well as humans in Myanmar (Aung et al., 2017), and *Necator gorillae* has been reported from Ugandan chimpanzees (*Pan troglodytes schweinfurthii*) (Hasegawa et al., 2017). Parasitic nematodes in the strongylid group form communities within host organisms, especially in large herbivores, and these communities consist of multiple coexisting species with various taxonomic relationships (Lichtenfels et al., 2008; Mclean et al., 2012b; Van Wyk et al., 2004). Traditional visual identification and molecular methods struggle to identify individual strongylid species or haplotypes in communities from noninvasively collected fecal samples (Lichtenfels et al., 2008; Pafčo et al., 2018).; high-throughput sequencing (HTS) serves as a better and more powerful tool for such analyses (Aivelo & Medlar, 2017; Avramenko et al., 2015; Tanaka et al., 2014).

3.1.2 Strongyloides

Strongyloides is a genus of nematodes with about 50 species of intestinal parasites that exclusively infect vertebrates such as amphibians, reptiles, birds, and mammals (Speare, 1989; Viney & Lok, 2015). Two *Strongyloides* species, *S. stercoralis* and *S. fuelleborni* are known to infect humans (Viney & Lok, 2015) with *S. stercoralis* being found worldwide in tropical and

subtropical areas (Schad, 1989) and *S. fuelleborni* and *S. fuelleborni kellyi* in Asia, Papua New Guinea, and various regions in Africa (Frias et al., 2018; Hasegawa et al., 2016a; Krolewiecki & Nutman, 2019; Thanchomnang et al., 2017a; White et al., 2019). The widespread occurrence of *S. stercoralis* in tropical and subtropical areas can be largely ascribed to elevated temperatures, increased moisture levels, insufficient sanitation, substandard hygiene practices, and occupations like farming and mining that raise the likelihood of individuals encountering soil contaminated larvae (Schär et al., 2013a).

Strongyloidiasis is a common infection in wild and domestic animals as well (Viney & Lok, 2015). Infection of *Strongyloides* is frequently documented in both free-ranging and captive primates across all continents except Antarctica, and with a possibility of missing data from captive primates in Australia (Nosková et al., 2024). *Strongyloides cebus* has exclusively been identified in the Central and South American primates (Dorris et al., 2002; Mati et al., 2013), with no records of human infections with this species. While it is believed that *S. fuelleborni* is the primary cause of infection, there have been reports of mixed infections involving both *S. stercoralis* and *S. fuelleborni* in wild central chimpanzee (*Pan troglodytes troglodytes*) in Tanzania (Hasegawa et al., 2010), indicating that simultaneous infections may be relatively common (Hasegawa et al., 2016a).

In addition to humans and primates, *S. stercoralis* can also infect dogs and cats (Thamsborg et al., 2016). In experimental settings, *S. stercoralis* has been effectively transmitted from humans to dogs (Jariwala et al., 2017; Thamsborg et al., 2016). However, recent comparative research found the presence of two distinct genetic populations of *S. stercoralis* in dogs: one population seemingly exclusive to dogs, while another population is found in both dogs and humans (Jaleta et al., 2017; Nagayasu et al., 2017).

3.1.3 Protists

Cryptosporidium, *Giardia*, and microsporidia are found in both humans and animals; the infectious diseases caused by them (cryptosporidiosis, giardiasis, and microsporidiosis respectively) have been documented in both developed and developing nations (Fayer, 2010a; Thellier & Breton, 2008a; Xiao & Fayer, 2008a). As of now, there are 51 recognized species of *Cryptosporidium* (Stensvold et al., 2024) with the literature describing over 150 genotypes, and in humans, at least 25 species and 3 genotypes have been detected (Fayer, 2010; Stensvold et al., 2024; Xiao, 2010). Between 1920 and 1930, over 50 *Giardia* species were proposed, but current research, focusing on trophozoite/cyst morphology, acknowledges only six species. *Giardia intestinalis* (syn. *G. lamblia, G. duodenalis*), the species infecting humans, comprises eight valid assemblages (A-H), among which assemblages A and B are the main causes of most human infections (Mohammed, 2024; Ryan & Cacciò, 2013). Certain genotypes of some microsporidia *Enterocytozoon bieneusi* exhibit a tendency to be primarily adapted to specific hosts, while others have the potential for zoonotic transmission (Thellier & Breton, 2008). *Cryptosporidium* spp., *G. intestinalis,* and several microsporidia that can be transmitted between animals and humans have been found in livestock, companion animals, and wildlife (Ryan & Cacciò, 2013; Thellier & Breton, 2008; Xiao & Fayer, 2008). Several studies have shown that NHPs are potential sources of cryptosporidiosis, giardiasis, and microsporidiosis in humans (Du et al., 2015); cases of human-pathogenic *Cryptosporidium* spp., *G. intestinalis* and *E. bieneusi* infections in wild, semi-wild, and captive primates have also been reported in Asia, Africa, and the Americas (Karim, Dong, et al., 2014; Mynářová et al., 2016; Nizeyi et al., 2002; Sak et al., 2013, 2014; Ye et al., 2012, 2014) owing to the close phylogenetic relationship between humans and primates (Du et al., 2015).

This chapter aims to address two major research questions:

Research Question 1: How do parasite prevalence and species richness vary among sympatric hosts, namely humans, vervet monkeys, livestock, and dogs at Lake Nabugabo, Uganda?

Research Question 2: Which species of the order Strongylida, genera *Strongyloides*, *Cryptosporidium, Giardia*, *Encephalitozoon*, and *Enterocytozoon* are shared among humans, vervet monkeys, livestock, and dogs at Lake Nabugabo, Uganda?

3.2 METHODS

3.2.1 Study Site

The study was conducted on the shores of Lake Nabugabo, Uganda (0°22′–12°S, 31°54′E, 1,136 m), a satellite of Lake Victoria that is mostly surrounded by wetlands, grasslands, patches of degraded forest, farmers' fields, and small buildings (Chapman et al., 2016). The area receives an average of 1,348 mm of rain annually (Chapman et al., 2016) in two seasons with high rainfall (March to May and September to November) and two seasons with low rainfall (December to February and June to August) (Schwegel et al., 2023). The Nabugabo Research Site on the shores of the lake is home to long-term research in three neighboring groups of vervet monkeys (Group M: since 2011, Groups HC & KS: since 2016), which served as subjects for this study.

3.2.2 Sample collection

Between July – September 2022, we non-invasively collected 75 fecal samples (mean = 2.03, range = 1-4) from adult and subadult males and females in each of the three vervet monkey study groups, 25 fecal samples from 25 different dogs, 25 fecal samples from 25 different species of livestock (9 cows, 7 goats, and 9 pigs), as well as 25 fecal samples from the 25 different pit latrines of households in Bbaale village nearby Lake Nabugabo, Uganda. The fecal samples from vervets, dogs, and livestock were collected as soon as the individuals were observed defecating to avoid contamination with the environment/soil. The collected samples were fixed in 10% formalin for

coproscopic analysis and 96% ethanol for molecular analysis. The samples were kept at room temperature until they were transported to the labs for the analyses.

3.3.3 Coproscopic analysis

The samples fixed in 10% formalin were analyzed at the Central Diagnostic Laboratory, College of Veterinary Medicine Animal Resources and Biosecurity, Makerere University, Kampala, Uganda using formalin-ether sedimentation technique (Ritchie, 1948; Ash & Orihel, 1987, Uga et al., 2010). In this technique, 5 mL from each thoroughly mixed sample was poured through a 20 μm sieve into a plastic beaker. The filtrate was transferred to a 15 mL centrifuge tube, adjusted to 15 mL with saline, and centrifuged at 500 G for 2 minutes. The supernatant was discarded, and the sediment was reconstituted in 10 mL saline, re-centrifuged, and the supernatant discarded again. The sediment was then reconstituted in 2 mL formalin and the volume adjusted to 10 mL. Next, 3 mL of ether was added to the mixture, the tube was shaken for 30 seconds and centrifuged at 500 G for 3 minutes. The top 3 layers were discarded, and the remaining fluid on the walls was drained back onto the sediment. The sediment was mixed with a disposable pipette tip, and two drops (~5 μL each) were placed on separate glass slides. To one slide, 2 drops of saline were added, and to the other, 2 drops of iodine. A coverslip was placed on top, and both slides were examined under a microscope under 10X magnification. The parasites were identified to the family and genus level wherever possible (Soulsby, 1982; Zajac & Conboy, 2006).

3.3.4 DNA isolation and sequencing

Total fecal DNA was extracted for detection of *Strongyloides* spp. from ethanol-preserved fecal samples using the DNeasy PowerSoil Pro kit (Qiagen, Hilden, Germany) after the aliquots were left overnight at 37°C to evaporate the residual ethanol. No modifications were made to the manufacturer's protocol, and the DNA was eluted in 100 μL of elution buffer. Eluted DNA was

stored at -20°C until further analyses. *Strongyloides* spp. DNA was detected by real-time quantitative PCR (qPCR) at the Real-Time PCR LightCycler® (Roche, Rotkreuz, Switzerland) targeting a conservative region (101 bp) of the gene for 18S rRNA (18S rDNA) using primers Stro18S-1530F, Stro18S-1630R and the probe Stro-18S-1586T as described by (Verweij et al., 2009). The PCR reaction comprised of 12.5 µl of PCRBIO Taq Mix Red (PCR Biosystems Ltd., London, UK), 1.25 µl of each primer, 5 µl of template DNA and filled up with PCR water up to the total volume of 25 µl. Cycling conditions were as follows: initial denaturation 1 min at 95°C followed by 40 cycles of 15s at 95°C, 15 s at 59°C and 7s at 72°C. Products were separated by electrophoresis in a 2% agarose gel stained by MIDORI Green Advance (Nippon Genetics Europe, Düren, Germany) and visualized by a UV transilluminator. Bands of corresponding size were cut off from the gel and purified using the GeneAid Gel/PCR DNA Fragments Kit (Geneaid, New Taipei, Taiwan). Products were sent for commercial sequencing to Macrogene (Macrogene Europe, Amsterdam, Netherlands).

The internal transcribed spacer 2 (ITS2) of strongylid nematodes was amplified using primers Strongyl_ITS-2_F and Strongyl_ITS-2_R using high-throughput sequencing (HTS) developed for strongylid nematodes in primates (Pafčo et al., 2018, 2019). Briefly, the HTS libraries were generated using a two-step-PCR approach following the Nextera primer design. Analyses were carried out in two technical replicates with different tag primer barcodes. DNA extractions from strongylid negative human feces and water were used as negative controls and synthetic DNA templates as positive controls. The final library was sequenced using MiSeq Reagent Kit v3 (2 × 300 bp pair-end reads, 600 cycles) by Illumina MiSeq platform.

Total genomic DNA (gDNA) for detection of *Cryptosporidium* spp., *G. intestinalis*, *E. bieneusi*, and *Encephalitozoon* spp. was isolated using the GeneAll® Exgene™ Stool DNA Mini

Kit (GeneAll Biotechnology Co., Ltd.; Seoul, South Korea) according to the manufacturer's guidelines, with the following modifications. The alcohol was evaporated from each sample at 65°C overnight. A 100 µl of 0.5 mm glass beads and 1,000 µl of lysis buffer was added to each tube and oo/cysts/spores were disrupted for 60 seconds at 5.5 m/s using glass beads in a FastPrep®-24 Instrument (MP Biomedicals, Santa Ana, CA, USA). The extracted gDNA was then stored at -80°C. Nested PCR protocols were used to identify *Cryptosporidium* spp. at partial sequences of gene encoding small subunits of rRNA (18S rDNA), *G. intestinalis* at partial sequences of gene encoding triosephosphate isomerase (TPI), and *E. bieneusi*, and *Encephalitozoon* spp. at partial sequences of gene encoding the internal transcribed spacer of rRNA (ITS) using established protocols and primers (Buckholt et al., 2002; Didier et al., 1995; Katzwinkel-Wladarsch et al., 1996; Sulaiman et al., 2003; Xiao et al., 1999). PCR amplicons were purified by GenElute™ Gel Extraction Kit (Sigma, St. Louis, MO, USA) according to the manufacturer‘s instructions and sequenced in both directions (SeqMe, Dobříš, Czech Republic).

3.3.5 Bioinformatics and data assembly

Gene-specific primers were trimmed using *skewer* (Jiang et al., 2014). Next, low-quality reads (expected error rate >2) were eliminated, and the filtered data set was denoised using *dada2* (Callahan et al., 2015) to obtain Amplicon Sequence Variants. Amplicon Sequence Variants (ASVs) are unique DNA sequences generated from targeted amplification of specific regions in the microbial genome, allowing for precise identification of distinct microbial taxa. Naive Bayesian *RDP classifier* (Wang et al., 2007) implemented in the *dada2* pipeline was used for taxonomic assignment of ASV with 80% posterior confidence. The reference training data set was downloaded from the National Center for Biotechnology Information database (200 top blast hits for each of our ASV, environmental samples were excluded). To avoid inflation of strongylid

diversity due to PCR/sequencing artifacts that were not corrected by *dada2*, we considered only those ASV that were consistently present in both technical duplicates for a given sample (Pafčo et al., 2018). We also excluded ASV that did not correspond to the Strongylida order. Read counts for ASV corresponding to the same genus were grouped within the resulting abundance matrix. Consequently, all further analyses focused on the variation in read counts among different strongylid genera. As different ASV for the same genus mostly corresponded to the same species, this step considerably reduced taxonomic redundancy of the dataset.

3.3.6 Phylogenetic analysis

The sequences obtained from the analyses were searched for the closest match to those in GenBank using the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information (NCBI). The sequences from this study are deposited in GenBank (Appendix B1; Appendix B2). We aligned sequences using Geneious Prime 2024.0.7 (www.geneious.com) and the phylogenetic trees were derived from IQ-tree (Minh et al., 2020) based on the maximum likelihood method with 1,000 bootstrap replicates.

3.3.7 Statistics

The prevalence of a parasite taxon was calculated by dividing the total number of individuals with a specific parasite taxon by the total number of individuals of a specific host group sampled, and the parasite species richness as the number of parasite taxa found in each host's fecal samples throughout the study period (Bush et al., 1997). Parasite infection rate was calculated as the presence of at least one parasite in the fecal sample divided by the number of samples for a particular host category. Chi-square tests of independence, followed by pairwise comparisons were conducted to test for significant differences in proportion of samples infected across different

host groups as well as proportion of samples infected with each parasite taxa across different host groups.

ASV prevalence was defined as the number of hosts infected with each ASV divided by the number of hosts sampled. Differences in alpha diversity of strongylid communities were investigated by using the number of ASVs per sample as a proxy measure. The number of different haplotypes per sample was highly correlated with the other commonly used alpha diversity indices, such as Shannon index (cor. coef. = 0.78), Simpson (cor. coef. = 0.63) or Inverse Simpson (cor. coef. = 0.78) and thus we used it as the only alpha diversity index in our analyses. The differences in haplotype diversity among host categories was tested by generalized linear model (GLM) with a quasibinomial error distribution, followed by a Tukey post-hoc test for pairwise comparison. Community composition was defined as prevalence and relative representation of ITS2 ASVs using two beta diversity metrics: Jaccard and Bray-Curtis ecological distances. Principal coordinate analysis (PCoA) was performed on both Jaccard and Bray-Curtis dissimilarities. Permutational analysis of variance (PERMANOVA) was performed, followed by analysis of similarity (ANOSIM), to test the interspecific differences in strongylid nematode community compositions among the hosts. Multivariate general linear models (GLMs) from the R package mvabund (Wang et al., 2012) were implemented to search for community-wide divergence and identification of significant ASVs that varied due to the different host species effect.

3.3 RESULTS

The coproscopic analysis of fecal samples showed that the parasitic infection rate was 40% (10/25) in dogs, 24% (6/25) in humans, 48% (12/25) in livestock, and 89% (67/75) in vervet monkeys. Dogs (mean ± SE = 0.4 ± 0.1) were found to be more infected than humans (mean ± SE = 0.24 ± 0.09) ($\chi^2 = 5.88$, df = 1, $p = 0.02$; Figure 3.1) but less than vervet monkeys (mean ± SE = 0.89 ± 0.04) ($\chi^2 = 52.43$, df = 1, $p < 0.001$; Figure 3.1), while the comparison between dogs and

livestock (mean ± SE = 0.48 ± 0.1) was not significant ($\chi^2 = 1.29$, df = 1, $p = 0.25$; Figure 3.1). Humans were found to be less infected than livestock ($\chi^2 = 12.5$, df = 1, $p < 0.001$; Figure 3.1) and vervet monkeys ($\chi^2 = 85.95$, df = 1, $p < 0.001$; Figure 3.1). Finally, livestock were found to be less infected than vervet monkeys ($\chi^2 = 38.95$, df = 1, $p < 0.001$; Figure 3.1).

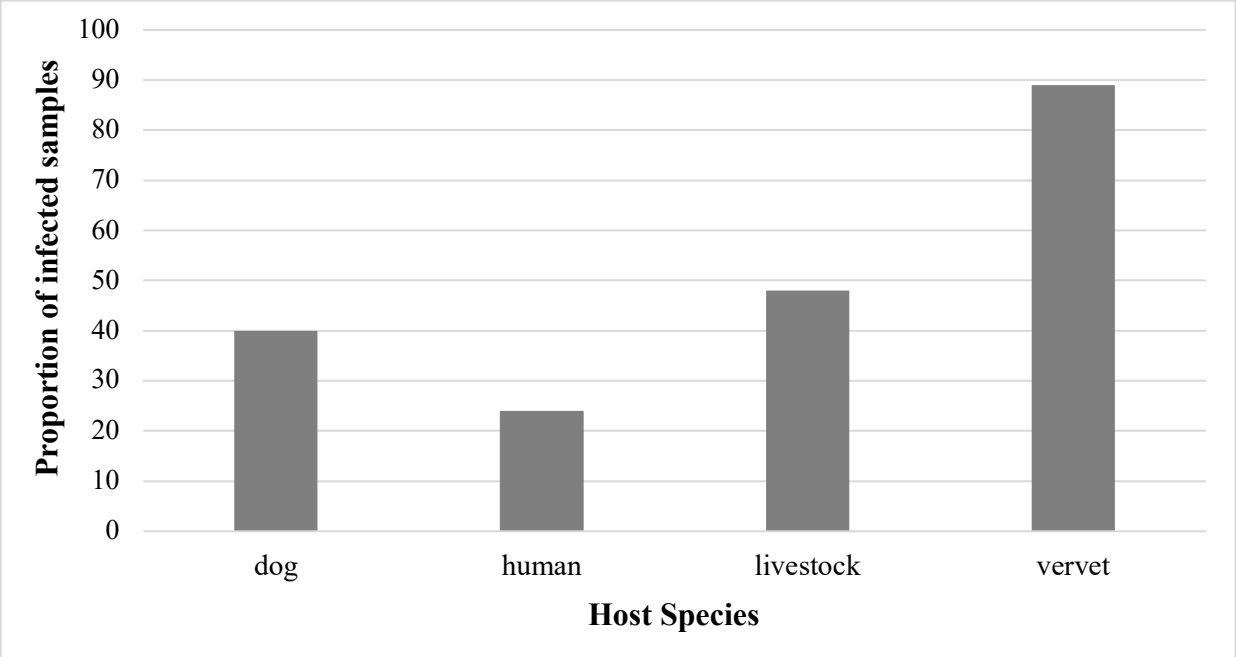

Figure 3.1: Proportion of infected samples from dogs (N = 25), humans (N = 25), livestock (N = 25), and vervet monkeys (N = 75) at the shore of Lake Nabugabo, Uganda.

The total number of parasite taxa identified by coproscopic and genetic analyses was 25 (Table 2.1, Table 2.2), with dogs harbouring 17 parasite taxa, livestock harbouring 15 parasite taxa, vervet monkeys harbouring 10 parasite taxa, and humans harbouring nine parasite taxa. Cestodes were found only in vervet monkeys (*Moniezia* sp.) and dogs (*Spirometra* sp.) (Table 2.1, Table 2.2). Trematodes (family Paramphistomidae) were found only in livestock (Table 2.1, Table 2.2). Among nematodes, *Trichuris* sp. in vervet monkeys (78.7%) was the most prevalent, followed by *Strongyloides fuelleborni* (36%), and *Ascaris* sp. (1.3%). *Trichuris* sp. was also found in humans (8%) and there was a significant difference in the proportion of samples infected with *Trichuris* sp. in vervet monkeys and humans ($\chi^2 = 98.91$, df = 1, $p < 0.001$). *Ascaris* sp. was also found in humans (4%) and livestock (4%), but there was no significant difference in the proportion of samples infected with *Ascaris* sp. in vervet monkeys, humans, and livestock ($\chi^2 = 1.68$, df = 2, $p = 0.43$). Other nematodes that were found in single host category included *Ancylostoma* sp. (16%), *Strongyloides stercoralis* lineage A (8%), *Toxocara* sp. (8%) in dogs, *Enterobius* sp. (4%) in humans, and *Strongyloides ransomi* (4%) and *Nematodirus* sp. (4%) in livestock (Table 2.1, Table 2.2). Among protists, *Giardia intestinalis* was found in dogs (16%), humans (12%), and vervet monkeys (1.3%), and there was a significant difference in the proportion of samples infected with *Giardia intestinalis* in dogs, humans, and vervet monkeys ($\chi^2 = 13.12$, df = 2, $p < 0.05$, Table 2.1, Table 2.2). *Cryptosporidium andersoni* was found only in dogs (4%) and livestock (8%) with no significant difference in the proportion of samples infected with *Cryptosporidium andersoni* ($\chi^2 = 0.79$, df = 1, $p = 0.37$, Table 2.1, Table 2.2). *Enterocytozoon bieneusi* was found only in humans (12%) (Table 2.1, Table 2.2). *Cryptosporidium canis* was found only in one dog (4%), *Cryptosporidium scrofarum* and *Cryptosporidium ubiquitum* were found only in two pigs (8%), and *Encephalitozoon intestinalis* was found only in 3 vervet monkeys (4%) (Table 2.1, Table 2.2).

Table 2.1: Prevalence of parasite taxa detected by coproscopic and genetic and their prevalence in the dogs, humans, livestock, and vervet monkeys at the shore of Lake Nabugabo, Uganda. *Parasite taxa identified from DNA sequencing.

Parasites	Taxa	Host type			
		Dogs (N = 25)	Humans (N = 25)	Livestock (N = 25)	Vervet monkeys (N = 75)
Cestodes	*Dipylidium* (Unsure)	8	4	0	0
	Moniezia	0	0	0	4
	Spirometra	8	0	0	0
Nematodes	**Ancylostoma*	56	4	4	0
	Ascaris	0	4	4	1.3
	**Cooperia*	4	0	0	0
	Enterobius	0	4	0	0
	**Haemonchus*	0	0	4	0
	**Hyostrongylus*	8	12	4	0
	**Murshidia*	24	36	4	0
	Nematodirus	0	0	4	0
	**Oesophagostomum*	36	36	16	11
	**Strongyloides fuelleborni*	0	0	0	36
	**Strongyloides ransomi*	0	0	4	0
	**Strongyloides stercoralis* lineage *A*	8	0	0	0
	Toxocara	8	0	0	0
	**Trichostrongylus*	0	0	0	8
	Trichuris	0	8	0	78.7
	**Unclassified*	20	28	0	4
Trematodes	Paramphistomidae	0	0	16	0
	Schistosoma (Unsure)	0	0	4	0
Protists	**Cryptosporidium andersoni*	4	0	8	0
	**Cryptosporidium canis*	4	0	0	0
	**Cryptosporidium scrofarum*	0	0	8	0

	**Cryptosporidium ubiquitum*	0	0	8	0
	**Microsporidia* sp.	0	0	0	4
	**Enterocytozoon bieneusi*	0	12	0	0
	**Giardia intestinalis*	16	12	0	1.3

Table 2.2: Number of identified amplicon sequence variants (ASVs), their proportion of total reads, number of ASVs in each host type and ASVs prevalence among host species.

Parasite taxa	**Number of identified ASVs**	**Total reads proportion (%)**	**Number of ASVs in dogs**	**Number of ASVs in humans**	**Number of ASVs in livestock**	**Number of ASVs in vervet monkeys**	**Prevalence in dogs (%)**	**Prevalence in humans (%)**	**Prevalence in livestock (%)**	**Prevalence in vervet monkeys (%)**
Ancylostoma braziliense	16	11.1	16	0	0	0	32	0	0	0
Ancylostoma caninum	20	25.3	20	0	1	0	48	0	4	0
Ancylostoma duodenale	13	15.3	13	1	0	0	28	4	0	0
Ancylostoma tubaeforme	3	5.3	3	0	0	0	8	0	0	0
Ancylostoma sp.	31	1.4	31	0	0	0	28	0	0	0
Cooperia punctata	3	1.9	3	0	0	0	4	0	0	0
Cooperia sp.	2	0.8	2	0	0	0	4	0	0	0
Haemonchus similis	18	3.7	0	0	18	0	0	0	4	0
Hyostrongylus sp.	12	1.1	2	3	12	0	8	12	4	0
Murshidia linstowi	11	4	10	11	1	0	24	36	4	0
Oesophagostomum bifurcum	2	0.5	0	0	1	1	0	0	4	3
Oesophagostomum dentatum	4	4.4	2	0	4	0	4	0	4	0
Oesophagostomum quadrispinulatum	2	0.2	0	0	2	0	0	0	4	0

Oesophagostomum stephanostomum	4	17.7	2	1	1	3	36	36	12	20
Trichostrongylus axei	1	0.3	0	0	0	1	0	0	0	1
Trichostrongylus colubriformis	3	3.8	0	0	0	3	0	0	0	8
Unclassified	12	3.2	2	3	0	7	20	28	0	4

3.3.1 Strongyles

In total 1,201,808 high-quality ITS2 reads were identified, with an average of about 22675.62 reads (SD: 31227.53; range: 223 - 166772) and median sequencing depth of 12422 reads per sample. In total, 157 individual ASVs were identified, including seven strongylid genera (Table 2.2; Appendix B1). Of the known units, the highest number of ASVs belonged to *Ancylostoma caninum*, followed by *Haemonchus similis* (Table 2.2). Out of 57 ASVs that could not be identified to the species level (present in 16% of the samples), 31 ASVs belonged to *Ancylostoma* sp., 2 ASVs belonged to *Cooperia* sp., 12 ASVs belonged to *Hyostrongylus* sp., and 12 ASVs belonged to order Rhabditida whose further taxonomy could not be analysed.

3.3.1.1 Composition of strongylid communities

The number of reads of ASVs varied significantly across host type ($\chi^2 = 15.63$, df = 3, p = 0.001) (Figure 3.2A), with dogs having a higher number of reads compared to humans (z = 37845, SE = 10439, df = 49, t = 3.63, p = 0.004) and vervet monkeys (z = 27881, SE = 9337, df = 49, t = 2.98, p = 0.02). The most prevalent variants belonged to three genera: *Ancylostoma*, *Murshidia*, and *Oesophagostomum* (Table 2.2). There was a significant interspecific difference in the relative abundances of strongylid nematode communities among host type (genus: $\chi^2 = 8.79$, df = 3, p = 0.03; species: $\chi^2 = 24.24$, df = 3, p < 0.001) (Figure 3.2B). At the genus level, humans harboured fewer genera compared to vervet monkeys (z = -0.28, SE = 0.10, df = 96, t = -2.77, p = 0.03; Figure 3.2B). At the species level, vervet monkeys harboured more species compared to dogs (z = -0.37, SE = 0.08, df = 124, t = -4.85, p < 0.001) and humans (z = -0.27, SE = 0.09, df = 124, t = -3.03, p = 0.02; Figure 3.2C).

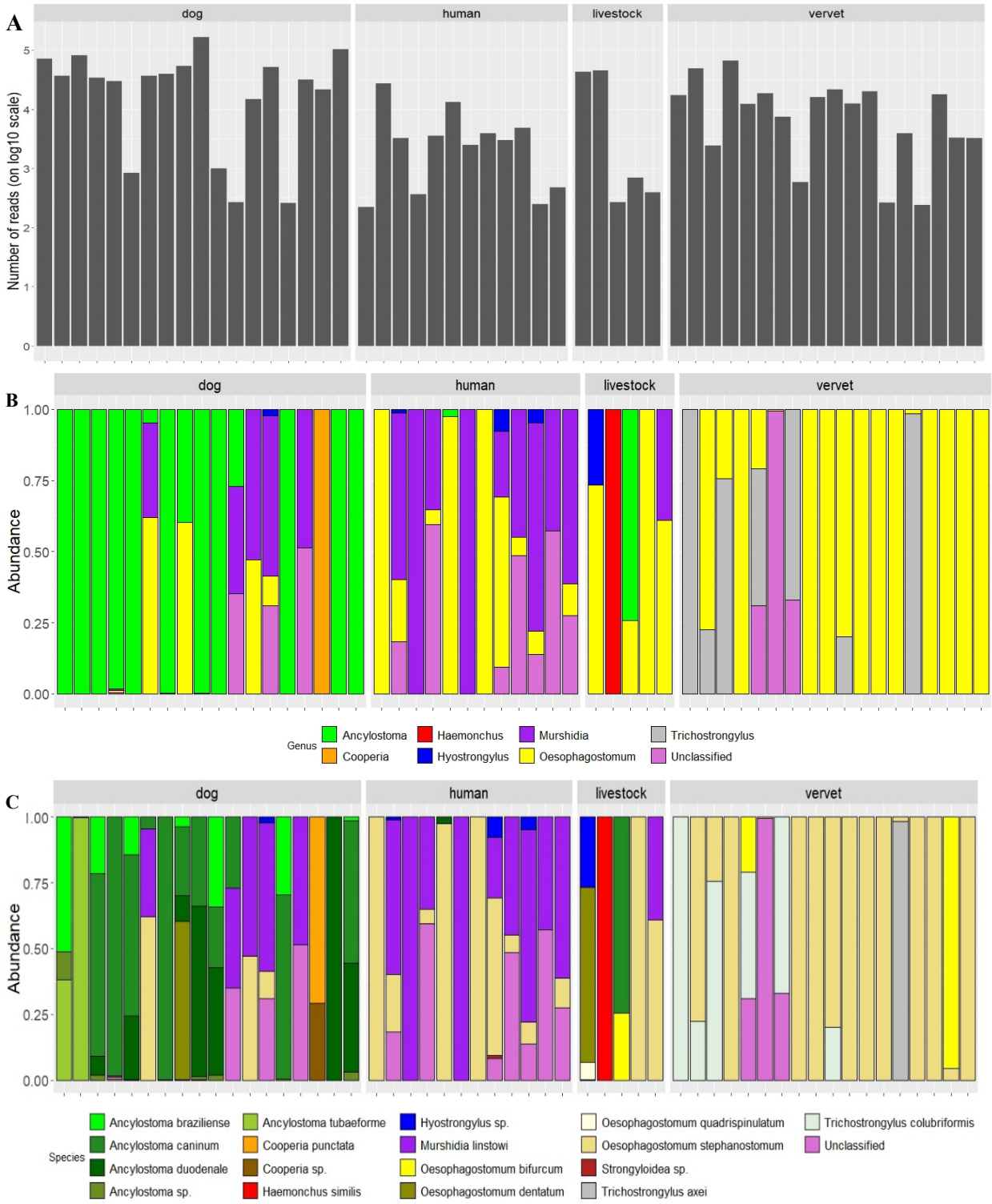

Figure 3.2: Bar plots showing A) number of reads in each individual sample on a log10 scale B) relative community composition of strongylid nematodes in examined samples at the genus level, C) relative community composition of strongylid nematodes in examined samples at the species level. Each column represents a sample. Numbers of reads (A) / relative abundances (B, C) of reads are depicted as color panels.

Among the three vervet groups, the number of reads of ASVs did not vary significantly across groups (χ^2 = 5.82, df = 2, p = 0.06) (Figure 3.3A). Furthermore, the relative abundance of strongylid variants did not vary significantly across groups at either the genus level (χ^2 = 4.83, df = 2, p = 0.09) or at the species level (χ^2 = 2.38, df = 2, p = 0.31) (Figure 3.3B & C).

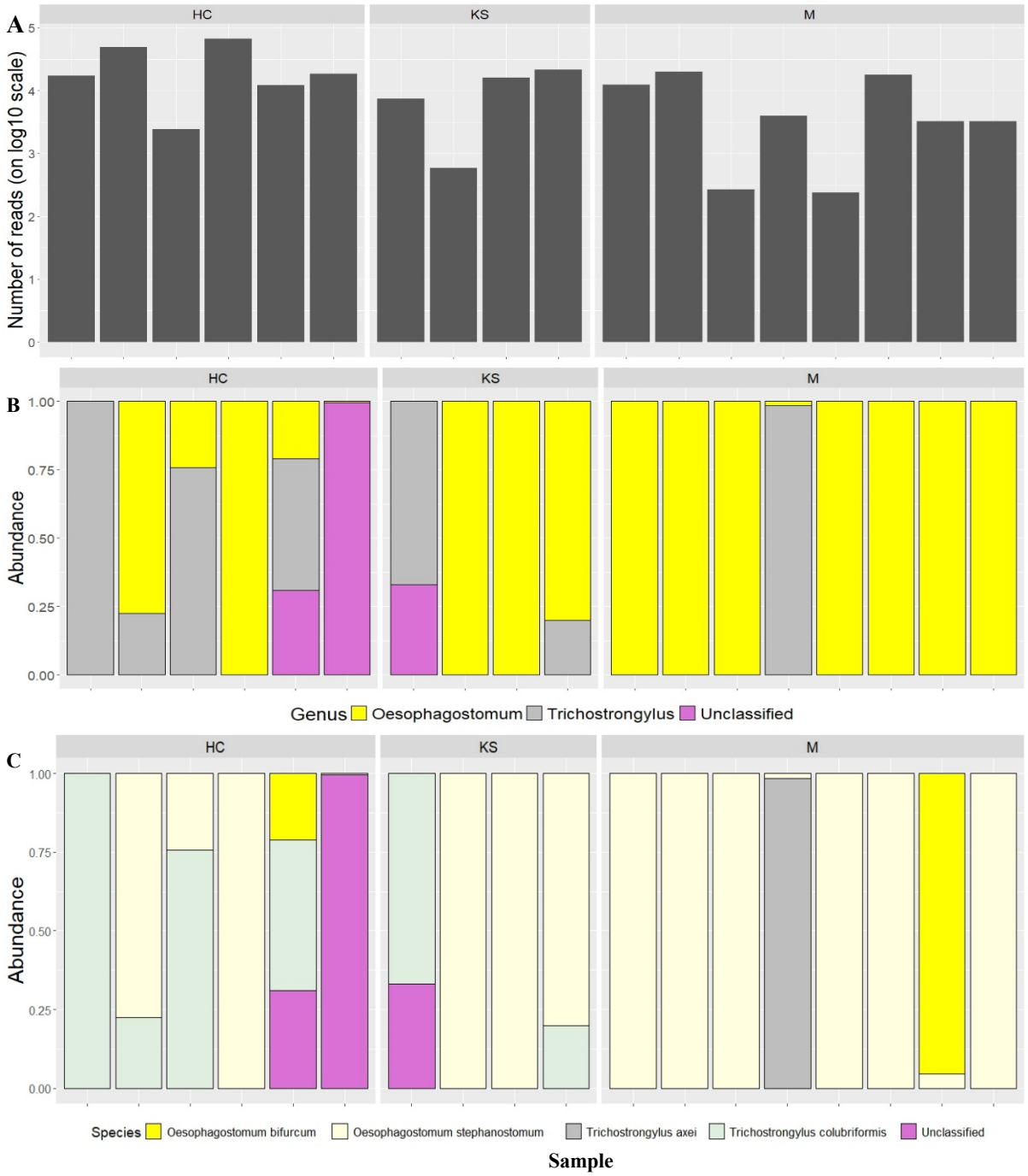

Figure 3.3: Bar plots showing A) number of reads ın eacn individual sample on a log10 scale B) relative community composition of strongylid nematodes in examined samples at the genus level, C) relative community composition of strongylid nematodes in examined samples at the species level of the three vervet monkey groups. Each column represents a sample. Numbers of reads (A) / relative abundances (B, C) of reads are depicted as color panels.

3.3.1.2 Alpha and beta diversity

Variant diversity differed significantly among host type (GLM: $F_{(3, 53)} = 21.59$, $p < 0.001$). Variant diversity in vervet monkeys was lower compared to dogs ($z = 1.78$, SE = 0.48, t ratio = 3.71, $p = 0.001$) (Figure 3.4), while there was no evidence of significant differences between dogs and humans, dogs and livestock, humans and livestock, humans and vervets, or between livestock and vervets (Figure 3.4). Variant diversity differed significantly among the three vervet monkey groups (GLM: $F_{(2,3)} = 7.03$, $p = 0.03$), with HC group harbouring greater diversity compared to M group ($z = 2.09$, SE = 0.79, t ratio = 2.65, $p = 0.05$) (Figure 3.5), though no significant difference was found between M and KS group (Figure 3.5).

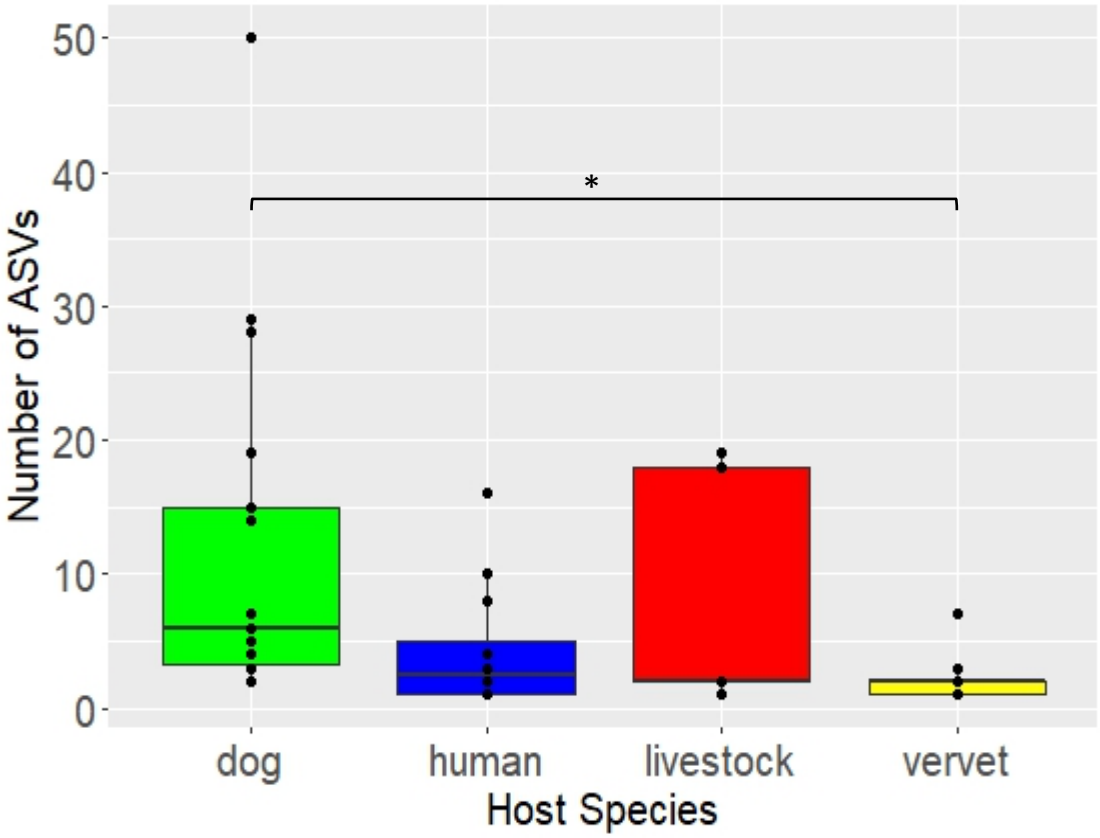

Figure 3.4: Boxplot of amplicon sequence variants (ASVs) counts according to host species.
* Significant pairwise comparison.

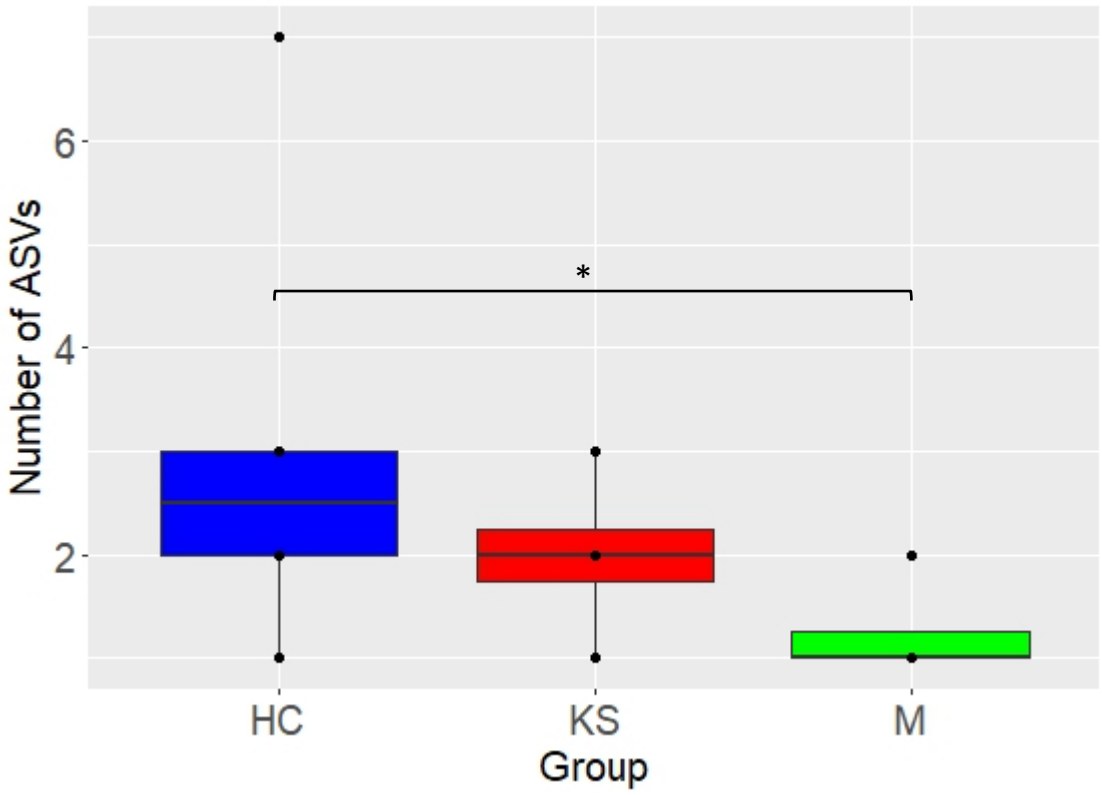

Figure 3.5: Boxplot of amplicon sequence variants (ASVs) counts according to the groups of vervet monkeys. * Significant pairwise comparison.

PCoA diagrams based on both Jaccard and Bray-Curtis ecological distances confirmed clear differences among host types in both composition and relative abundance of strongylid ASVs (Figure 3.6). Significant differences between different host species in the composition of their strongylid nematode communities were further confirmed by PERMANOVA (Jaccard: $F_{(3,53)} = 1.71$, $p < 0.001$; Bray-Curtis: $F_{(3,53)} = 2.76$, $p < 0.001$) and ANOSIM (Jaccard: $R = 0.32$, $p = 0.001$; Bray-Curtis: $R = 0.32$, $p = 0.001$) tests. Tukey post-hoc testing revealed significant differences between dogs and humans, dogs and vervets, and humans and vervets for both Jaccard and Bray-Curtis distances ($p < 0.05$), while all other pairwise comparisons were not statistically significant.

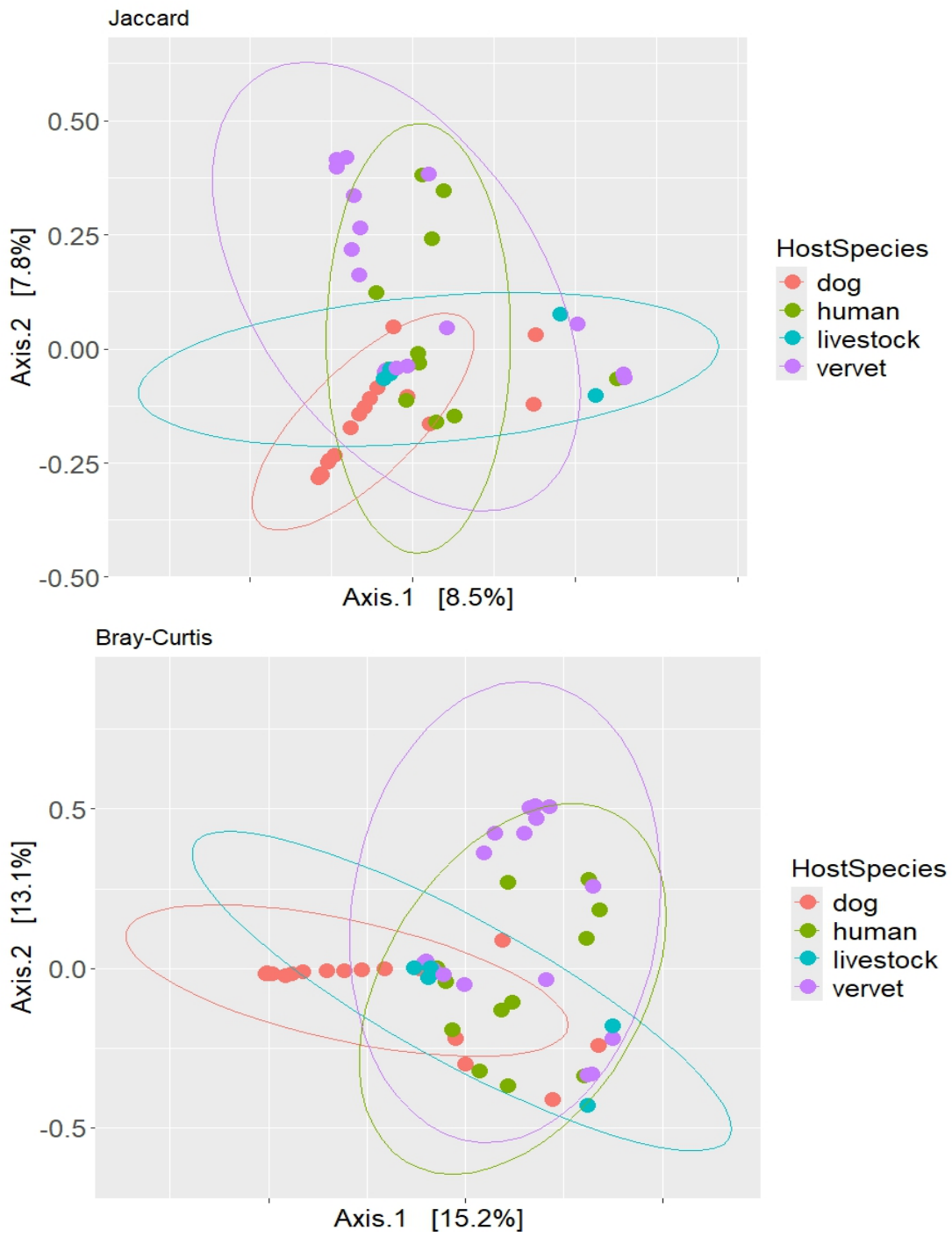

Figure 3.6: PCoA ordination diagrams of beta diversity of strongylid nematode communities based on Jaccard ecological distance (Presence/absence of amplicon sequence variants (ASVs)); Bray-Curtis ecological distance (relative abundances of reads).

Mvabund testing confirmed the interspecific differences (mvabund: $\Delta DF = 3$, $\chi 2 = 749.1$, $p < 0.05$) and identified 11 ASVs with whose different relative abundances were the main driving force of diversity among different host species in contrast to shared haplotypes (Figure 3.7). Differences among hosts were mainly due to greater frequencies of *Ancylostoma caninum*, *A. duodenale*, *A. braziliense* in dogs, *Murshidia linstowi* in humans, and *Oesophagostomum stephanostomum* in vervets (Figure 3.7).

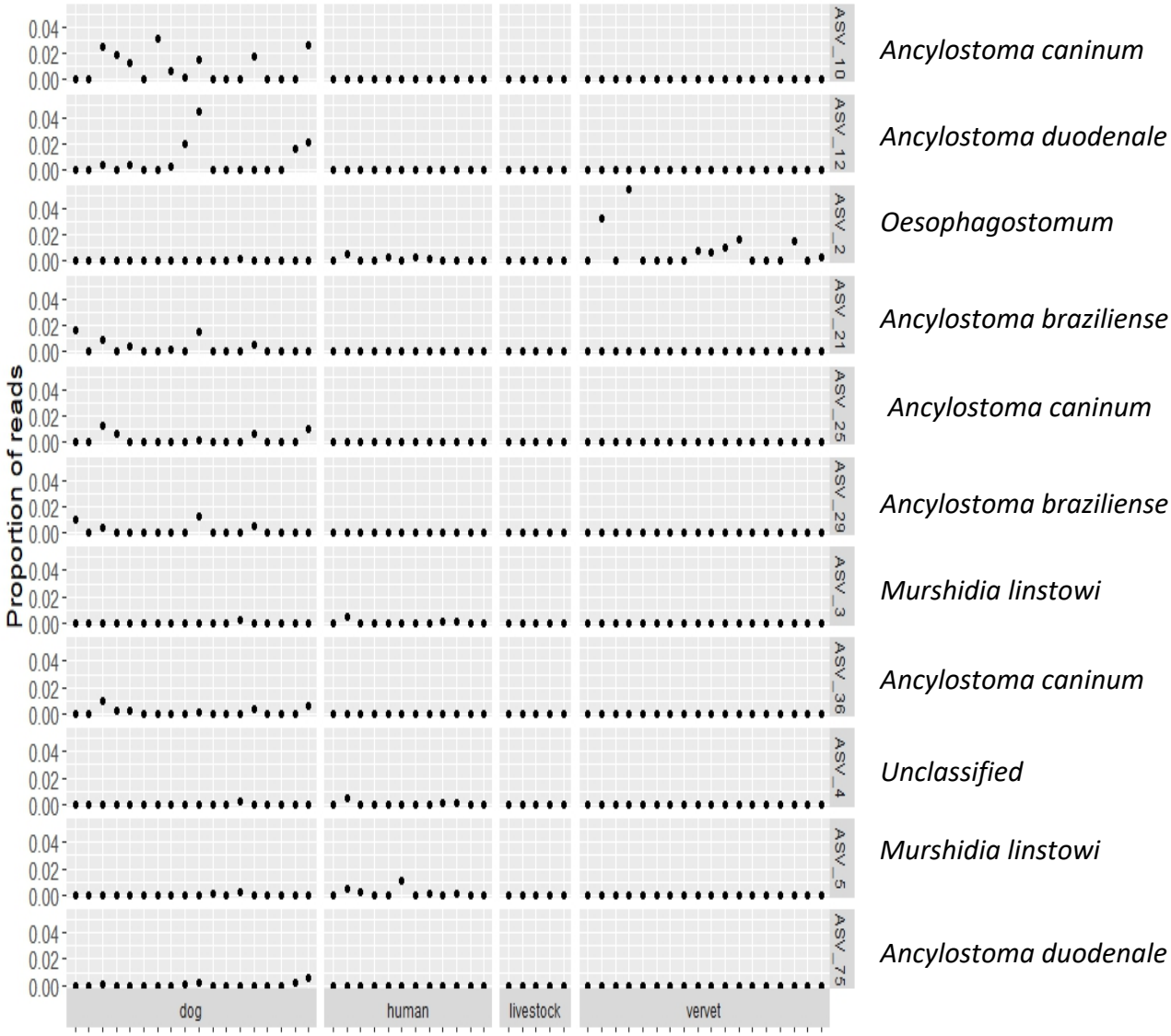

Figure 3.7: Plot showing relative abundance of amplicon sequence variants (ASVs) indicated by Mvabund analyses as a driving force of differences among studied hosts.

3.3.2 *Strongyloides*

The phylogenetic relationships among *Strongyloides* spp. were structured according to the host taxonomic groups and geographical location of their hosts (Figure 3.8). Molecular analysis revealed that 27 vervet monkeys samples were infected with *Strongyloides fuelleborni* and the *S. fuelleborni* arrangements of HVR-IV found in the vervet monkeys clustered with the isolates on GenBank sampled from yellow baboons, chimpanzees, humans, gorillas, and Japanese macaques from East and Central Africa as well as East Asia (Figure 3.8). Similarly, molecular analysis revealed that dogs were infected with *S. stercoralis* lineage A. A few dogs were also found to be infected with *S. ransomi*, most likely a spurious parasitism as a consequence of eating pig feces. One pig was also found to be infected with *S. ransomi*. The *S. ransomi* found in dogs and pig clustered with the isolates of *S. ransomi* on GenBank sampled from wild boar in Brazil and the isolates of *S. venezuelensis* from brown rat in Japan (Figure 3.8). The *S. stercoralis* lineage A found in dogs clustered with the isolates of *S. stercoralis* on GenBank sampled from chimpanzees in East Africa and Sumatran orangutans in Europe, humans in Central Africa and Southeast Asia, and dogs in Europe and Southeast Asia (Figure 3.8).

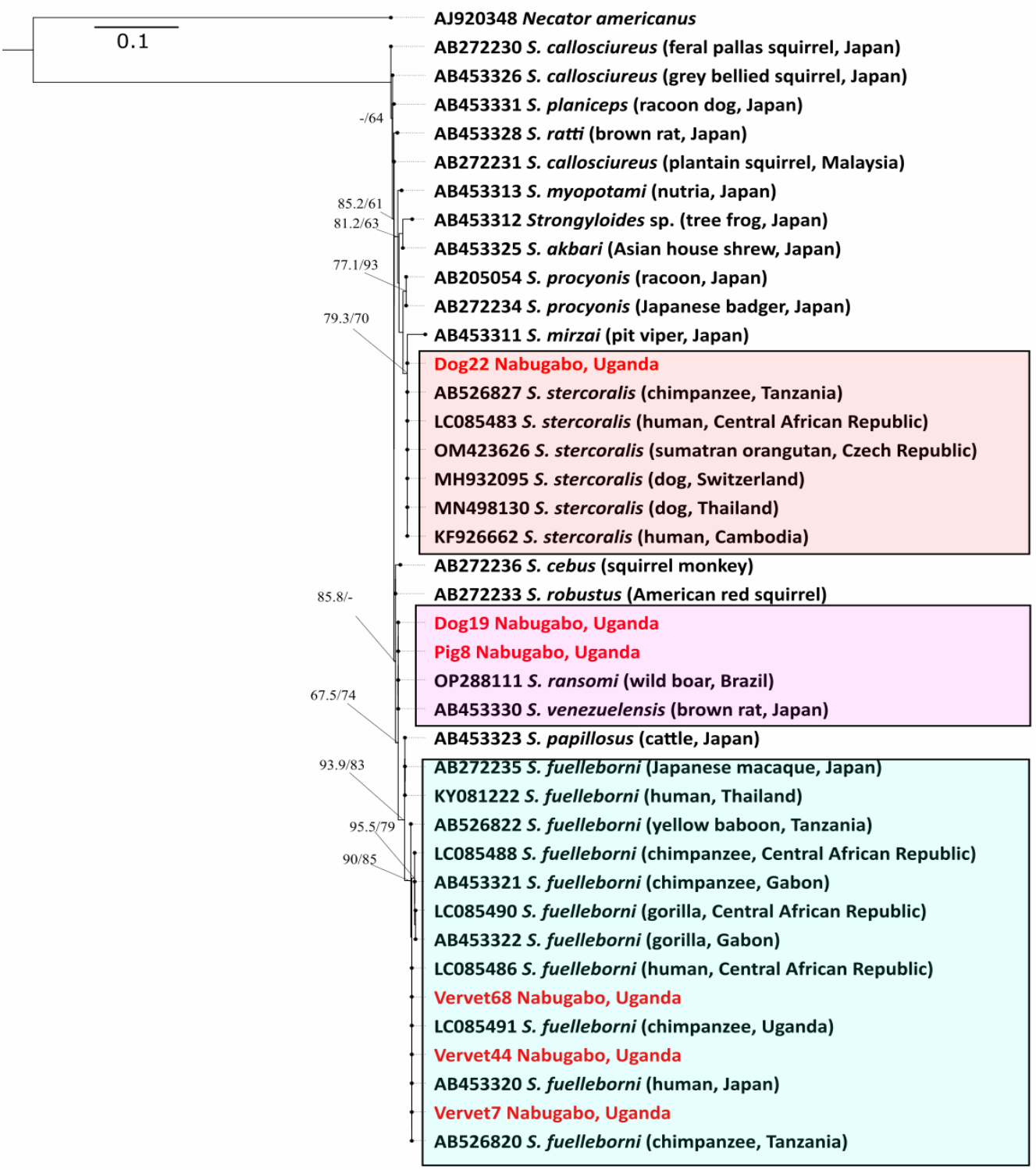

Figure 3.8: Phylogenetic relationship of *Strongyloides* spp. genotypes identified in this study (red in color) and other genotypes previously deposited in GenBank as inferred by the Maximum Likelihood analysis of HVR-IV sequences based on genetic distances calculated by the Kimura 3-parameter (K3P) model. Bootstrap values of >50% from 1000 replicates are shown on nodes. Each sequence from GenBank is identified by its accession number, host origin, and country.

3.3.3 Protists

3.3.3.1 *Cryptosporidium* spp.

Out of the 25 fecal samples collected from livestock, 24% (n = 6) tested positive for *Cryptosporidium* spp., with infection rates ranging from 0% to 8% (Table 2.1). Similarly, out of the 25 fecal samples collected from dogs, 8% (n =2) tested positive for *Cryptosporidium* spp., with infection rates ranging from 0% to 4% (Table 2.1). In this study, we identified four *Cryptosporidium* spp., namely *C. andersoni* (n = 3) in one dog and two cows, *C. canis* (n = 1) in one dog, *C. scrofarum* (n = 2) in two pigs, and *C. ubiquitum* (n = 2) in two goats. *Cryptosporidium* SSU sequences from a dog clustered with the isolates of *C. canis* on GenBank sampled from dogs (*Canis lupus familiaris*) in Europe and racoon dogs (*Nyctereutes procyonoides*), minks, blue foxes (*Vulpes lagopus*), and dogs in East Asia (Figure 3.9). The *Cryptosporidium* SSU sequences from a dog also clustered with *C. canis* found in water in Spain (Figure 3.9). The *Cryptosporidium* SSU sequences obtained from goats clustered with the isolates of *C. ubiquitum* on GenBank sampled from goats (*Capra aegagrus hircus*) and Tibetan sheep (*Ovis ammon hodgsoni*) in China, hosts such as roe deer (*Capreolus capreolus*), common ostrich (*Struthio camelus*), nutria (*Myocastor coypus*) in Europe, alpaca (*Vicugna pacos*) in South America, long-tailed chinchilla (*Chinchilla lanigera*) in East Asia, and eastern grey squirrel (*Sciurus carolensis*) and American red squirrel (*Tamiasciurus hudsonicus*) in North America (Figure 3.9).

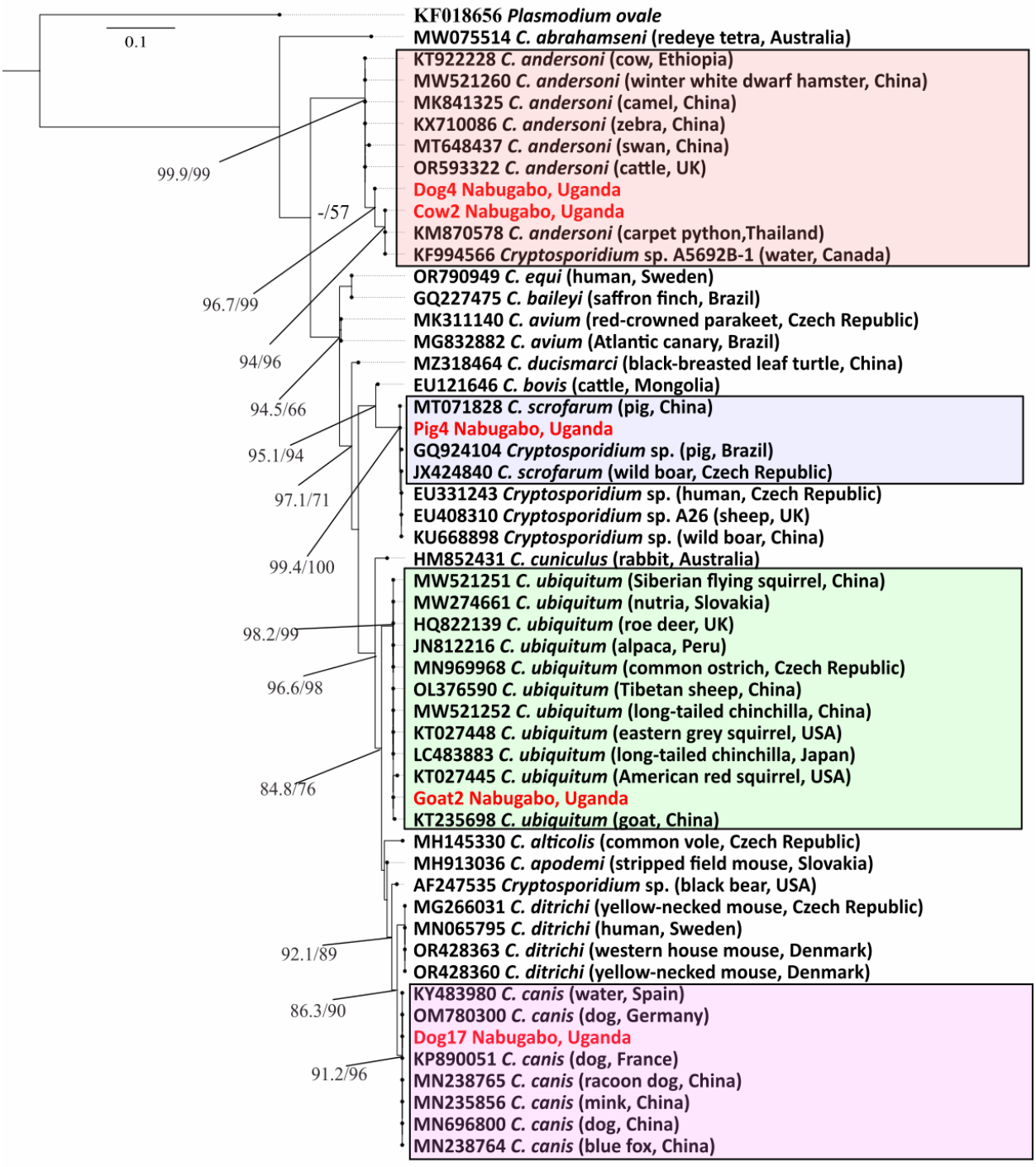

Figure 3.9. Phylogenetic relationship of *Cryptosporidium* spp. genotypes identified in this study (red in color) and other genotypes previously deposited in GenBank as inferred by the Maximum Likelihood analysis of SSU sequences based on genetic distances calculated by the Tamura-Ito (TIM2) model. Bootstrap values of >50% from 1000 replicates are shown on nodes. Each sequence from GenBank is identified by its accession number, host origin, and country.

3.3.3.2 *Giardia intestinalis*

Out of the 25 fecal samples collected from dogs, 16% (n = 4) tested positive for *Giardia intestinalis* assemblage A (Table 2.1). Similarly, out of the 25 samples collected from humans, 12% (n = 3) tested positive for *G. intestinalis* assemblage A (Table 2.1). Out of the 75 fecal samples collected from vervet monkeys, only one sample (1.3%) tested positive for *G. intestinalis* assemblage A (Table 2.1). The TPI sequences obtained from dogs, humans, and vervet monkeys clustered with the isolates of *G. intestinalis* assemblage A on GenBank sampled from rhesus macaque (*Macaca mulatta*), goat, sheep (*Ovis aries*), François' leaf monkey (*Trachypithecus francoisi*), cattle (*Bos taurus*) in China, sheep in USA, alpaca in Australia, and humans in China, Australia, and Malaysia (Figure 3.10).

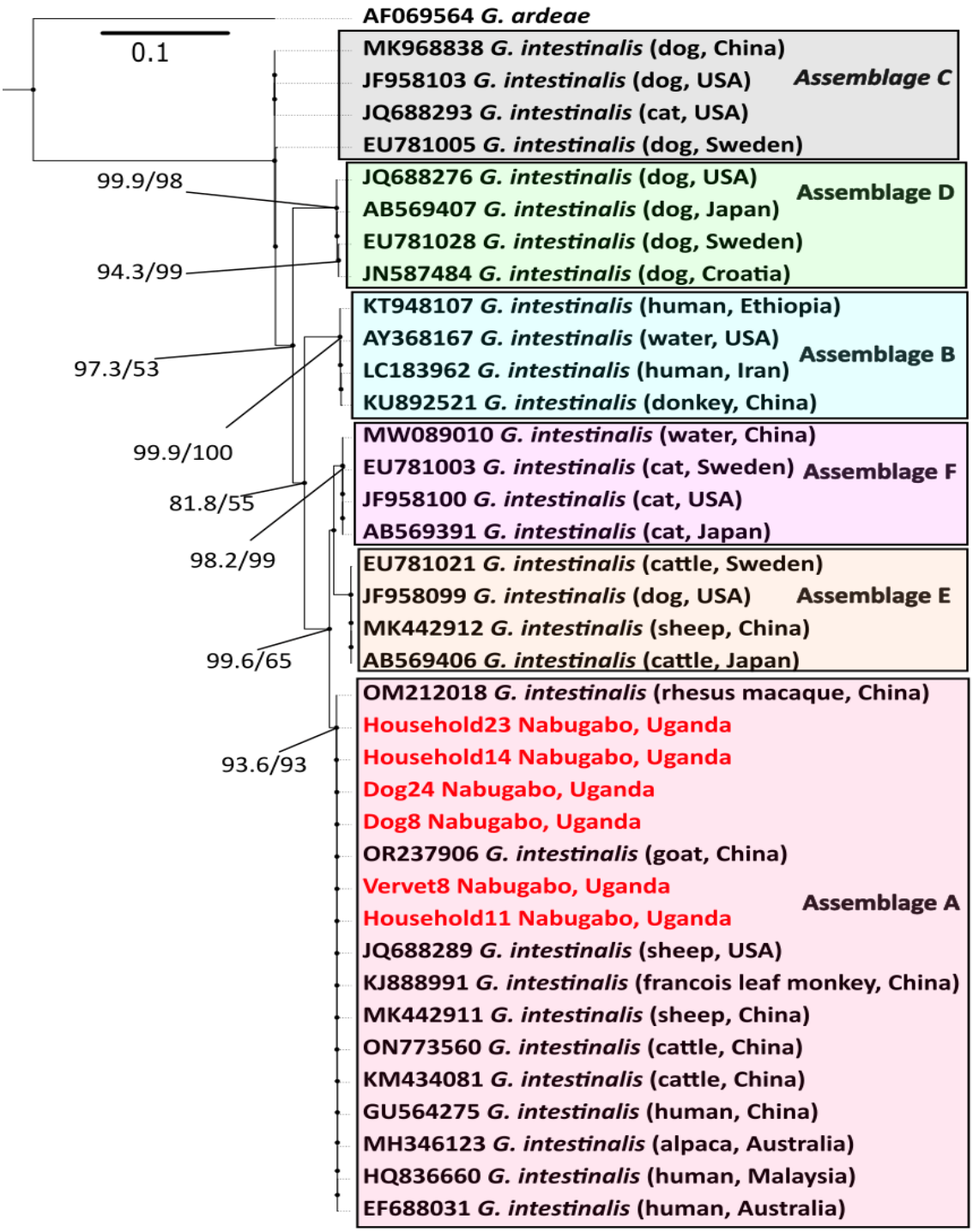

Figure 3.10: Phylogenetic relationship of *Giardia* spp. genotypes identified in this study (red in color) and other genotypes previously deposited in GenBank as inferred by the Maximum Likelihood analysis of the triosephosphate isomerase (TPI) sequences based on genetic distances calculated by the Tamura-Nei (TN) Model. Bootstrap values of >50% from 1000 replicates are shown on nodes. Each sequence from GenBank is identified by its accession number, host origin, and country.

3.3.3.3 Microsporidia

Out of the 25 fecal samples collected from households, 12% (n=3) tested positive for *Enterocytozoon bieneusi* (Table 2.1). The ITS sequences obtained from two human fecal samples clustered with the isolates of *Enterocytozoon bieneusi* genotype Peru8 on GenBank sampled from human, guereza colobus (*Colobus guereza*), rhesus and Assamese macaques (*Macaca assamensis*) in China, and humans in Peru (Figure 3.11). Similarly, the ITS sequence obtained from one human fecal sample clustered with the isolates of *Enterocytozoon bieneusi* genotype D on GenBank sampled from dogs, golden snub-nosed monkeys (*Rhinopithecus roxellana*) and northern white-cheeked gibbons (*Nomascus leucogenys*) in China, humans in China and Egypt, foxes in Poland, mountain gorillas (*Gorilla beringei beringei*) in Rwanda, genotype gorilla4 from mountain gorillas in Rwanda, genotype CM8 from human in China, genotype Peru10 from cats in Colombia, and genotype S6 from humans in Malawi (Figure 3.11).

Out of 75 fecal samples collected from vervet monkeys, only 2.7% (n = 2) tested positive for *Encephalitozoon* species (Table 2.1). One of the ITS sequences obtained from vervet samples clustered with the isolates of *Encephalitozoon intestinalis* on GenBank from red panda (*Ailurus fulgens*) in China, Central African chimpanzee (*Pan troglodytes troglodytes*), moustached guenon monkey (*Cercopithecus cephus*) in Cameroon, and humans in Russia and Iran (Figure 3.12). The other two ITS sequences obtained from vervet samples were found 86.2% homologous with *Encephalitozoon cuniculi* on GenBank from red panda in China, 83.7% homologous with *E. cuniculi* from mountain gorilla in Rwanda, 82.9% homologous with *E. cuniculi* from cat (*Felis catus*) in Austria, and 82.6% homologous with *E. cuniculi* from rabbit in Japan (Figure 3.12).

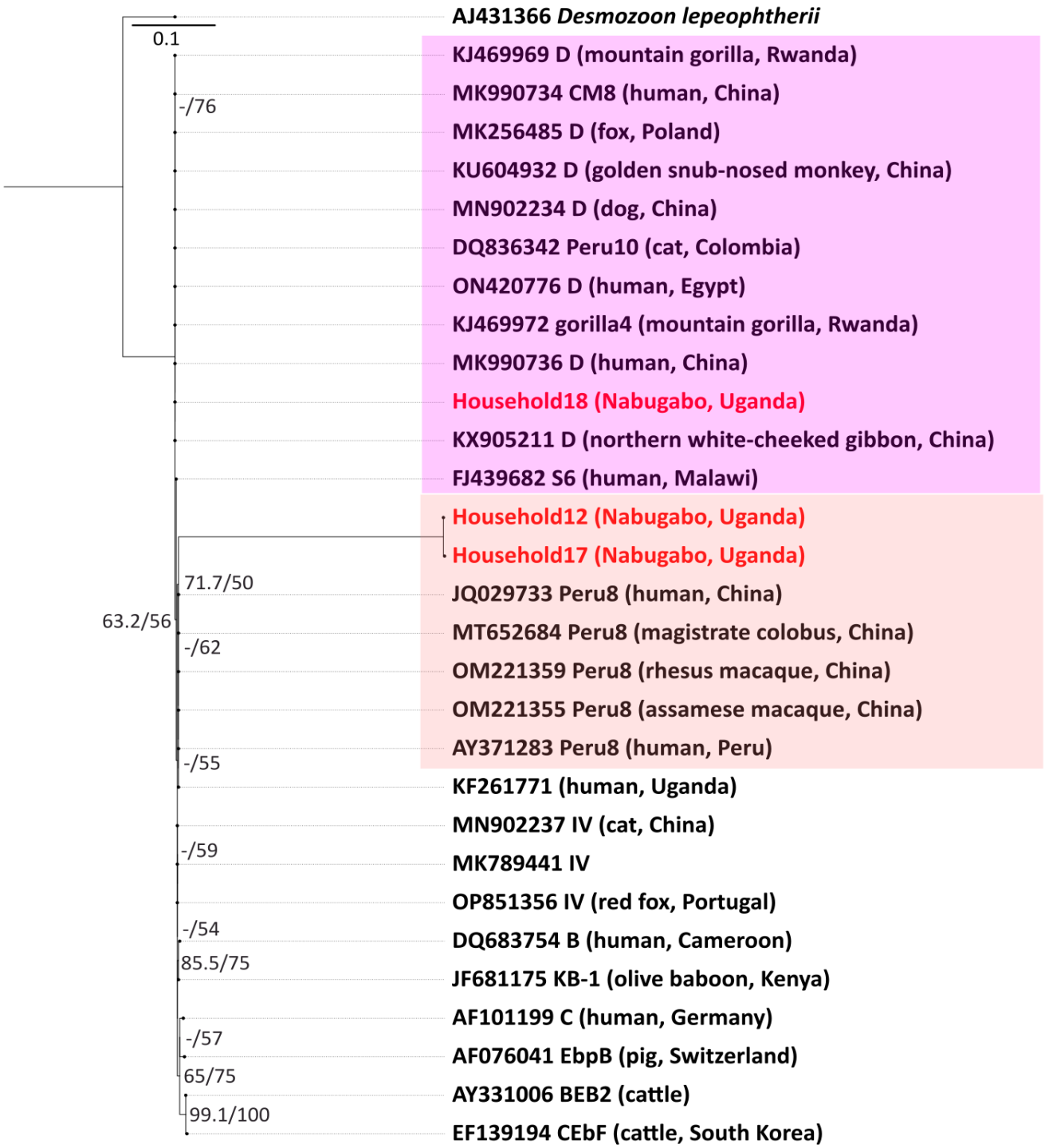

Figure 3.11: Phylogenetic relationship of *Enterocytozoon bieneusi* genotypes identified in this study (red in color) and other genotypes previously deposited in GenBank as inferred by the Maximum Likelihood analysis of internal transcribed spacer (ITS) sequences based on genetic distances calculated by the Kimura's Two Parameter (K2P) Model. Bootstrap values of >50% from 1000 replicates are shown on nodes. Each sequence from GenBank is identified by its accession number, host origin, and country.

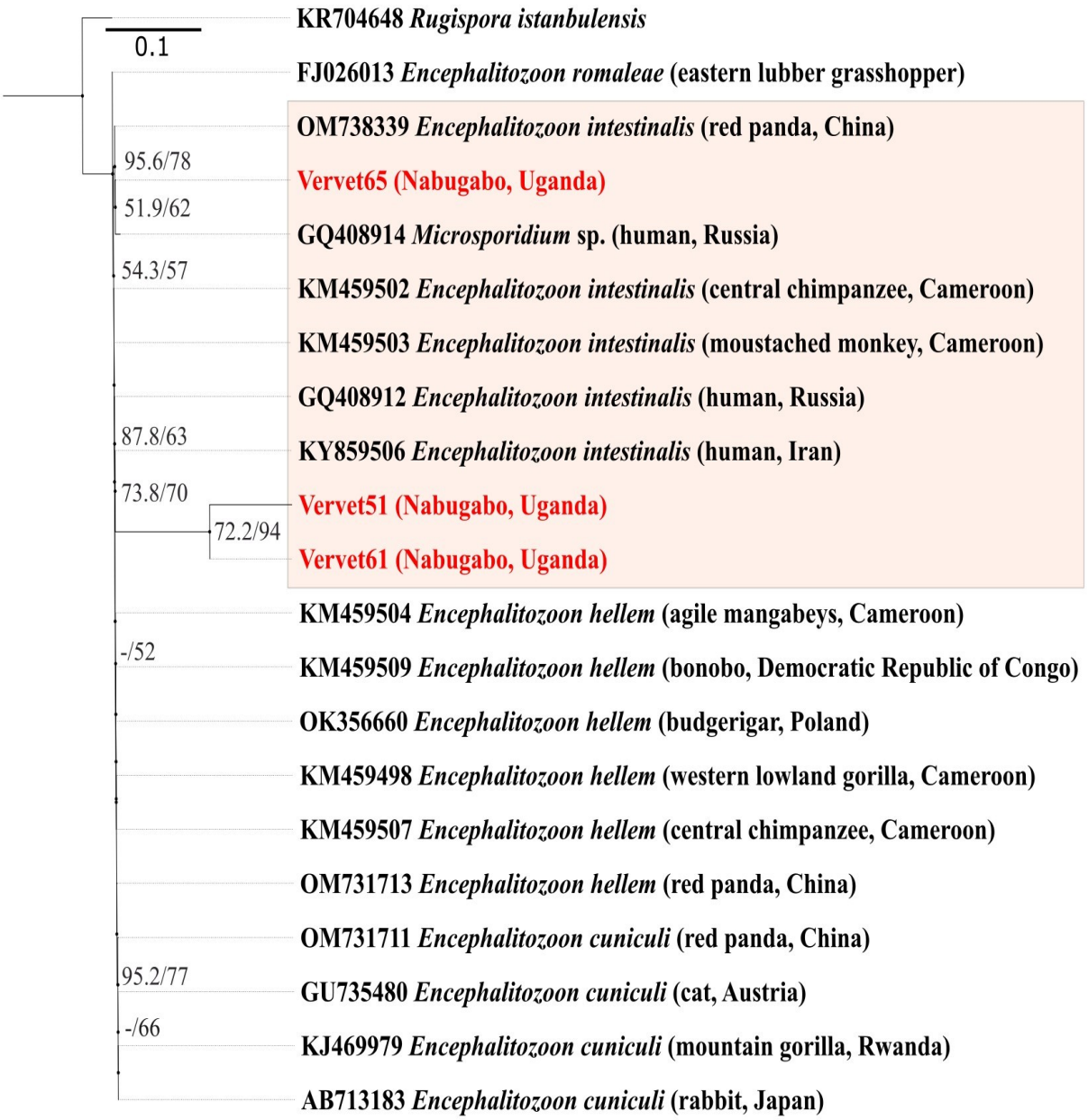

Figure 3.12: Phylogenetic relationship of *Encephalitozoon intestinalis* genotypes identified in this study (red in color) and other genotypes previously deposited in GenBank as inferred by the Maximum Likelihood analysis of internal transcribed spacer (ITS) sequences based on genetic distances calculated by the Jukes-Cantor (JC) Model. Bootstrap values of >50% from 1000 replicates are shown on nodes. Each sequence from GenBank is identified by its accession number, host origin, and country.

3.4 DISCUSSION

In this study, we assessed the parasite prevalence, species richness, and infection rate in dogs, humans, livestock, and vervet monkeys at Lake Nabugabo, Uganda by employing both microscopy and molecular techniques, identifying a total of 25 parasite taxa across the four host groups. The findings highlight important differences in parasite diversity and prevalence, shedding light on potential parasite transmission dynamics among wildlife, domestic animals, and humans, along with species-specific differences in susceptibility or exposure (Bielby et al., 2015; Fenton & Pedersen, 2005).

We found a higher diversity of parasites in dogs, with 17 parasite taxa identified, compared to the other host species, likely due to their coprophagy behavior, close contact with humans, and exposure to various parasites in domestic environments. Free-roaming dogs at Nabugabo are more prone to encountering contaminated areas. Given these factors, our findings are consistent with established research, which highlights dogs as a major source of zoonotic parasites, facilitating the transmission of these parasites between livestock, wildlife, and humans, and are linked to emerging human diseases like eosinophilic enteritis, alveolar echinococcosis, and thus may pose risks for immunocompromised individuals (Salb et al., 2008). Common enteric parasites in dogs include *Toxocara canis*, *Ancylostoma caninum*, *Taenia hydatigena*, *Echinococcus* spp., *Dipylidium caninum*, *Trichuris vulpis*, *Giardia* spp., *Cryptosporidium* spp., and *Isospora canis* (Papajová et al., 2021), some of which were also found in this study. These parasites can impair immune responses, growth, and overall health in both dogs and humans (Abdelkareem et al., 2022).

A previous study reported that the vervet monkeys of Lake Nabugabo have the highest recorded parasite diversity (11) among vervet monkeys (Valenta et al., 2017), thus it was not surprising that we also found a high number of parasite taxa (10) in this study as well. In addition

to finding six taxa previously reported for this population, we discovered *Moniezia sp.*, *Trichostrongylus axei*, *T. colubriformis*, and *Microsporidia* sp. in vervet monkeys, which were not observed in the earlier study (Valenta et al., 2017). This suggests that vervet monkeys may serve as a significant reservoir for a variety of parasites (Dalimi et al., 2016), which could be relevant for understanding zoonotic transmission risks.

The presence of cestodes (*Moniezia* sp. in vervet monkeys and *Spirometra* sp. in dogs) was limited to these two host species, underscoring the possibility of host-specific transmission pathways for these parasites. Despite their global occurrence, the taxonomy of *Moniezia* spp. remains unclear, with genetic data available for only three of the seven proposed species (*M. benedini*, *M. expansa,* and *M. monardi*) (Guo, 2017). The life cycle of *Moniezia* spp. is completed with oribatids (mites) acting as intermediate hosts and ruminants as definitive hosts (Guo, 2017), thus *Moniezia* spp. are typically found in ruminants like cattle, goats, sheep, antelopes, and deer (Tam et al., 2020). However, they have also been reported in Assamese macaques (*Macaca assamensis*) in Nepal, likely due to their close proximity to ruminants (Pokhrel & Maharjan, 2014). *Spirometra* spp. affect humans and certain domestic and wild animals that come into contact with humans, and infected secondary intermediate hosts can be consumed by paratenic hosts (in which the parasite does not develop) like nonhuman primates, pigs, rodents, and birds, helping the pathogen survive in the environment over time (Morales et al., 2022).

While *Dipylidium* sp. was found in both dogs and humans, it was challenging to distinguish between species using coproscopic methods, highlighting the need for more refined diagnostic techniques for accurate parasite identification, especially since *Dipylidium* sp. is regarded as the

most common tapeworm infecting companion animals, although cases of dipylidiasis in humans are uncommon (Rousseau et al., 2022).

Trematodes (Paramphistomidae and *Schistosoma* sp.) were exclusively found in livestock, which highlights the importance of domestic animals as hosts for these parasites, particularly in agricultural settings (Megersa et al., 2024). The finding of trematodes in livestock, but not in humans, suggests that while livestock can be infected, humans may not directly acquire the parasite from the same environmental sources, or there may be differences in exposure risk as the intermediate gastropod hosts of *Schistosoma* spp. are known to be absent at Lake Nabugabo (Efitre et al., 2001; Nakirya et al., 2015).

The difference in *Trichuris* sp. prevalence between vervet monkeys and humans suggests potential spillover risks, as two *Trichuris* genotypes infect both human and non-human primates across Africa, Europe, and Asia (Ravasi et al., 2012). Studies indicate *Trichuris* is among the 20% of helminths capable of cross-infecting human and non-human primates, with genetic evidence supporting multiple infective species (Ghai et al., 2014; Ravasi et al., 2012).

3.4.1 Strongyles

The overall taxonomic classification of the 157 ASVs identified in this study suggests that humans, vervet monkeys, dogs, and livestock at Lake Nabugabo harbor at least seven known genera of strongylid nematodes. The most prevalent genera were *Ancylostoma*, *Murshidia*, and *Oesophagostomum,* which have previously been found in both human and non-human primates (Brooker et al., 2004; Cibot et al., 2015; Ghai, Chapman, et al., 2014; Pafčo et al., 2019). We identified 52 ASVs of *Ancylostoma* spp. (33.12% from the total of 157 ASVs found) being shared between multiple hosts.

Ancylostoma spp.

Ancylostoma caninum, one of the most common parasitic nematodes in dogs globally (Nezami et al., 2023), was found in 12 dogs and one cow, suggesting a possible infection by passage in the cow through contaminated soil, water, or feces. Similarly, *A. duodenale* was found in 7 dogs and one human sample. Although *A. duodenale* coexists with *Necator americanus* in many endemic areas, where people are frequently infected with both species (Adenusi & Ogunyomi, 2003), we did not detect any *Necator* sp. in this study. *A. duodenale* is known to be a human-specific parasite. One previous study documented its presence in humans in the Dzanga-Sangha Protected Areas of the Central African Republic, reinforcing its established role as a human pathogen (Pafčo et al., 2019). In this study, *A. duodenale* was detected in only one human sample, which raises the possibility that its presence may not reflect a true human infection. This could be an artifact resulting from the sample collection process, particularly given the potential for cross-contamination in the environment where the samples were gathered. The finding of *A. duodenale* in a single human sample in the present study, therefore, warrants caution in interpreting it as a definitive human infection. While the presence of *A. duodenale* in a single sample here may be questionable, the species' prevalence in other studies supports the likelihood that humans are indeed hosts for this parasite (Adenusi & Ogunyomi, 2003; Pafčo et al., 2019). Dogs were also found to be infected with three other species of *Ancylostoma*: *A. braziliense, A. tubaeforme*, and an unclassified species. *Ancylostoma tubaeforme* is commonly found in cats, but it is related to dog hookworms (*A. caninum,* and *A. braziliense*), and *A. braziliense* has been found in dogs in the United States of America (Lucio-Forster et al., 2012).

Murshidia linstowi

Murshidia linstowi was found in dogs, humans, and livestock (goats). *M. linstowi* is primarily known to infect elephants (Chel et al., 2020; Mclean et al., 2012a), making this likely

the first study to report *M. linstowi* in dogs and goats. The detection of *M. linstowi* in human samples requires further consideration. It is possible that the presence of the parasite in human samples was influenced by the method of sample collection. Specifically, the samples were obtained from pit latrines, where various materials, including livestock feces, could have been discarded. This creates a risk of cross-contamination, which might explain the unexpected finding of *M. linstowi* in human samples. It is also important to note that multiple individuals may have used the same pit latrine, and/or a single individual may have used more than one pit latrine, potentially resulting in multiple "pit latrine" infections.

***Oesophagostomum* spp**.

This study identified four species of *Oesophagostomum* across different host species, highlighting the broad distribution of these parasites in both domestic and wild animals, as well as humans. A single pig sample was found to be infected with *O. stephanostomum, O. quadrispinulatum*, and *O. dentatum*, aligning with the findings from a study on Tibetan pigs in the high-altitude Tibetan Plateau, where these same species were present in large numbers (Li et al., 2017). This supports the widespread nature of *Oesophagostomum* infections in pigs, which are known to be globally distributed (Boes et al., 2007; Joachim et al., 2001; Lai et al., 2011; Weng et al., 2005).

The detection of *O. stephanostomum* in a pig is particularly significant as it was also found in a human and a goat sample, vervet monkeys, and dogs in this study, suggesting *O. stephanostomum* may have a broader host range, including both domestic and wild animals, and could serve as a potential zoonotic parasite. However, further evaluation is needed, as the parasite may have been accidentally passed through the ingestion of contaminated water, food, or soil. The detection of *O. bifurcum* in vervet monkeys is another notable finding. *O. bifurcum* is

found in humans, especially in West Africa (Ziem et al., 2006), and its presence in vervet monkeys suggests that non-human primates may act as reservoirs for this species. Furthermore, a cow in this study was also infected with *O. bifurcum*, further supporting the idea that this species has a wide host range, which includes both livestock and wildlife.

The finding that *O. dentatum* was shared between pigs and dogs is consistent with previous studies suggesting that *Oesophagostomum* species can be transmitted across different host species, further complicating the ecological dynamics of these parasites, although the presence of *O. dentatum* is more likely a result of coprophagy. Two *Oesophagostomum* species are commonly found in both human and non-human primates in Africa: *O. stephanostomum* in great apes (Cibot et al., 2015; Narat et al., 2015) and *O. bifurcum* in humans (Ziem et al., 2006). While other *Oesophagostomum* species have been observed, they are much less common (Ota et al., 2015).

Other strongylids

Among other strongylid nematodes detected in various host species, *Hyostrongylus* sp. was found in human, dog, and pig samples. *Hyostrongylus* sp. is typically found in pigs (Kouam & Ngueguim, 2022), and the presence of *Hyostrongylus* in dogs could be a spurious infection, while its presentin humans could be a result of sampling method from pit latrines. Thus, this finding requires further examination. The genus *Cooperia* includes Trichostrongyloid nematodes that are important in veterinary medicine, as they play a role in mixed-species helminth infections, leading to production losses in livestock worldwide (Stromberg et al., 2012). In this study, variants of *C. punctata* and a *Cooperia* sp. were found in dogs, which could again be the result of coprophagy.

Alpha and beta diversity

At Nabugabo, dogs exhibited higher strongylid alpha diversity than vervets. This high diversity among dogs was attributed primarily to the prevalence and dominance of *Ancylostoma caninum* variants, which not only exhibited high infection rates but also contributed substantially to the overall relative abundance of strongyles in the host population. Specifically, dogs were found to harbor 11 distinct species of strongyle nematodes, raising the possibility of dogs as a major reservoir of these parasites. However, it should be highlighted that the majority of these infections are likely due to coprophagy of infected feces from animals or humans. That said, dogs can still spread eggs or larvae that may remain infectious to other hosts, which warrants further investigation. Notably, 12 samples from dogs were confirmed to be infected with *A. caninum*, underscoring its prominent role in shaping the helminth community composition within this host group. On the other hand, the strongylid communities of humans, livestock, and vervets were dominated by variants belonging to *Oesophagostomum stephanostomum*, *Trichostronglyus colubriformis*, and *Murshidia linstowi*. As previously noted, however, the detection of *M. linstowi* in human samples warrants careful consideration.

3.4.2 *Strongyloides*

We did not detect any *Strongyloides* infections in humans at Lake Nabugabo, Uganda. However, we did identify *S. fuelleborni* and *S. stercoralis* in vervet monkeys and dogs, both of which are *Strongyloides* species that have been previously found in humans (Hasegawa et al., 2009, 2016b; Schär et al., 2014; Thanchomnang et al., 2017b). Of particular concern is *S. stercoralis*, a soil-transmitted helminth known to infect humans, dogs, and non-human primates (Olsen et al., 2009). Globally, *S. stercoralis* is a major public health issue, infecting over 100 million people, and is widely considered the primary species responsible for strongyloidiasis (Anderson et al., 2012; Schär et al., 2013b).

While human infections with *S. fuelleborni* have also been reported, these are less common and are typically associated with individuals who frequent areas inhabited by non-human primates, where *S. fuelleborni* is believed to originate (Hasegawa et al., 2010). Although we did not detect human infections in this study, the presence of this species in vervet monkeys and dogs indicates a potential risk of zoonotic transmission. This is especially concerning given the close proximity between humans and these animals, as well as the possibility of human exposure to environmental contamination with parasite larvae.

Additionally, *S. stercoralis* is one of the most challenging helminths to manage due to its ability to infect humans through skin penetration and its capacity for endogenous autoinfection, allowing the parasite to multiply within the host (Schär et al., 2013b). This makes *S. stercoralis* a major cause of long-term health issues and suffering (Prendki et al., 2011; Schär et al., 2013b; Vadlamudi et al., 2006). A pig sample and three dog samples were found to be infected with *S. ransomi. S. ransomi* are known to infect pigs and dogs globally (Barratt et al., 2019; Tam et al., 2020), thus finding pig and dog samples infected with *S. ransomi* was not surprising. However, dogs might have been infected because of consumption of pig feces, resulting in spurious parasitism.

3.4.3 Protists

Cryptosporidium spp., *Giardia* spp. and microsporidia are opportunistic pathogens known for their ability to cross species barriers, owing to their low host specificity (Franzen, 2008; Thompson, 2004). Despite numerous reports of *Cryptosporidium* spp. in primates (Butel et al., 2015; Da Silva et al., 2003; Du et al., 2015; Karim et al., 2014b; Legesse & Erko, 2004; Lim et al., 2008; van Zijll Langhout et al., 2010), our study did not detect any *Cryptosporidium* infections in either humans or vervet monkeys at the study site. *Cryptosporidium andersoni*, a

common species in ruminants (Du et al., 2015), was detected only in two cows in this study. The finding that only a small number of host samples tested positive for other *Cryptosporidium* species—such as *C. andersoni* and *C. canis* in two dogs, *C. scrofarum* in two pigs, and *C. ubiquitum* in two goats—suggests that these species may be present at a low prevalence in the studied animal populations. The limited detection could point to sporadic exposure or infection, or it might indicate that these species have minimal impact on the health of the animals. This finding could also suggest cross-species transmission or be influenced by host-specific factors that affect the prevalence of these species. Additionally, the small sample sizes for each host species may mean the results are not fully representative of the broader populations, or that these species are relatively rare in the region or under the study conditions. Larger sample sizes would be necessary for a more thorough analysis.

Among the two assemblages of *Giardia intestinalis* found most commonly in humans, dogs, cats, livestock, and wild animals including primates (Cama & Mathison, 2015; Feng & Xiao, 2011; Kváč et al., 2017), we discovered that humans, dogs, and a vervet monkey were infected with assemblage A, suggesting a potential for zoonotic transmission. *Giardia* is among the most prevalent intestinal parasites affecting humans, with an estimated 200 million people in Asia, Africa, and Latin America suffering from symptomatic infections (Yason & Rivera, 2007). Once infected, individuals typically experience a self-limiting illness known as giardiasis, which is marked by symptoms such as diarrhea, abdominal cramps, bloating, weight loss, and malabsorption (Cama & Mathison, 2015). However, asymptomatic cases of giardiasis are also common, particularly in developing countries (Hellard et al., 2000; Thompson, 2000). The presence of assemblage A in both humans and animals at Lake Nabugabo underscores the

potential role of animals as reservoirs for human infections, particularly given that there is close contact between human populations and domestic animals and vervet monkeys.

In this study, *Enterocytozoon bieneusi* was detected exclusively in human samples, which aligns with previous research indicating that this species is the primary causative agent of microsporidiosis in humans. *E. bieneusi* is responsible for over 90% of human microsporidiosis cases worldwide, making it the most significant species of microsporidia in terms of public health impact (Khanduja et al., 2017; Qiu et al., 2019; Tao et al., 2020; Xu et al., 2016). The fact that we found *E. bieneusi* only in human samples is consistent with its well-established role as a human pathogen, primarily transmitted through environmental sources, contaminated water, and possibly zoonotic routes involving animals (Amer et al., 2019; Khanduja et al., 2017). However, one surprising and somewhat unexpected finding of this study is that only 12% of household samples tested positive for *E. bieneusi*. This low prevalence within household samples contrasts with the global distribution of *E. bieneusi* infections and raises important questions about the factors influencing the parasite's transmission in this region. Given the established zoonotic potential of *E. bieneusi* and its known presence in a variety of hosts, including livestock, pets, and wildlife (Tao et al., 2020), one might expect a higher prevalence of infection within households where humans often interact with animals. One possibility is that household-level transmission may be less common in this region, either due to effective sanitation practices or the fact that *E. bieneusi* may primarily be transmitted through waterborne routes, as is commonly seen in other endemic areas (Xu et al., 2016). In addition, asymptomatic infections could also be an important factor. Asymptomatic carriers, who may not exhibit clinical symptoms, could potentially harbor the parasite without shedding it in significant amounts, reducing the chance of detection in household samples. As *E. bieneusi* infections are often subclinical or mild,

especially in immunocompetent individuals, this may explain the relatively low prevalence observed in our study. Another potential explanation for the low prevalence of *E. bieneusi* in household samples could be related to the diagnostic methods employed in this study. While molecular techniques such as PCR are highly sensitive, the detection of *E. bieneusi* can sometimes be limited by the timing of sample collection or the presence of low parasite loads. Therefore, it is possible that the 12% prevalence reflects only the most overt cases of infection, while subclinical or lower-level infections may have gone undetected.

Finally, among microsporidia, a microsporidium closely related to *Encephalitozoon intestinalis* was detected only in vervet monkeys with a prevalence of 4%. Although this microsporidia or *E. intestinalis* was not detected in other host species, including humans, in our study, previous research has shown that *E. intestinalis* does infect humans in other regions. Studies have reported *E. intestinalis* infections in humans, particularly in immunocompromised individuals, such as those with HIV/AIDS or undergoing chemotherapy (Sokolova et al., 2011; Tavalla et al., 2017). While our study did not detect *E. intestinalis* in other species, such as dogs or livestock, it is important to consider the possibility that the parasite could still be circulating in these populations at low levels or that other, undetected reservoirs may exist. This underscores the complexity of microsporidial transmission and the challenges of detecting such infections, especially when they may not manifest with obvious clinical signs in animals. The low prevalence of *E. intestinalis* observed in vervet monkeys in this study may reflect similar low prevalence rates in other animal species in the region, which could be influenced by factors such as local environmental conditions, hygiene practices, and the ecological overlap between human and animal populations.

The presence of parasites in human samples could potentially be influenced by the method of sample collection, given the samples were gathered from pit latrines. Pit latrines are common areas where human waste is discarded, but they can also contain other materials, including livestock and dog feces. The mixing of human and animal waste in these environments could raise the risk of cross-contamination, particularly with parasites that rely on livestock or dogs as their definitive and/or reservoir hosts, which may compromise the accuracy of the findings. As livestock and dog feces can harbor a variety of zoonotic parasites, it is possible that the observed parasites in human samples reflect a mixing of fecal samples in the latrine, rather than a true zoonotic infection or one that relies on human-to-human transmission. Therefore, future studies should consider alternative sampling methods to minimize potential cross-contamination and provide more reliable data on parasite prevalence in human populations.

3.5 CONCLUSION

This study underscores the complex and diverse nature of parasitic infections in humans, domestic animals, and wildlife, with vervet monkeys and livestock hosting the highest diversity and prevalence of parasitic taxa. The identification of 25 parasite taxa across these host groups highlights the complex ecological interactions between wildlife, domestic animals, and humans, and underscores the potential zoonotic risks associated with certain parasites. Dogs, with their coprophagic behavior and close proximity to humans, exhibited the highest diversity of parasites, including some responsible for potential zoonotic diseases. These findings emphasize the need to address domestic animal parasite management as a critical public health issue (Giannelli et al., 2024). Vervet monkeys, exhibiting high parasite richness, may serve as a significant reservoir for a range of parasites, with potential implications for both wildlife conservation and zoonotic disease transmission. The study also draws attention to the role of livestock in harboring trematodes and strongylid nematodes like *Oesophagostomum* species, with the potential for

cross-species transmission between livestock and humans. The presence of certain parasite taxa, such as *Trichuris*, *Dipylidium*, and *Strongyloides*, further illustrates the potential for complex interspecific transmission dynamics in this region. Additionally, although no direct *Strongyloides* infections were detected in humans, the presence of these parasites in non-human primates and dogs presents a potential zoonotic risk that warrants continued monitoring. Although the results of this study reveal potential spillover risks, particularly from animals to humans, they also highlight the need for improved diagnostic techniques to accurately identify parasite species and understand their transmission patterns. Addressing the health risks posed by these parasites requires coordinated efforts across veterinary, environmental, and public health sectors to mitigate potential zoonotic transmission and safeguard both animal and human health.

3.6 CONTRIBUTIONS STATEMENT

PU and VAMS developed the research design; PU collected fecal samples; Lordrick Alinaitwe (LA) conducted coproscopic analysis, Barbora Červená (BC), Martin Kváč (MK), Kelly M. Sambucci (KMS), Eva Noskova (EN), Vladislav Ilik (VI), and Barbora Pafčo (BP) conducted molecular analyses; PU analysed the data, wrote the manuscript; BC, MK and VAMS thoroughly edited the manuscript.

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CHAPTER 4: EFFECTS OF GASTROINTESTINAL PARASITES ON FECAL GLUCOCORTICOIDS AND BEHAVIOURS IN VERVET MONKEYS (*Chlorocebus pygerythrus*)

Published as:
Upadhayay P, Chapman CA, Mastromonaco GF, Schoof VAM (2025) Effects of gastrointestinal parasites on fecal glucocorticoids and behaviour in vervet monkeys (*Chlorocebus pygerythrus*). PLoS ONE 20(1): e0316728. https://doi.org/10.1371/journal.pone.0316728

Chapter Summary

Relationships between parasites, host physiology, and behaviours are complex. Parasites can influence host hormonal microenvironment and behaviour through "sickness behaviours" that generally conserve energy. Using a parasite removal experiment, we examined the effects of gastrointestinal parasites on fecal glucocorticoid metabolites (fGC) and behaviours of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. We collected parasitological, hormonal, and behavioural data from adult and subadult male and female vervets (N = 19) in 2014 across four study phases: pre-deworming, post-deworming, early reinfection, and late reinfection as well as in 2015. Overall, there was no decrease in fGC after deworming, but there was an increase following natural reinfection. There was no change in feeding across study phases; however, moving, grooming, and resting changed between the post-deworming and late reinfection phases, but not always in the predicted direction. Comparing behaviour across the same months in the following year as in the 2014 experimental study period, we found no differences in moving, feeding, grooming, and resting events. Despite behavioural variation between study phases, we cannot conclude that behavioural changes are due to parasitism rather than other seasonal variation. However, fGC increased following reinfection, which is consistent with parasitism being costly for hosts.

Keywords: Gastrointestinal parasites, deworming experiment, fecal glucocorticoid metabolites, hormones, behaviour, primates

4.1 INTRODUCTION

Parasites live on or in a host organism, from whom they extract resources (e.g., nutrients) at the expense of their host (Nunn & Altizer, 2006). Parasites can affect host health, behaviours, reproduction, survival, and overall fitness (Chapman et al., 2005; Nunn & Altizer, 2006), and at

the population level, can affect host density and distribution (Laurenson et al., 1998; Nunn & Altizer, 2006). Although gastrointestinal parasites are less likely to be lethal to their hosts compared to viruses and bacteria, chronic infections from these parasites can lead to increased host morbidity (Alum et al., 2010), and induce various physiological and behavioural changes in their hosts by modulating and disrupting the immune system (Raveh et al., 2011).

Organisms can respond physiologically and behaviourally to environmental or biological stressors (MacDougall-Shackleton et al., 2019). One physiological response in vertebrates is the activation of the hypothalamic-pituitary-adrenal (HPA) axis, which leads to the release of glucocorticoid hormones like corticosterone and cortisol (O'Dwyer et al., 2020). However, the relationships between host physiology and parasites are complex and ambiguous. Glucocorticoid hormones (GCs) increase temporarily in response to stressors and mobilize energy stores required to maintain homeostasis (Sapolsky, 1994). However, GCs can also have immunosuppressive effects leaving the hosts more susceptible to infections (Beldomenico & Begon, 2016). While a positive correlation between GCs and parasites may be due to HPA axis activation in response to parasite-imposed energetic stress (Coop & Kyriazakis, 1999), it is unclear whether the relationship is influenced by the resulting immunosuppression, the host's stress response itself, or both (Foerster et al., 2015; Muehlenbein, 2006). Conversely, a negative relationship between GCs and parasites may arise from chronic stress causing HPA axis dysfunction (Hufschmid et al., 2013), which can result in low GC levels (Defolie et al., 2019). Previous studies examining the link between parasites and GCs have shown mixed results, with some finding positive or negative relationships and others showing none; this variable relationship could be due to differences in factors such as parasite type, infection severity, and host age and sex (Defolie et al., 2019). A phylogenetic meta-analysis of 65 studies between parasites and mammalian host GCs revealed

stronger support for a positive association than negative association. This could potentially be explained by a variety of mechanisms, including host manipulation by parasites, host responses to infection, cumulative stress effects, and the neuro-immunomodulatory functions of GCs (Defolie et al., 2019).

Sickness behaviours are considered an adaptive response by the host's immune system to fight infection and maintain homeostasis (Hart, 1988; Johnson, 2002; Poulin, 1994). Sickness behaviours include general inactivity or lethargy, increased sleep, reduced exploratory behaviour, feeding, social, and sexual interactions, and postures that reduce heat loss and facilitate a fever response (Hart, 1990; Lopes et al., 2021). The species studied both in controlled and natural environments exhibit common sickness behaviors, such as anorexia, reduced nest building (Prendergast et al., 2008), decreased activity (Ramirez-Otarola et al., 2019; Stockmaier et al., 2018), less allogrooming (Stockmaier et al., 2018), and increased somnolence (Friedman et al., 1996) and resting (Ghai et al., 2015). Host sickness behaviours may also reduce contact with potentially infectious individuals by reducing movement and social grooming (Bohn et al., 2016). For example, studies have found that reduced movement in immune-challenged mice led to social disconnection (Lopes et al., 2016), and *Trichuris*-infected vervet monkeys spent less time grooming conspecifics (Wren et al., 2021). Alternatively, pathogens may directly influence host sickness behaviours that increase transmission opportunities, and in some cases may even alter the behaviour of uninfected individuals (Demandt et al., 2018).

We used a parasite removal experiment and subsequent natural reinfection to examine the effects of gastrointestinal (GI) parasites on fGC and behaviours in a group of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. Previous research on this population found that it had greater parasite species richness than any other wild vervet population examined

(Valenta et al., 2017). The Nabugabo vervet parasite community included trematodes such as *Dicrocoeliida* and *Schistosoma*, nematodes such as *Ascaris,* order Strongylida*,* and *Trichuris*, unidentified cestodes, protists such as *Entamoeba a*nd *Giardia*, and three parasite genera previously undocumented in vervets: *Metastrongylus, Toxocara,* and *Fasciola* (Valenta et al., 2017). Unidentified trematodes were the most prevalent, occurring in 92% of individuals at least once, followed by *Fasciola* spp. (38%), unidentified cestodes (38%), *Ascaris* spp. (33%), and *Strongyloides* spp. (29%) (Valenta et al., 2017). Experimental removal of GI parasites demonstrated resting events decreased and traveling events increased following deworming, as well as an increase in the number of nearest neighbors, especially for juveniles (Chapman et al., 2016). The current study expands on the previous study by examining fGC and behavioural response to deworming and reinfection, and behavioral variation was compared to a matched control phase the following year. We tested the hypothesis that if vervets respond physiologically to parasite infection, then we predict 1) a decrease in fGC after deworming and increase following reinfection. The logic of this prediction is that infection can activate the HPA, leading to GC secretion, as the host reallocates resources from non-essential functions to critical functions. If vervets respond behaviourally to parasite infection, we predict that 2) after deworming, there will be an increase in moving, feeding, and grooming behaviour and a decrease in resting but 3) a decrease in moving, feeding, and grooming and an increase in resting following natural reinfection.

4.2 METHODS

4.2.1 Study site and subjects

The study was conducted on the shores of Lake Nabugabo, Uganda (0°22′–12°S, 31°54′E, 1,136 m), a satellite of Lake Victoria, that is mostly surrounded by wetlands, grasslands, patches of degraded forest, and farmers' fields (Chapman et al., 2016). The area receives an average of

1348 mm of rain annually (Chapman et al., 2016) in two seasons with high rainfall (March to May and September to November) and two seasons with low rainfall (December to February and June to August) (Schwegel et al., 2023).

During the experimental study (29 May – 13 December 2014), the group had an average of 28 individuals (5 adult males, 10 adult females, 1 subadult male, 2 subadult females, 10 juveniles and infants), each of whom was identifiable based on natural markings. Infants and juveniles were excluded from the experimental design. For our analyses, the category "male" includes adult (> 5 years) and subadult (4-5 years) males, "female with infant" includes females with infants < 6 months, and "female" includes all other adult (after first birth) and subadult (after first observed copulation) females.

4.2.2 Study design

Parasitological, hormonal, and behavioural data were collected during all phases except the experimental deworming phase (see below). Subjects were dewormed to examine fecal glucocorticoid and behavioural changes in the presence and absence of gastrointestinal parasites.

***Pre-deworming phase*:** In the three weeks prior to experimental deworming treatment (29 May - 21 June 2014), we collected a mean of 4.2 fecal samples (range: 1-7) per individual for parasite and hormone analyses (see below). Daily behavioural activity scan sampling occurred from dawn to dusk every 30 minutes (see below).

***Deworming treatment*:** All subjects were treated twice using ivermectin at a dose of 0.3 mg/kg to kill helminth parasites, with a minimum of 5 days and a maximum of 7 days between treatments (treatment dates 22 June - 02 July 2014). Oral ivermectin was placed within a banana and opportunistically given to specific individuals when they were foraging in isolation from other individuals.

***Post-deworming phase*:** In the month following the ivermectin treatment (i.e., July 2014), we collected a mean of 3.4 fecal samples (range: 1-7) per individual and once again started activity scan sampling.

Reinfection phases: Scan sampling was reduced to approximately 10 days per month for 8-hours per day during the early reinfection phase (August 2014) and late reinfection phase (September–December 2014). We collected 2 fecal samples per individual in the early reinfection phase and a mean of 3.8 fecal samples (range: 1-6) per individual in the late reinfection phase.

4.2.2.1 Parasitological data

Fecal samples (N = 225, Appendix C1) were collected immediately upon defecation and placed in vials labeled with individual, date, and time of collection, and then stored in a cooler with icepacks. At the end of the day, 1.0 g of wet fecal material was stored in 2 mL of 10% formalin solution for parasite identification, and approximately 0.1 g was placed in polyvinyl alcohol (PVA) for protozoan analysis. Parasites were identified to the family and genus level where possible at the Central Diagnostic Laboratory, College of Veterinary Medicine Animal Resources and Biosecurity, Makerere University, Kampala, Uganda using a modified ethyl acetate sedimentation method (A. M. Zajac & Conboy, 2012). We calculated the prevalence of a parasite taxon by dividing the total number of individuals infected with a specific parasite taxon by the total number of individuals sampled. Maximum parasite species richness (MPSR) was tabulated from the unique number of parasite taxa found in each host's fecal samples during each study phase (Bush et al., 1997).

4.2.2.2 Hormonal data

We transferred ~1.0 g of wet feces from 182 (Appendix C1) fecal samples to a labelled tube and stored these at -20°C until hormone extraction. Hormones were extracted from 0.5 g

sample of thawed feces using a 10 mL solution of 50:50 deionized water: 95% ethanol, vortexed for 10 minutes, then centrifuged for 20 minutes. A 2 mL portion of the hormone extract was pushed through Prevail C18 Maxi-Clean 300mg Solid Phase Extraction cartridges (Alltech Associates, Inc., Deerfield, IL) and the cartridges were then washed with 2 mL of deionized water. Capped cartridges were stored in a cool, dark, and dry location before transport to McGill University for elution. SPE cartridges were washed with 1 mL of 5% methanol, and hormone extracts eluted from the cartridges with 2 mL of 100% methanol. Hormone-methanol extracts were stored at -4˚C before transport and fGC analyses (L'Allier et al., 2022).

Fecal cortisol metabolites were assayed by enzyme immunoassays (EIA) at the Toronto Zoo's Reproductive Endocrinology Lab using a previously published protocol (Majchrzak et al., 2015) with modification. Plates were coated with 50 ul of antibody (R4866; C. Munro, UC Davis) diluted 1:12,000 in coating buffer. After overnight incubation, plates were washed with 0.15 M NaCl and 0.05% Tween 20 and the wells loaded with 50 uL of hormone standards or reconstituted extracts followed by 50 uL of horseradish peroxidase conjugate diluted 1:33,400 in EIA buffer. For each sample, a 450 uL portion of the hormone-methanol extract was dried and resuspended in 150 uL assay buffer. To fit within the linear range of the standard curve, one sample was diluted 1:1 (150 ul evaporated extract, reconstituted in 150 ul buffer). After a two-hour incubation, plates were washed and 100 uL of colour developing substrate solution (i.e., ABTS) was added. After approximately 30 minutes of color development, absorbance was measured at 405 nm using a spectrophotometer (MRX microplate reader, Dynex Technologies, Chantilly, VA, USA). All samples and standards were run in duplicate, and all hormone values are reported in ng/g of wet fecal weight as a mean of the sample duplicates.

All assays included a 9-point standard curve (GC standard: Sigma H0135, 78–20,000 pg/mL) and two external fecal extract controls. The intra-assay CV was 7.4% at 55% binding, and inter-assay CVs were 9.7% and 6.4% for the low control (60% binding) and high control (19% binding), respectively. Assay sensitivity was 41.8 pg/ml. To test for parallelism between the standard curve and a representative sample pool, the pool was serially diluted two-fold from 1.25x (concentrated) to 1:13 in EIA buffer for fGC. Parallel displacement between the standard curve and serial dilutions of fecal extract was used as an indirect measure of assay specificity. Pooled reconstituted fecal extracts were serially diluted two-fold in assay buffer and visually compared to the respective standard curve. The data were plotted as log (relative dose) vs. percent antibody bound. The slopes of the lines within the linear portion of the curves were determined using linear regression analysis and compared ($t=0.69$, $p=0.51$, $df=7$, Appendix C2) where $p>0.05$ indicates the slopes are not significantly different and thus interpreted as parallel (Soper, 2021). The relative standard deviation between samples in the dilution series was calculated using the method outlined by (Andreasson et al., 2015). The %CV between neat and each dilution in series was ≤30% demonstrating parallelism (Desilva et al., 2003).

Recovery of known amounts of cortisol was calculated to examine possible interference of fecal extract components with antibody binding. Increasing concentrations of hormone standard were added to an equal volume of pooled fecal extracts of known concentration. The percent recovery was calculated using the formula: amount observed/amount expected x 100%, where amount observed is the value from the spiked sample minus the endogenous hormone in the unspiked extract, and the amount expected is the concentration of hormone standard added. Recovery was mean ± SE = 92.6 ± 2.2% and the amount of cortisol recovered was correlated with the amount added (Pearson's correlation coefficient (r) = 0.99, $p < 0.001$, Appendix C3). Fecal GC

measured using a cortisol EIA have been previously validated for biological relevance in captive vervets as evidenced by an fGC increase in response to an ACTH challenge (Young et al., 2017).

4.2.2.3 Behavioural data

The occurrence of general activities, such as moving, feeding, resting, grooming (both receiving and giving), other affiliative behaviours (playing, groom solicit, etc.), agonism (chase, avoid, supplant), and mating behaviours (copulations, mating presentations) were recorded every 30 minutes following an established ethogram. At each behavioural activity scan sample, the behaviour and nearest neighbor were recorded for five subjects. All subjects were sampled at least once a day (Appendix C1). Data were collected by 2 observers. The observers went through extensive training to ensure consistency in how they recorded behaviours and to limit interobserver variation. Given this training and since the behaviours are easy to distinguish between (e.g., resting versus moving) we believe there was little interobserver variation in how behaviour was assessed.

4.2.3 Statistics

We analyzed the effect of maximum parasite species richness on fGC using linear mixed effects models (LMMs). The vervets continued to excrete parasites in their feces shortly after deworming, likely consisting of inactive/dead parasites. Considering that the typical life cycles and prepatent periods of the identified nematodes, trematodes, and cestodes ranges from 14 to 44 days (Bresciani et al., 2017; Yoshihara et al., 2013), we inferred a delay of approximately one month between the parasite presence in feces and on-going gastrointestinal infection, and thus compared excreted fecal parasite species richness in one month to fecal glucocorticoid levels (fGC) in the previous month. This predictor variable is herein referred to as “lagged MPSR” (e.g., MPSR in August was examined in relation to July fGC levels). For the LMM, we created a repeated-measures global model with fGC levels as the response variable and lagged MPSR (0, 1, ≥ 2 taxa),

study phase (4 phases: pre-deworming, post-deworming, early reinfection, and late reinfection), sex/reproductive state (male, female without infant, and female with infant) as fixed effects; we included individual identity as a random effect. Although the goal of the study is not to examine sex/reproductive status differences, we included it as a predictor variable because it is a possible source of variation that we can account for since females may have different baseline GC levels than males due to the energetic demands associated gestation and lactation (Khokhlova et al., 2002). Since some of the females gave birth during the study, we occasionally characterised the same individual as adult female without infant (pre-parturition) and female with infant (post-partum) within the same phase (N = 2).

Activity budgets were calculated from 4710 scans in 2014 and 5330 in 2015 for males, females, and females with infants. The number of study individuals changed between 2014 and 2015 due to demographic changes (Appendix C1). We divided general activity into four categories: moving, feeding, social grooming (i.e., giving and receiving grooming), and resting. Generalized linear mixed effects models (GLMMs) with binomial link function (package lmerTest) (Kuznetsova et al., 2017) were used to examine the effect of lagged MPSR on moving, feeding, grooming, and resting activity scans. For each behaviour, we created a repeated-measures global model with lagged MPSR (0, 1, ≥ 2 taxa), study phase (4 phases: pre-deworming, post-deworming, early reinfection, and late reinfection), mean individual monthly fGC, and sex/reproductive status (male, female without infant, and female with infant) as fixed effects and vervet identity as a random effect. We used the total number of activity scans per individual per phase as weights to account for the variable contribution of individuals to the dataset (Hector, 2021). If a female gave birth during a study phase, we characterised the individual as "female without infant" if the number of days of activity scan data collection before the birth exceeded the

number of days of data collection after the birth and characterised the individual as "female with infant" if the reverse was true. For each model, we used the 'dredge' function in the Multi-model Inference (MuMIN) package (Barton, 2023) to identify the "top" models within Δ7 AICc (Burnham et al., 2011). When multiple top models were identified, we conducted model averaging and calculated 95% confidence interval for each predictor (Buckland et al., 1997; Burnham et al., 2011).

To examine whether the behavioural changes in 2014 were associated with the deworming experiment rather than naturally-occurring social (e.g., conceptive vs. birth peaks) or ecological (e.g., rain and temperature variation) seasonal variations, we compared behaviour categories (i.e., proportion of activity scans for moving, feeding, grooming, and resting) across months in 2015 (non-experimental period) using separate generalized linear models (GLMs) with month, and sex/reproductive status as predictor variables. The total activity scans per individual per month were used as weights to account for the variable contribution of individuals to the dataset in each period (Hector, 2021). Despite potential effects of social (i.e., conception or birth "peaks") and ecological season on hormones and behaviour, we did not include these in the model because births can and did occur outside of the birth "peak", and the ecological seasonality (wet and "wetter" seasons) both occur in the late-reinfection phase. In order to avoid overfitting and unwarranted model complexity, and to focus on the relevant predictor variables, we did not include any interactions in our models. All statistical analyses were conducted in R statistical software RStudio (version 4.0.3) (R Core Team, 2020).

Ethical Note

This research was approved by the Uganda Wildlife Authority and Uganda National Committee for Science and Technology to CAC (2011-2015) and VAMS (2015-present), as well

as the McGill University Animal Care Committee to CAC and York University Animal Care Committee to VAMS.

4.3 RESULTS

4.3.1 Parasites and study phases

We collected 225 fecal samples to identify gastrointestinal parasites during the 2014 experimental study phases, with a mean ± SE = 0.97 ± 0.07 (range = 0-4, median = 1), of which 154 (68.4%) were positive for at least one parasite taxon. Of the 154 positive samples, 62.9% were positive for a single parasite taxon, while 33.1% were positive for two taxa, 2.6% for three taxa, and 1.3% for four taxa. The most commonly found parasites were unidentified trematodes, followed by unidentified cestodes and coccidian oocysts (Appendix C4). *Schistosoma* spp. was the only identified trematode, no cestode taxa were identified, and *Strongyloides* spp. were found to be most prevalent nematodes (Appendix C4). Among protists, *Iodomoeba* spp. were the most prevalent (Appendix C4). Of the 72 fecal samples collected during the pre-deworming phase, 81% were positive for at least one parasite (Appendix C4). Following deworming and reinfection, 87% of fecal samples collected (n = 52) were infected, and all parasite taxa were present. Consistent with the average life cycles and prepatent periods of known vervet parasites, we found that: 1) the first month of reinfection (i.e., August) was marked by the absence of shed trematodes, cestodes, or nematodes (n = 32), with only 9% of samples testing positive for protists, and 2) the second month of reinfection, 100% samples were positive for parasites, with 87% for trematodes, 57% for cestodes, 0% for nematodes, and 9% for protists (Appendix C5).

4.3.2 Effect of gastrointestinal parasites on fecal glucocorticoids

Across the experimental study period, the mean ± SE fGC was 16.51 ng/g ± 1.71 ng/g (median: 8.62 ng/g, range: 2.29 – 297.49 ng/g; Appendix C6). Changes in mean fGC were best

described by three top models, all of which included study phase, while lagged MPSR and sex/reproductive state each appeared in two models (Table 4.1). Contrary to our prediction, mean fGC did not decrease from pre- to post-deworming. As predicted, fGC levels were higher during the reinfection phases [both early (b = 13.07, SE = 3.67, CI: 5.83 – 20.30) and late (b = 19.74, SE = 2.47, CI: 14.86 – 24.61)] than during the post-deworming phase (Figure 4.1; Appendix C7).

Table 4.1: Model selection for the outcome variable fecal glucocorticoid metabolites (fGC) during deworming experimental year (2014) in vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda.

Outcome	**Predictors**	**df**	**loglik**	**AICc**	**ΔAICc**	**weight**
fGC	Phase + Lagged MPSR + Sex	9	-660.37	1339.80	0	0.75
	Phase + Lagged MPSR	7	-664.27	1343.20	3.39	0.14
	Phase + Sex	8	-663.51	1343.90	4.06	0.09

Predictors include study phase (pre-deworming, post-deworming, early reinfection, late reinfection), lagged maximum parasite species richness (lagged MPSR), and sex (sex/reproductive state = males, females without infants, and females with infants). The models are within < 7 ΔAICc.

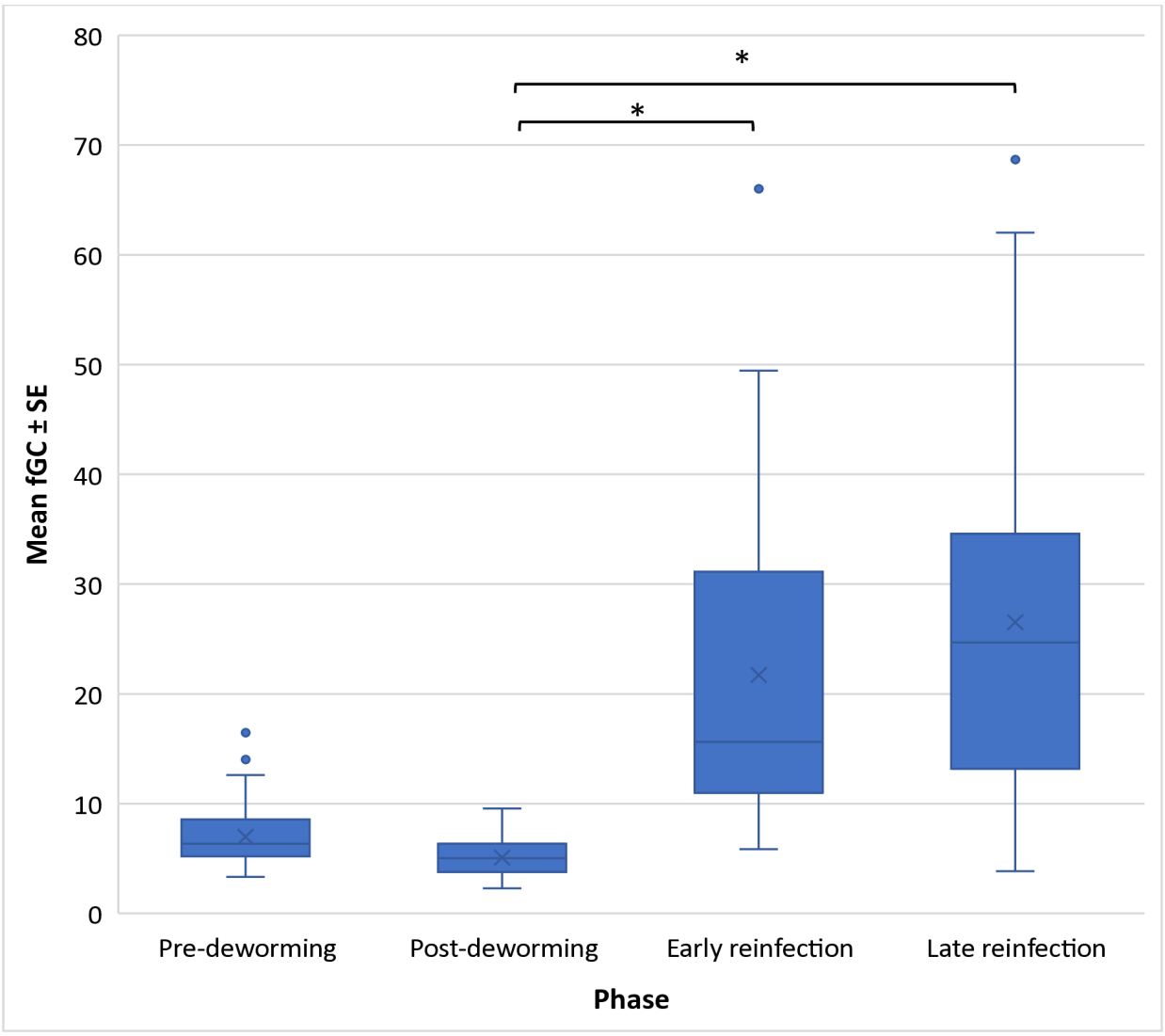

Figure 4.1: Fecal glucocorticoid (fGC) metabolite levels in vervet monkeys across study phases. The estimated mean fGC levels (X) in vervet monkeys during each study phase at Lake Nabugabo, Uganda, from June-December 2014. *Significant pairwise comparison.

4.3.3 Effects of gastrointestinal parasites on behaviours

On average, the proportion of moving, feeding, grooming, and resting activity scans were 17%, 30%, 16%, and 16% respectively from June to December 2014 (Appendix C1), which is similar to the proportion of moving, feeding, grooming, and resting activity scans of 17%, 34%, 13%, and 15% respectively in June to December 2015

4.3.3.1 Moving

Variation in moving was best described by eight top models, all of which included phase, while lagged MPSR, mean fGC, and sex/reproductive state each appeared in four models (Table 4.2). Moving was lower in the late reinfection phase compared to the post-deworming phase (b = -0.34, SE = 0.13, CI: -0.58 to -0.08) (Appendix C8; Figure 4.2A), but there were no other differences between study phases. Moving behaviour did not differ across months in 2015 (Appendix C9).

Table 4.2: Model selection for the behavioural outcome variables during experimental deworming year in vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda.

Outcomes	Predictors	df	loglik	AICc	ΔAICc	weight
Proportion of moving scans	Phase + Lagged MPSR	6	-203.39	419.90	0	0.37
	Phase + Lagged MPSR + Mean fGC	7	-202.78	421.10	1.17	0.21
	Phase + Lagged MPSR + Sex	8	-201.69	421.40	1.45	0.18
	Phase	5	-205.91	422.60	2.69	0.09
	Phase + Lagged MPSR + Mean fGC + Sex	9	-201.25	423.00	3.09	0.08
	Phase + Sex	7	-204.08	423.70	3.76	0.06
	Phase + Mean fGC	6	-205.39	423.89	3.98	0.05
	Phase + Mean fGC + Sex	8	-203.77	425.51	5.60	0.02
Proportion of feeding scans	Phase + Sex	7	-225.92	467.35	0	0.28
	Phase + Mean fGC + Sex	8	-224.98	467.93	0.58	0.21
	Mean fGC + Sex	5	-228.61	468.01	0.65	0.20
	Mean fGC + Lagged MPSR + Sex	6	-227.67	468.46	1.11	0.16
	Phase + Lagged MPSR + Sex	8	-225.92	469.80	2.45	0.08
	Phase + Mean fGC + Lagged MPSR + Sex	9	-224.98	470.45	3.10	0.06
Proportion of grooming scans	Phase + Sex	7	-200.56	416.60	0	0.45
	Phase + Lagged MPSR + Sex	8	-199.72	417.40	0.76	0.31
	Phase + Mean fGC + Sex	8	-200.44	418.90	2.21	0.19
	Phase + Mean fGC + Lagged MPSR + Sex	9	-199.58	419.70	3.02	0.09
Proportion of resting scans	Phase	5	-234.47	479.74	0	0.33
	Phase + Lagged MPSR	6	-233.81	480.75	1.01	0.20
	Phase + Mean fGC	6	-233.88	480.89	1.15	0.18
	Phase + Mean fGC + Lagged MPSR	7	-233.16	481.82	2.09	0.12
	Phase + Sex	7	-233.51	482.52	2.79	0.08
	Phase + Mean fGC + Sex	8	-233.05	484.07	4.34	0.04
	Phase + Lagged MPSR + Sex	8	-233.05	484.08	4.34	0.04
	Phase + Mean fGC + Lagged MPSR + Sex	9	-232.53	485.56	5.82	0.02

Predictors include study phase, lagged maximum parasite species richness (lagged MPSR), mean fGC, and sex. The models are within < 7 ΔAICc.

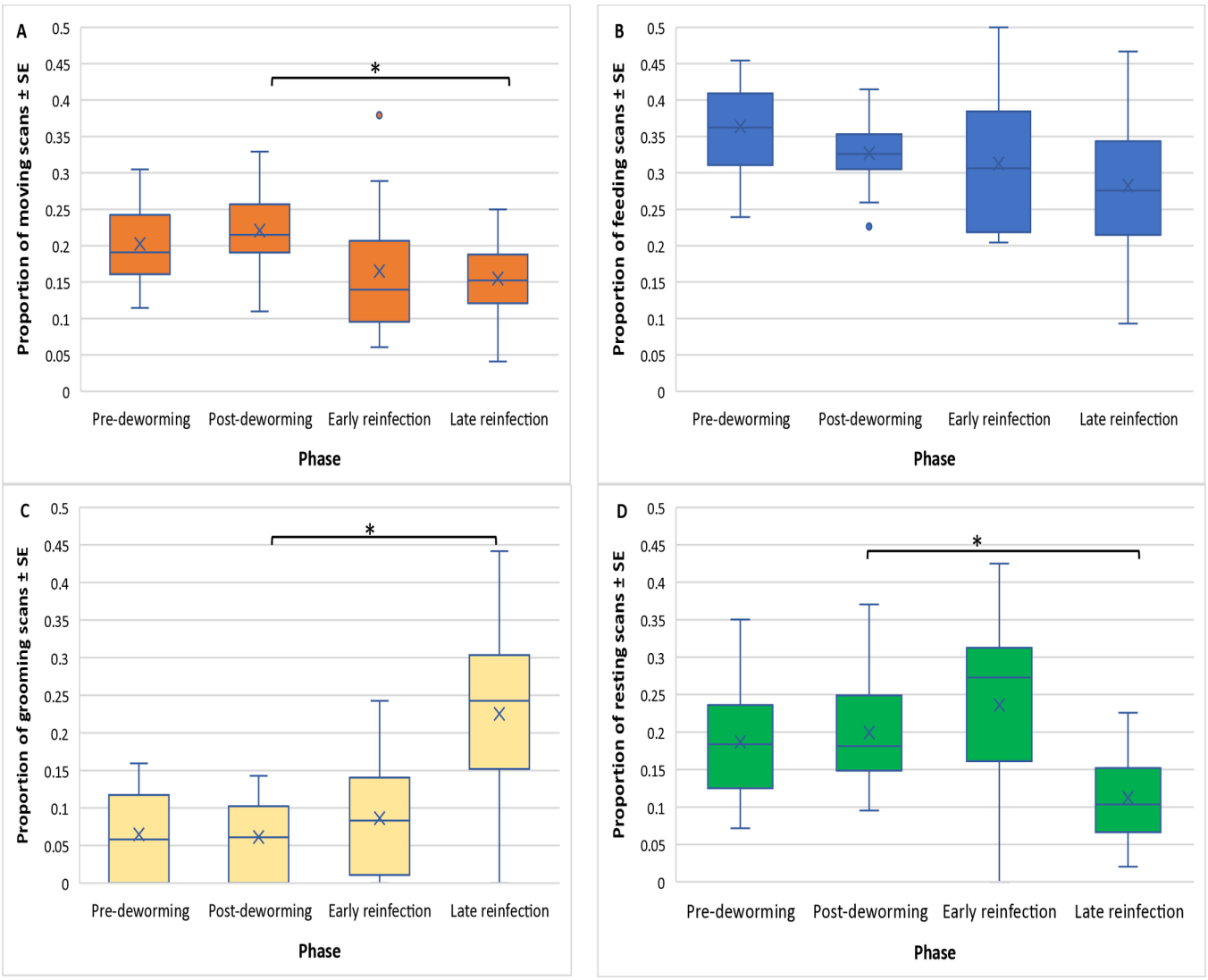

Figure 4.2: The proportion of (A) moving, (B) feeding, (C) grooming, and (D) resting activity scans in vervet monkeys across study phases. The estimated mean proportion (X) of moving, feeding, grooming, and resting activity scans in vervet monkeys (*Chlorocebus pygerythrus*) during each study phase at Lake Nabugabo, Uganda, from June-December 2014. *Significant pairwise comparison.

4.3.3.2 Feeding

Variation in feeding was best described by six top models, with the variable sex/reproductive state appearing in all six models, phase and mean fGC appearing in four models, and lagged MPSR appearing in three models (Table 4.2). There was no difference in feeding behaviour across phases (Appendix C8; Figure 4.2B), but females with infants fed less than females without infants (b = -0.38, SE = 0.09, CI: -0.56 to -0.18) (Appendix C8). Similarly, there was no variation in feeding behaviour across months in 2015 (Appendix C9).

4.3.3.3 Grooming

Variation in grooming was best described by four top models, all of which included phase and sex/reproductive state, with lagged MPSR and mean fGC each appearing in two top models (Table 4.2). Grooming was higher in the late reinfection phase compared to the post-deworming phase (b = 1.39, SE = 0.15, CI: 1.11 to 1.69) (Appendix C8; Figure 4.2C), but there were no other differences between study phases. Additionally, males spent less time grooming than females without infants (b = -2.44, SE = 0.34, CI: -3.13 to -1.75) (Appendix C8; Figure 4.2C). There was no variation in grooming behaviour throughout 2015 (Appendix C9).

4.3.3.4 Resting

Variation in resting was best described by eight top models, all of which included phase, with lagged MPSR, mean fGC, and sex/reproductive state each appearing in four of the top models (Table 4.2). Resting was lower in late reinfection phase (b = -0.71, SE = 0.13, CI: -0.96 to -0.45) (Appendix C8; Figure 4.2D), but there were no other differences between study phases. There was no variation in resting behaviour throughout 2015 (Appendix C9).

4.4 DISCUSSION

We examined changes in fecal glucocorticoids and behaviour of vervet monkeys in response to an experimental ivermectin deworming treatment and natural reinfection. Contrary to our predictions, there was no decrease in fecal glucocorticoids, nor were there any behavioural changes in response to deworming. However, fGCs increased following reinfection. Our behavioural analyses provide limited support for the presence of sickness behaviours in response to reinfection, with a decrease in moving in the late reinfection phase as predicted. However, in contrast to our predictions, there was no change in feeding behaviour, while following reinfection grooming and resting changed in the opposite direction from what we had predicted (an increase in grooming, a decrease in resting). Furthermore, there were differences in behaviour across the experimental phases but not in the non-experimental year, suggesting that vervets adjust their behaviour in response to parasite infection.

4.4.1 Effectiveness of ivermectin treatment

Species richness of parasites shed in vervet feces decreased in the second month after deworming. This is consistent with a study where silver foxes were treated with ivermectin, resulting in parasite-free fecal samples 3- to 6-weeks post-treatment (Conboy & Adams, 1995). The “delayed” decrease in excreted parasites following ivermectin treatment may be because the vervets were shedding inert parasites during the first month after deworming. Given that ivermectin is an anti-helminthic treatment, it is not surprising that only protists were shed in the second month after deworming.

4.4.2 Effects of parasites on fecal glucocorticoids

Contrary to our prediction, mean fecal glucocorticoids (fGC) did not decrease following ivermectin treatment, but it did increase following parasite reinfection. The absence of a decrease in GC may be the result of the fact that a parasite may have diminished effects on a host if the

host's tolerance to the damage caused by the parasite is chronic (Medzhitov et al., 2012) and/or it may suggest they use compensatory behavioural mechanisms, such as sickness behaviours (but see below) to limit the detrimental effects of parasite infection. Our findings are consistent with those of a parasite reduction experiment in racoons that also found no decrease in fecal glucocorticoids (Monello et al., 2010). Parasite infected reindeer had slightly lower glucocorticoid levels than uninfected reindeer, leading to authors to hypothesize that they may use a tolerance strategy to cope with infection (Carlsson et al., 2016). Another possible explanation for the lack of GC decrease following deworming may be due to individual variation in the impact of parasitism, influenced by factors such as age, sex, reproductive state, dominance status, or sociality (Akinyi et al., 2019; Nunn & Altizer, 2006), which we were unable to examine since model averaging makes the interpretation of interactions very difficult (Engqvist, 2005). However, if parasites are indeed costly, it is difficult to imagine a scenario where an individual would not benefit from deworming; that said, individual characteristics (e.g., dominance rank) may influence the occurrence and response to other (non-parasite) stressors (Anestis et al., 2006).

As predicted, there was an elevation in fGC levels as the vervets became reinfected. This may reflect a stress response to reinfection and aligns with the idea that short-term elevations in GCs are adaptive due to their anti-inflammatory effects as a part of the immune reaction (Holub et al., 2007; O'Dwyer et al., 2020). This has been observed in mice where initial parasite infection was associated with elevations in blood glucocorticoids (Roggero et al., 2006). Possibly the process of deworming disrupted any homeostatic state that may have been reached by hosts and that a new infection is more likely to illicit a response than an on-going, low-grade infection. A diminished or incomplete immune response has been observed in rats infected with *Nippostrongylus brasiliensis*, with immune response returning to normal following

antihelminthic treatment (Jarrett, 1971). However, both hosts and parasites can influence GC levels when parasite infection occurs (Defolie et al., 2019). Some parasites manipulate GC levels, which can increase susceptibility to additional infections (Banu et al., 2005). Some parasites may also be associated with secondary infections by other parasites (Ulrich & Schmid-Hempel, 2012) by causing immunosuppression due to long-term elevation of GCs (Beldomenico & Begon, 2016). This could explain the observed increase in fGC levels during the early and late reinfection phase. Nevertheless, other factors could have influenced the increase, along with parasite reinfection. For example, glucocorticoids are known to vary with social interactions as well as with social and ecological seasonality (Higham, 2016).

4.4.3 Effects of parasites on behaviours

Contrary to our predictions, there was no evidence of sickness behaviours that changed the balance of moving, feeding, grooming, or resting in response to experimental deworming. However, we observed changes in moving, grooming, and resting between the post-deworming and late reinfection phase, though the direction of these behavioural changes were only partially consistent with the hypothesis that parasite infection can lead to reduced energy budgets (Hart, 1990). Consistent with our prediction, movement, an energetically expensive behaviour, was lower in the late reinfection phase. This reduced movement could be a strategy to preserve energy while mounting an immune response, which is consistent with our findings that fGCs also increased at this time. A decrease in moving behaviour could also be a host strategy to decrease the chances of encountering parasites in the environment when they are already fighting an existing parasite infection (Agostini et al., 2023; Friant et al., 2016).

In contrast to our predictions, resting decreased while grooming increased during the reinfection phase, and feeding behaviour did not change between study phases. We had expected

resting, an energetically conservative behaviour, to increase during the reinfection phase compared to the post-deworming phase. We had also expected that grooming and feeding, energetically expensive behaviours and one that also have the potential to increase parasite exposure risk, would decrease during the reinfection phase (Agostini et al., 2023; Wren et al., 2021). Grooming is an important behaviour in developing and maintaining social bonds but is also a source of disease transmission (Kappeler et al., 2015). One study found that parasite-infected Barbary macaques (*Macaca sylvanus*) continued to maintain social interactions despite elevated glucocorticoids, a finding which highlights the importance of social relationships (Müller-Klein et al., 2019).

The observed decrease in moving and resting behaviour and increase in grooming during the late reinfection phase could be driven by a subset of individuals: females with infants. This period coincides with a birth peak in the Nabugabo vervet population, such that females with infants may be constrained by parental care, possibly including increased grooming towards infants and decreased moving (such as during breastfeeding) and therefore have less time for other activities. In our study, five females gave birth during the late reinfection phase, compared to two in the early reinfection phase and one during the post-deworming phase. That said, this seems unlikely given that behaviour did not vary across 2015 despite the birth of three infants during late reinfection phase, although we did find that females with infants fed less than females without infants in the experimental year. Increased grooming may be associated with the birth season, when not only mothers but many individuals are drawn to new infants and access to them may be used as a commodity in exchange for grooming (Fruteau et al., 2011). Unfortunately, we were not able to test this hypothesis because we would need to incorporate interactions into our models, which can complicate interpretation and lead to falsely interpreting biologically significant interactions as statistically non-significant when model averaging (Engqvist, 2005).

Another possible alternative explanation for changes in moving, resting, and grooming across the experimental year could be ecological seasonality. Despite the occurrence of two wet and two dry seasons at the Lake Nabugabo field site, there is no seasonality in the availability of the most consumed natural foods, nor in the consumption of anthropogenic foods. Furthermore, we did not find any behavioural variation during the corresponding time periods in the non-experimental year. Another limitation of model averaging that we need to keep in mind is that it focuses on prediction rather than causality. While it excels at identifying a set of predictors that best explain the variation, it does not provide insight into the underlying mechanisms or causal pathways. Thus, some observed behavioural changes were consistent with sickness behaviour-related changes (i.e., decreased moving during late reinfection), while others were not (i.e., increase in grooming and decrease in resting).

Overall, our ivermectin treatment experiment provided mixed support of the hypothesis that gastrointestinal parasites are costly for hosts. Deworming had no impact on fGC levels or any of the behaviours examined, which suggests that helminth parasites may not be costly to hosts or that infections are sufficiently low-grade that parasite removal has a limited impact. The fact that behaviours did not change in response to the deworming, suggesting that they do not appear to use compensatory behavioural mechanisms to mitigate costs of parasite infection. Another possible explanation for our findings is the "old friends" derivative of the "hygiene hypothesis", which suggests that because parasitic helminths have co-evolved with the immune system, they play a crucial role in supporting normal immune development (Sironi & Clerici, 2010; Strachan, 1989). Thus, it is possible that these parasites may contribute to maintaining a healthy immune response rather than being solely detrimental in the vervets. Additionally, the pathogenicity of the identified parasite taxa could influence the results, as previous research has shown that only certain parasites

are associated with elevated fGC levels (Akinyi et al., 2019). That said, there was an increase in fGC following natural reinfection and a decrease in movement behaviour, as would be predicted if parasites are costly for hosts. Although we cannot exclude the possibility that the observed fGC and behavioural variation is tied to seasonality rather than parasitism, it is possible that gastrointestinal parasites are not as costly as previously hypothesized or host physiological responses to parasitism are sufficient to limit the expression of sickness behaviours.

4.5 ACKNOWLEDGEMENTS

We thank the Uganda Wildlife Authority, and Uganda National Council for Science and Technology for permission to conduct this research. We also thank the Community Nkima Project, Nabugabo: Dr. Dennis Twinomugisha, Matovu Ponsyano, Katwere Livingstone, and Hillary Tashobya for assistance with the data collection. We are grateful to Primate Behavioural Endocrinology Lab for assistance with the behavioural data entry. Finally, we thank Megan Schwegel and Alessandro Filazzola for the help with statistics, Tony Goldberg for advice on the ivermectin treatment, and Christine Gilman for assistance with the hormone analyses.

4.6 CONTRIBUTIONS STATEMENT

PU managed data, developed and implemented statistical analyses, interpreted results, wrote the manuscript; Colin C. Chapman (CAC) developed and implemented study design, managed data, reviewed and edited manuscript; Gabriela F. Mastromanaco (GFM) conducted hormone analyses, reviewed and edited manuscript; VAMS developed and implemented the hormone aspect of the study design, extracted hormones, managed data, interpreted results, and contributed to manuscript writing.

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CHAPTER 5: GENERAL CONCLUSION

5.1 Conclusion

This dissertation contributes to a growing but still fragmented body of research on human-wildlife coexistence, offering a comparative, interdisciplinary exploration of conflict and parasitism across contrasting East African landscapes. While much of the literature on human-wildlife conflict (HWC) focuses either on protected areas or non-protected regions in isolation (Treves & Karanth, 2003; Woodroffe et al., 2005), this research bridges that divide by directly comparing two socio-ecological contexts: a Ugandan village in a non-protected area and a Kenyan village adjacent to a conservancy (Chapter 2). These contrasts revealed notable differences not only in the frequency and severity of conflict but also in how local socio-economic factors—such as land size and education—shape human responses. This supports recent findings that advocate for moving beyond simplistic conservation-vs-livelihood frameworks and instead adopting place-based strategies that integrate local knowledge and lived realities (Barua et al., 2013; Kidane et al., 2024; Redpath et al., 2013). A key insight from this work is that management strategies must be tailored to the socio-ecological context of each site. For instance, while protected areas may experience more frequent but less severe HWCs due to regulatory structures and wildlife habituation, non-protected areas may suffer from fewer but more damaging interactions, often exacerbated by land tenure issues and lower conservation support. These findings echo calls for adaptive, community-driven conservation models that center equity and local participation (Büscher & Dressler, 2007). The comparative lens not only illuminates the diversity of conflict experiences but also emphasizes the importance of integrating social and ecological data to better inform policy.

Chapters 3 and 4 expand this socio-ecological perspective by embedding human-wildlife conflict within broader One Health concerns—namely, parasitism transmission at the human-

animal interface. The discovery of shared gastrointestinal parasites among humans, livestock, dogs, and vervet monkeys reinforces the notion that these landscapes are not only socially but biologically entangled (Hassell et al., 2017). While not all parasites showed cross-species transmission, the presence of shared taxa like *Giardia intestinalis* and *Enterocytozoon bieneusi* suggests ongoing or historical interspecies exchange, possibly facilitated by overlapping land use and limited sanitation infrastructure. Vervet monkeys, due to their ecological flexibility and close genetic relatedness to humans, are particularly significant in this context and warrant closer inclusion in zoonotic disease surveillance systems (Wolfe et al., 1998).

This research also highlights the often-understudied physiological costs of parasitism in wild hosts. Although no significant change in mean fecal glucocorticoid (fGC) levels was observed post-deworming, the increase in fGC during natural reinfection (Chapter 4) suggests that parasitism may act as a stressor, particularly when compounded by other environmental pressures. However, the complexity of behavioral responses across the study phases suggests that wildlife stress is multifactorial—likely influenced by seasonal shifts, social dynamics, and habitat disturbances (Behringer & Deschner, 2017; MacIntosh et al., 2010). These findings call for a more nuanced understanding of wildlife health that accounts for both proximate (e.g., parasitism) and distal (e.g., climate variability, land use change) stressors.

Collectively, this dissertation underscores the value of interdisciplinary, site-specific research in addressing the intertwined challenges of conservation, public health, and community well-being. It aligns closely with the One Health framework, which emphasizes the interconnectedness of people, animals, and ecosystems (Destoumieux-Garzón et al., 2018). Importantly, it identifies key research gaps that merit future attention: (1) the need to link local perceptions of wildlife with epidemiological data, (2) the role of sanitation, infrastructure, and

land access in mediating parasitism risk, and (3) long-term monitoring of physiological stress in wildlife as an indicator of ecosystem health. As a researcher, this work has helped shape my identity as an integrative scientist committed to producing socially relevant, ecologically informed knowledge that bridges conservation biology, disease ecology, and community-based research. In increasingly human-modified landscapes, such interdisciplinary approaches are essential for designing interventions that are both ethically grounded and ecologically sustainable.

5.2 Future directions

This study provides valuable insights into human-wildlife conflict (HWC), parasitic interactions, and stress responses in vervet monkeys, but there are several areas for future research. Expanding the study to multiple sites is crucial to assess the generalizability of the findings. Future research could replicate the methods across diverse regions to evaluate how HWC dynamics and socio-economic factors vary in different ecological and cultural contexts. This would help identify region-specific conflict mitigation strategies. Additionally, integrating interdisciplinary research that combines ecological, geographic, and socio-economic data with wildlife health monitoring could offer a more holistic view of HWC. Understanding how environmental factors, community behaviors, and wildlife health intersect will enable the development of tailored conflict management strategies. Incorporating social science into wildlife management could also foster more collaborative conservation efforts, improving the success of mitigation strategies.

Equally important is the translation of research findings into policy and practice. Collaborations with wildlife management authorities, public health sectors, and local communities will be essential to apply insights from this research toward the development of evidence-based conservation and health policies. Incorporating participatory approaches and

local knowledge systems into research and intervention design will enhance the cultural relevance, acceptance, and effectiveness of conflict mitigation and parasite control strategies.

Another significant future direction lies in studying other species beyond vervet monkeys. While this research has focused on vervet monkeys and their parasitic dynamics, it would be valuable to extend similar experimental parasite studies to other vervet populations, to other non-human primates, as well as to other mammalian species that coexist with human populations. Different populations and different species may exhibit varying levels of parasitic infections and stress responses and understanding whether the findings from the vervet monkey study population are applicable to other species is crucial for understanding the costs of parasitism – if any – and for developing more comprehensive wildlife health management strategies. By exploring similar parasite communities in other populations and among other species that interact with human populations, researchers can build a more generalized understanding of zoonotic disease dynamics and the health impacts of human-wildlife interactions. Furthermore, future studies could also build on the long-term impacts of deworming interventions on wildlife health. While this study focused on vervet monkeys and the potential benefits of deworming, additional studies could assess the sustainability and long-term effects of such interventions, not only on parasite loads but also on overall wildlife health and behavior. This could include monitoring changes over several seasons or years to determine whether the benefits of deworming persist and how it influences the broader ecosystem, particularly in relation to wildlife stress and reproduction.

Future studies should also consider employing a variety of methodological approaches, such as remote sensing, GPS tracking, and non-invasive physiological sampling (e.g., fecal glucocorticoid analysis), to quantify spatial overlap, behavioral adaptations, and stress

physiology in wildlife exposed to human pressures. Longitudinal studies using controlled deworming trials, coupled with systematic behavioral and ecological monitoring, would help establish causal links between parasitic infection, stress, and fitness outcomes.

Additionally, expanding the scope of the human-wildlife parasite study to include other ecosystems or human-wildlife contexts would provide important insights into the broader ecological and health risks of parasitic transmission between humans, domestic animals, and wildlife. This could include areas with different socio-economic dynamics, sanitation or cultural practices, or climatic conditions, offering a more global perspective on the ways in which human activities influence wildlife health and parasite transmission.

In summary, future research in these areas will provide critical insights into the complexities of human-wildlife interactions, contributing to the development of more effective conservation strategies and improving our ability to manage conflicts between humans and wildlife in diverse settings. Expanding the scope to include multiple sites, diverse species, and long-term studies will ensure that conservation efforts are adaptable, sustainable, and more widely applicable across different ecosystems.

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APPENDIX A

Appendix A1: Survey questionnaire

COMMUNITY PERCEPTION OF WILDLIFE AND RESEARCH – Initial survey

Name of Interviewer: _____

Date: _____ Start Time: _____

Household ID:_____ Consent form completed: YES NO

GPS of Household: UTM-N_____UTM-E_____

Village, District, Country

_____

PART 1 – HOUSEHOLD DEMOGRAPHICS:

1. Please list the people in this household, including gender, age, occupations and level of education:

Position Within Family	Sex	Age	Occupation(s)	Level of Education	
□ Grandparent (GP) □ Parent (P) □ Child (C) □ Grandchild (GC) □ Other Relative (OR) □ House-Helper (HH)	M/F	yrs	Please Specify:	□ None (N) □ Some Primary (SP) □ Completed Primary (CP) □ Some Secondary (SS)	□ Completed Secondary (CS) □ Vocational Training (V) □ College, University or Higher (CUH)

2. What is your primary source of livelihood (*multiple answers allowed*)?

(i) Crop farming (ii) Trading (iii) Cattle raising (iv) Other(s) _____

_____

_____

3. a) How much land do you currently cultivate?

   (i) Less than 100m^2 (ii) 100-500 m^2 (iii) 500-1000m^2 (iv) 1000-5000 m^2 (v) none

   b) What percentage of cultivated food is for your household food consumption?

   (i) 100% (all food for family) (ii) More than 50% (iii) Less than 50% (iv) none (all sold)

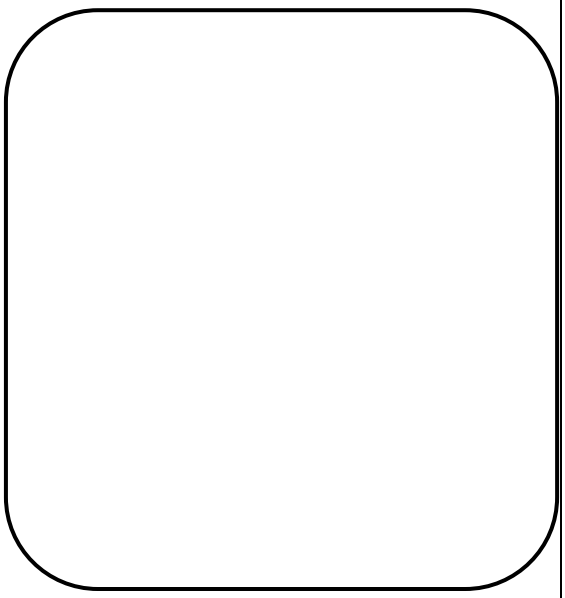
   (v) not applicable, n/a

4. How close to your home is the land you cultivate?

   (i) Adjacent (ii) 100-500 m (iii) 500-1000 m (iv) More than 1km away (v) n/a

5. CURRENTLY, how many food types are you growing in your garden? In column A, please give the food/plant name. In column B, what percentage of your CURRENT garden is made up of each food/plant type? (You can also use the diagram on the right if this is easier)

Plant Name	Garden %



6. For how long have you lived in this area?

   (i) Less than 5 yrs (ii) 6-10 yrs (iii) 11-15 yrs (iv) 16-20 yrs (v) Over 20yrs

7. Which of the following does your household have? *Check all that apply*

Electricity? From the electrical lines _____ From solar ____ Bicycle_____(no.) Motorcycle_____(no.) Car_____ Radio_____(no.) CD/DVD player _____(no.) Television_____	Mobile phone_____(no.) Refrigerator_____ Milking bucket/cans_____ Mattress _____(no.) Couches _____(no.) Chickens _____(no.) Goats _____(no.) Cows _____(no.)

PART 2 – WILDLIFE EXPERIENCES & PERCEPTIONS

8. What animals do you see in your community? (Interviewer should check off answers in the table below. If the participant doesn't know, read them the list below and for each "yes", ask them how often they see this animal type).

Species	Every day	1-2/week	1-2/month	Few times/year	Not every year	Other (specify)
Wild dogs						
Domesticated dogs						
Vervet monkeys						
Colobus monkeys						
Red tail monkeys						
Baboon						
Small birds						
Birds of prey						
Snakes						
Rodents/Rats						
Small Antelope						
Other: _____						

Notes:

_____

_____

_____

_____

9. Have you experienced any conflict with wild animals in the last year?

   (i) Yes (ii) No

10. If Yes, what type of conflict did you face? (rank out of 4; with 1=less severe & 4=most severe)

	Type of conflict	Severity Rank			
1	Crop raiding	1	2	3	4
2	Destruction of food store	1	2	3	4
3	Scaring or threatening livestock	1	2	3	4
4	Killing or threatening people	1	2	3	4
5	Others (specify)	1	2	3	4

11. Which type of animal have you had conflict with in the past 2 years? (rank out of 4; with conflict rank 1=less severe & 4=most severe; with conflict type 1= crop raiding, 2 = destruction of food store, 3 = scaring or threatening livestock, 4 = killing or threatening people, 5 = other/specify)

	Type of Animal	Severity Rank				Conflict type(s)
1	Wild dogs	1	2	3	4	
2	Domesticated dogs	1	2	3	4	
3	Vervet monkeys	1	2	3	4	
4	Colobus monkeys	1	2	3	4	
5	Red tail monkeys	1	2	3	4	

6	Baboon	1	2	3	4	
7	Small birds	1	2	3	4	
8	Birds of prey	1	2	3	4	
9	Snakes	1	2	3	4	
10	Rodents/Rats	1	2	3	4	
11	Small Antelope	1	2	3	4	
12	Others (specify)	1	2	3	4	

Notes:

_____

_____

_____

12. What words would you use to describe the vervet monkeys that you see?

_____

_____

_____

13. What words would you use to describe the birds that you see?

_____

_____

_____

14. How often do you experience wildlife problems in this area?

(i) More than once a day

(ii) Once a day (daily)

(iii) Once a week

(iv) 2-3 times a week

(v) Once every two weeks

(vi) Once a month

15. During which month(s) of the year do you frequently experience conflict with wild animals? (*multiple responses allowed*)

(i) Jan. (ii) Feb. (iii) March (iv) April (v) May (vi) June

(vii) July (viii) Aug. (ix) Sept. (x) Oct. (xi) Nov. (xii) Dec.

16. What time do these incidences frequently occur? (*multiple responses allowed*)

(i) Morning (ii) Afternoon (iii) Evening (iv) At night (v) don't know

17. Which method(s) do you use to guard against wildlife problems? (*multiple responses allowed*)

(i) Scare crow
(ii) Throw stones
(iii) Bon fire
(iv) Fencing
(v) Shouting
(vi) Bang tins
(vii) Tie up dogs in plot
(viii) Release dogs
(ix) Poison
(x) Trap and release
(xi) Trap and kill
(xii) Do nothing
(xiii) Do something else (describe) _____

_____

_____

18. What preventive measures do you think would help reduce wildlife problems in your area, and why?

_____

_____

_____

19. How often do you touch, handle, or are bitten by wild animals from the forest?

(i) No contact or unknown

(ii) Less than one time per month

(iii) More than one time per month, but less than once per week

(iv) Once or more per week

20. In your opinion, when do you think problems between humans and wildlife began in this area?

(i) Less than 5 yrs (ii) 6-10 yrs (iii) 11-15 yrs (iv) 16-20 yrs (v) Always (vi) Don't know

21. What do you think has been the cause of these problems in this area over the years? (*multiple responses are allowed*)

(i) Increase in wild animals' population

(ii) Increase in human settlement taking away wildlife habitat

(iii) Not enough wild animal food in their habitat

(iv) Researchers coming to the area

(v) Tourists coming to the area

(vi) Others (specify)

_____

_____

_____

22. How would you rate the severity of wildlife problems in this area?

(i) Very severe

(ii) Moderate

(iii) Less severe

(iv) Not sure

23. How would you rate your liking for the Nabugabo Fish & Monkey Research Project?

(i) Not at all (ii) Not that much (iii) Half&half (don't like or dislike) (iv) I like it (v) I like it very much

24. Could you please list some of the benefits this household (H) or community (C) receives from living in a village close to where researchers come? Please rank the benefits based on how important they are for this household or community.

Benefits (H – Household; C – Community)	Rank

25. Could you please list some of the negative effects this household (H) or community (C) receives from living close where researchers come? Please rank the negative effects based on how important they are for this household or community.

Negative effects (H – Household; C – Community)	Rank

26. Do you have any ideas as to how to improve community-researcher relations and conservation efforts?

_____

_____

End time: _____

Appendix A2: Negative effects reported by the respondents from having the Nabugabo Fish & Monkey Project on the shores of Lake Nabugabo, Uganda, and Lewa-Borana Conservancy in Kenya.

Nabugabo		
Negative effects from the researchers	**Negative effects from the animals**	**No negative effect**
Researchers following monkeys to the gardens	Destruction of crops	
Ill behavior from the researchers towards the villagers	Overpopulation of the monkeys	
Monkeys not being looked after by the researchers	Monkeys becoming fearless	
Empty promises made by the researchers		
Researchers making monkeys their friends.		
Lewa		
Negative effects from the researchers/Conservancy	**Negative effects from the animals**	**No negative effect**
No electricity	Destruction of crops	
Less response from the researchers	Threatening and killing of livestock	
Not enough opportunities for everyone		
No improvement of infrastructures		
Not enough markets for local products		

Appendix A3: Socio-demographic information obtained from the respondents from Nabugabo and Lewa. Totals for each category may not sum to N = 73 for Nabugabo and N = 50 for Lewa because respondents may have opted not to answer a particular question.

Age categories	**Nabugabo**	**Lewa**
18-30	18	3
31-40	18	12
41-50	17	14
51-60	10	11
61-70	7	5
Above 70	3	5
Self-identified gender		
Male	29	26
Female	44	24
Education		
None	6	5
Primary	50	31
Secondary	17	10
Cultivable land		
Less than 100 acres	16	2
100-500 acres	37	10
500-1000 acres	19	12
More than 1000 acres	0	26
Distance between households and cultivable land		
Adjacent	43	34
100-500 m	13	13
500-1000 m	12	2
More than 1000 m	4	1
Sources of income		
Single source	40	6
Multiple sources	33	44

Appendix A4: Model averaged parameter estimates for the top models for the outcomes: number of types of conflicts, severity of conflicts and frequency of conflicts. The table contains relative importance (∑), regression coefficient (b), unconditional standard error (SE), odds ratio (OR), and 95% confidence interval (CI) for b. Statistically significant predictors are in bold. The reference for gender is "Female", for education is "None", for the cultivable land is "Less than 100 acres", for distance is "Adjacent", and for sources of income is "Multiple" and for site is "Lewa".

Outcomes	**Predictors/levels**	∑	***b***	**SE**	**OR**	**95% CI for *b***
Number of types of conflicts	Age	0.27	0.01	0.01	1.01	-0.02 to 0.03
	Gender_Male	0.25	-0.20	0.22	0.82	-0.98 to 0.58
	Education_Primary	0.10	-0.33	0.23	0.72	-1.67 to 1.01
	Education_Secondary		-0.65	0.31	0.52	-2.20 to 0.91
	Cultivable land_100-500 acres	**1.00**	-0.19	0.58	0.83	-1.34 to 0.96
	Cultivable land_500-1000 acres		0.00	0.63	1.00	-1.24 to 1.24
	Cultivable land_More than 1000 acres		**3.48**	**1.02**	**32.45**	**1.46 to 5.49**
	Distance_100-500 m	0.35	-0.75	0.47	0.47	-1.78 to 0.28
	Distance_More than 500 m		-0.73	0.45	0.48	-1.70 to 0.24
	Sources of income_Single	0.29	0.31	0.26	1.37	-0.49 to 1.12
	Site_Nabugabo	0.41	-0.62	0.44	0.54	-1.61 to 0.37
Severity of conflicts	Age	0.23	0.00	0.01	1.00	-0.05 to 0.05
	Gender_Male	0.22	0.03	0.29	1.03	-1.19 to 1.25
	Education_Primary	**1.00**	-1.02	1.33	0.36	-3.65 to 1.61
	Education_Secondary		**-3.35**	**1.42**	**0.04**	**-6.17 to -0.52**
	Cultivable land_100-500 acres	1.00	-0.76	1.19	0.47	-3.13 to 1.60
	Cultivable land_500-1000 acres		0.66	1.42	1.93	-2.15 to 3.46
	Cultivable land_More than 1000 acres		2.47	1.49	11.83	-0.48 to 5.42
	Distance_100-500 m	0.08	0.18	0.27	1.20	-1.66 to 2.02
	Distance_More than 500 m		-0.59	0.34	0.55	-2.64 to 1.45
	Sources of income_Single	0.70	1.65	1.05	5.22	-0.08 to 3.39
	Site_Nabugabo	**1.00**	**4.02**	**0.85**	**55.62**	**2.34 to 5.70**
Frequency of conflicts	Age	0.23	0.00	0.01	1.00	-0.03 to 0.03
	Gender_Male	0.24	-0.17	0.22	0.84	0.67 to 0.84
	Education_Primary	0.25	-0.06	0.38	0.94	-1.58 to 1.45

	Education_Secondary		-0.85	0.56	0.43	-2.51 to 0.81
	Cultivable land_100-500 acres	0.20	-0.39	0.31	0.67	-1.57 to 0.78
	Cultivable land_500-1000 acres		-0.42	0.33	0.66	1.71 to 0.86
	Cultivable land_More than 1000 acres		1.57	0.84	4.79	-0.96 to 4.10
	Distance_100-500 m	0.15	0.68	0.33	1.97	-0.43 to 1.79
	Distance_More than 500 m		0.46	0.27	1.58	-0.63 to 1.54
	Sources of income_Single	0.25	0.26	0.25	1.29	-0.61 to 1.12
	Site_Nabugabo	**0.99**	**-1.66**	**0.57**	**0.19**	**-2.73 to -0.58**

APPENDIX B

Appendix B1: List of identified strongylid nematodes Amplicon Sequences Variants (ASVs), organisms found in studied hosts, isolation source, and NCBI Accession numbers.

Sequence ID	Organism	Host	Isolation source	Accession no.
ASV2a	*Oesophagostomum stephanostomum*	Dog	Feces	PQ785588
ASV2b	*Oesophagostomum stephanostomum*	Human	Latrine feces	PQ785589
ASV2c	*Oesophagostomum stephanostomum*	Goat	Feces	PQ785590
ASV2d	*Oesophagostomum stephanostomum*	Pig	Feces	PQ785591
ASV2e	*Oesophagostomum stephanostomum*	Vervet	Feces	PQ785592
ASV3a	*Murshidia* sp.	Dog	Feces	PQ785593
ASV3b	*Murshidia* sp.	Human	Latrine feces	PQ785594
ASV4a	*Strongyloidea* sp.	Dog	Feces	PQ785595
ASV4b	*Strongyloidea* sp.	Human	Latrine feces	PQ785596
ASV5a	*Murshidia* sp.	Dog	Feces	PQ785597
ASV5b	*Murshidia* sp.	Human	Latrine feces	PQ785598
ASV5c	*Murshidia* sp.	Goat	Feces	PQ785599
ASV6a	*Murshidia* sp.	Dog	Feces	PQ785600
ASV6b	*Murshidia* sp.	Human	Latrine feces	PQ785601
ASV7a	*Murshidia* sp.	Dog	Feces	PQ785602
ASV7b	*Murshidia* sp.	Human	Latrine feces	PQ785603
ASV8a	*Strongyloidea* sp.	Dog	Feces	PQ785604
ASV8b	*Strongyloidea* sp.	Human	Latrine feces	PQ785605
ASV10a	*Ancylostoma caninum*	Dog	Feces	PQ785606
ASV10b	*Ancylostoma caninum*	Cattle	Feces	PQ785607
ASV12a	*Ancylostoma duodenale*	Dog	Feces	PQ785608
ASV12b	*Ancylostoma duodenale*	Human	Latrine feces	PQ785609
ASV13	*Oesophagostomum bifurcum*	Vervet	Feces	PQ785610
ASV14	*Oesophagostomum quadrispinulatum*	Pig	Feces	PQ785611
ASV16a	*Murshidia* sp.	Dog	Feces	PQ785612
ASV16b	*Murshidia* sp.	Human	Latrine feces	PQ785613
ASV18a	*Hyostrongylus* sp.	Dog	Feces	PQ785614
ASV18b	*Hyostrongylus* sp.	Human	Latrine feces	PQ785615
ASV18c	*Hyostrongylus* sp.	Pig	Feces	PQ785616
ASV19a	*Oesophagostomum dentatum*	Dog	Feces	PQ785617
ASV19b	*Oesophagostomum dentatum*	Pig	Feces	PQ785618
ASV21	*Ancylostoma braziliense*	Dog	Feces	PQ785619
ASV22	*Oesophagostomum stephanostomum*	Vervet	Feces	PQ785620
ASV23a	*Hyostrongylus* sp.	Human	Latrine feces	PQ785621
ASV23b	*Hyostrongylus* sp.	Pig	Feces	PQ785622
ASV24	*Ancylostoma tubaeforme*	Dog	Feces	PQ785623
ASV25	*Ancylostoma caninum*	Dog	Feces	PQ785624
ASV27	*Trichostrongylus colubriformis*	Vervet	Feces	PQ785625

ASV28a	*Murshidia* sp.	Dog	Feces	PQ785626
ASV28b	*Murshidia* sp.	Human	Latrine feces	PQ785627
ASV29	*Ancylostoma braziliense*	Dog	Feces	PQ785628
ASV32	*Strongyloidea* sp.	Vervet	Feces	PQ785629
ASV33	*Trichostrongylus colubriformis*	Vervet	Feces	PQ785630
ASV34a	*Hyostrongylus* sp.	Dog	Feces	PQ785631
ASV34b	*Hyostrongylus* sp.	Human	Latrine feces	PQ785632
ASV34c	*Hyostrongylus* sp.	Pig	Feces	PQ785633
ASV36	*Ancylostoma caninum*	Dog	Feces	PQ785634
ASV40	*Oesophagostomum stephanostomum*	Vervet	Feces	PQ785635
ASV44a	*Murshidia* sp.	Dog	Feces	PQ785636
ASV44b	*Murshidia* sp.	Human	Latrine feces	PQ785637
ASV45	*Cooperia punctata*	Dog	Feces	PQ785638
ASV46	*Ancylostoma caninum*	Dog	Feces	PQ785639
ASV47	*Ancylostoma braziliense*	Dog	Feces	PQ785640
ASV50	*Trichostrongylus colubriformis*	Vervet	Feces	PQ785641
ASV51	*Murshidia* sp.	Human	Latrine feces	PQ785642
ASV60	*Ancylostoma duodenale*	Dog	Feces	PQ785643
ASV61a	*Murshidia* sp.	Dog	Feces	PQ785644
ASV61b	*Murshidia* sp.	Human	Latrine feces	PQ785645
ASV62	*Hyostrongylus* sp.	Pig	Feces	PQ785646
ASV64	*Haemonchus similis*	Cattle	Feces	PQ785647
ASV74	*Ancylostoma tubaeforme*	Dog	Feces	PQ785648
ASV75	*Ancylostoma duodenale*	Dog	Feces	PQ785649
ASV84	*Ancylostoma braziliense*	Dog	Feces	PQ785650
ASV85	*Haemonchus similis*	Cattle	Feces	PQ785651
ASV87	*Ancylostoma caninum*	Dog	Feces	PQ785652
ASV88	*Haemonchus similis*	Cattle	Feces	PQ785653
ASV90a	*Oesophagostomum dentatum*	Dog	Feces	PQ785654
ASV90b	*Oesophagostomum dentatum*	Pig	Feces	PQ785655
ASV100	*Ancylostoma duodenale*	Dog	Feces	PQ785656
ASV105	*Oesophagostomum bifurcum*	Cattle	Feces	PQ785657
ASV129a	*Murshidia* sp.	Dog	Feces	PQ785658
ASV129b	*Murshidia* sp.	Human	Latrine feces	PQ785659
ASV139	*Cooperia punctata*	Dog	Feces	PQ785660
ASV147	*Strongyloidea* sp.	Vervet	Feces	PQ785661
ASV150a	*Murshidia* sp.	Human	Latrine feces	PQ785662
ASV150b	*Murshidia* sp.	Human	Latrine feces	PQ785663
ASV166	*Hyostrongylus* sp.	Pig	Feces	PQ785664
ASV184	*Ancylostoma caninum*	Dog	Feces	PQ785665
ASV197	*Ancylostoma duodenale*	Dog	Feces	PQ785666
ASV204	*Cooperia* sp.	Dog	Feces	PQ785667
ASV207	*Ancylostoma* sp.	Dog	Feces	PQ785668
ASV214	*Ancylostoma* sp.	Dog	Feces	PQ785669
ASV236	*Hyostrongylus* sp.	Pig	Feces	PQ785670

ASV264	*Cooperia* sp.	Dog	Feces	PQ785671
ASV270	*Ancylostoma caninum*	Dog	Feces	PQ785672
ASV286	*Cooperia punctata*	Dog	Feces	PQ785673
ASV288	*Trichostrongylus axei*	Vervet	Feces	PQ785674
ASV289	*Strongyloidea* sp.	Vervet	Feces	PQ785675
ASV326	*Ancylostoma* sp.	Dog	Feces	PQ785676
ASV345	*Ancylostoma* sp.	Dog	Feces	PQ785677
ASV352	*Strongyloidea* sp.	Vervet	Feces	PQ785678
ASV395	*Ancylostoma tubaeforme*	Dog	Feces	PQ785679
ASV411	*Ancylostoma braziliense*	Dog	Feces	PQ785680
ASV437	*Oesophagostomum* sp.	Vervet	Feces	PQ785681
ASV521	*Ancylostoma caninum*	Dog	Feces	PQ785682
ASV589	*Ancylostoma braziliense*	Dog	Feces	PQ785683
ASV794	*Haemonchus similis*	Cattle	Feces	PQ785684
ASV905	*Haemonchus similis*	Cattle	Feces	PQ785685
ASV931	*Ancylostoma braziliense*	Dog	Feces	PQ785686
ASV937	*Hyostrongylus* sp.	Pig	Feces	PQ785687
ASV947	*Ancylostoma caninum*	Dog	Feces	PQ785688
ASV953	*Haemonchus similis*	Cattle	Feces	PQ785689
ASV985	*Haemonchus similis*	Cattle	Feces	PQ785690
ASV1012	*Ancylostoma* sp.	Dog	Feces	PQ785691
ASV1085	*Ancylostoma duodenale*	Dog	Feces	PQ785692
ASV1137	*Ancylostoma* sp.	Dog	Feces	PQ785693
ASV1142	*Ancylostoma caninum*	Dog	Feces	PQ785694
ASV1150	*Ancylostoma caninum*	Dog	Feces	PQ785695
ASV1161	*Ancylostoma braziliense*	Dog	Feces	PQ785696
ASV1176	*Ancylostoma duodenale*	Dog	Feces	PQ785697
ASV1220	*Ancylostoma* sp.	Dog	Feces	PQ785698
ASV1242	*Ancylostoma* sp.	Dog	Feces	PQ785699
ASV1255	*Ancylostoma braziliense*	Dog	Feces	PQ785700
ASV1300	*Ancylostoma duodenale*	Dog	Feces	PQ785701
ASV1315	*Ancylostoma braziliense*	Dog	Feces	PQ785702
ASV1323	*Ancylostoma* sp.	Dog	Feces	PQ785703
ASV1360	*Haemonchus similis*	Cattle	Feces	PQ785704
ASV1471	*Strongyloidea* sp.	Human	Latrine feces	PQ785705
ASV1563	*Ancylostoma* sp.	Dog	Feces	PQ785706
ASV1616	*Ancylostoma caninum*	Dog	Feces	PQ785707
ASV1653	*Ancylostoma braziliense*	Dog	Feces	PQ785708
ASV1731	*Strongyloidea* sp.	Vervet	Feces	PQ785709
ASV1756	*Haemonchus similis*	Cattle	Feces	PQ785710
ASV1815	*Oesophagostomum dentatum*	Pig	Feces	PQ785711
ASV1872	*Ancylostoma* sp.	Dog	Feces	PQ785712
ASV1911	*Ancylostoma* sp.	Dog	Feces	PQ785713
ASV1970	*Ancylostoma* sp.	Dog	Feces	PQ785714
ASV2038	*Hyostrongylus* sp.	Pig	Feces	PQ785715

ASV2060	*Ancylostoma braziliense*	Dog	Feces	PQ785716
ASV2147	*Ancylostoma* sp.	Dog	Feces	PQ785717
ASV2153	*Ancylostoma* sp.	Dog	Feces	PQ785718
ASV2159	*Ancylostoma* sp.	Dog	Feces	PQ785719
ASV2210	*Ancylostoma* sp.	Dog	Feces	PQ785720
ASV2257	*Ancylostoma caninum*	Dog	Feces	PQ785721
ASV2327	*Oesophagostomum quadrispinulatum*	Pig	Feces	PQ785722
ASV2381	*Hyostrongylus* sp.	Pig	Feces	PQ785723
ASV2422	*Hyostrongylus* sp.	Pig	Feces	PQ785724
ASV2445	*Ancylostoma duodenale*	Dog	Feces	PQ785725
ASV2607	*Ancylostoma caninum*	Dog	Feces	PQ785726
ASV2640	*Ancylostoma* sp.	Dog	Feces	PQ785727
ASV2761	*Ancylostoma* sp.	Dog	Feces	PQ785728
ASV2863	*Ancylostoma* sp.	Dog	Feces	PQ785729
ASV3057	*Ancylostoma caninum*	Dog	Feces	PQ785730
ASV3104	*Oesophagostomum stephanostomum*	Dog	Feces	PQ785731
ASV3260	*Haemonchus similis*	Cattle	Feces	PQ785732
ASV3365	*Ancylostoma* sp.	Dog	Feces	PQ785733
ASV3369	*Hyostrongylus* sp.	Pig	Feces	PQ785734
ASV3526	*Haemonchus similis*	Cattle	Feces	PQ785735
ASV3590	*Hyostrongylus* sp.	Pig	Feces	PQ785736
ASV3783	*Ancylostoma caninum*	Dog	Feces	PQ785737
ASV3785	*Haemonchus similis*	Cattle	Feces	PQ785738
ASV3866	*Ancylostoma caninum*	Dog	Feces	PQ785739
ASV3906	*Ancylostoma duodenale*	Dog	Feces	PQ785740
ASV3959	*Ancylostoma* sp.	Dog	Feces	PQ785741
ASV3982	*Ancylostoma braziliense*	Dog	Feces	PQ785742
ASV4150	*Ancylostoma* sp.	Dog	Feces	PQ785743
ASV4234	*Oesophagostomum dentatum*	Pig	Feces	PQ785744
ASV4278	*Strongyloidea* sp.	Vervet	Feces	PQ785745
ASV4579	*Ancylostoma caninum*	Dog	Feces	PQ785746
ASV4757	*Ancylostoma* sp.	Dog	Feces	PQ785747
ASV4848	*Ancylostoma duodenale*	Dog	Feces	PQ785748
ASV4872	*Haemonchus similis*	Cattle	Feces	PQ785749
ASV4966	*Haemonchus similis*	Cattle	Feces	PQ785750
ASV5270	*Ancylostoma caninum*	Dog	Feces	PQ785751
ASV5301	*Ancylostoma caninum*	Dog	Feces	PQ785752
ASV5712	*Ancylostoma* sp.	Dog	Feces	PQ785753
ASV5770	*Ancylostoma* sp.	Dog	Feces	PQ785754
ASV6003	*Ancylostoma* sp.	Dog	Feces	PQ785755
ASV6138	*Ancylostoma* sp.	Dog	Feces	PQ785756
ASV6144	*Ancylostoma* sp.	Dog	Feces	PQ785757
ASV6565	*Ancylostoma* sp.	Dog	Feces	PQ785758
ASV6583	*Haemonchus similis*	Cattle	Feces	PQ785759
ASV7013	*Ancylostoma braziliense*	Dog	Feces	PQ785760

ASV7023	*Haemonchus similis*	Cattle	Feces	PQ785761
ASV7138	*Ancylostoma duodenale*	Dog	Feces	PQ785762
ASV7357	*Ancylostoma duodenale*	Dog	Feces	PQ785763
ASV8250	*Ancylostoma* sp.	Dog	Feces	PQ785764
ASV8748	*Haemonchus similis*	Cattle	Feces	PQ785765
ASV8983	*Ancylostoma* sp.	Dog	Feces	PQ785766
ASV9032	*Haemonchus similis*	Cattle	Feces	PQ785767
ASV9351	*Ancylostoma* sp.	Dog	Feces	PQ785768

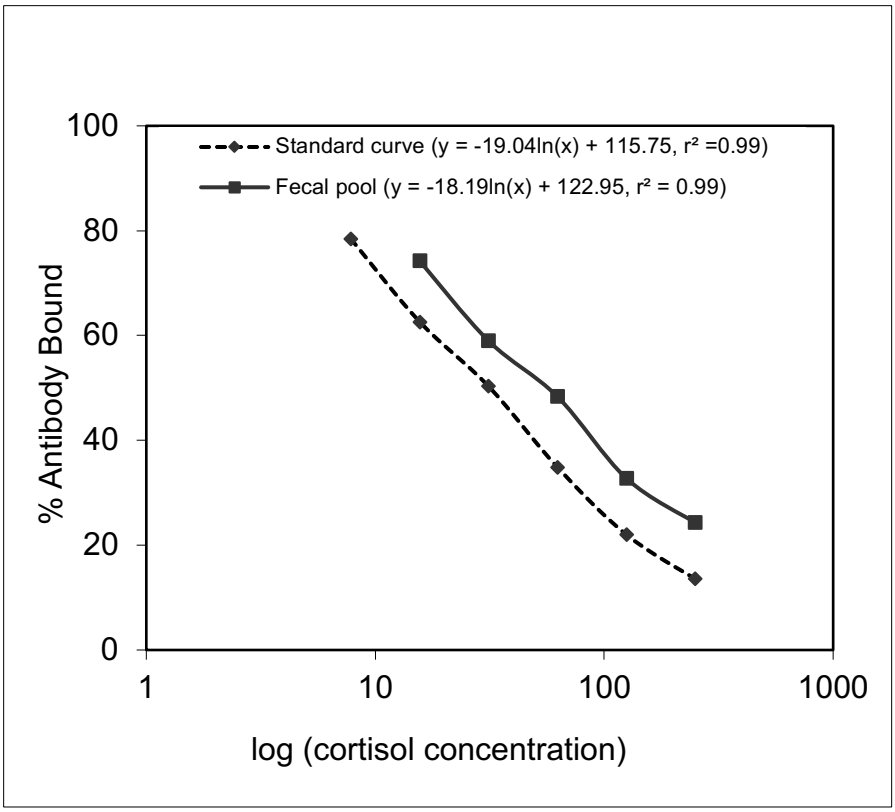
Appendix B2: List of identified *Strongyloides*, *Cryptosporidium, Giardia*, and Microsporidia spp. found in studied hosts, isolation source, and NCBI Accession numbers.

Sequence ID	**Organism**	**Host**	**Isolation source**	**Accession no.**
D22	*Strongyloides stercoralis*	Dog	Feces	PQ786134
P8	*Strongyloides ransomi*	Pig	Feces	PQ786135
VT7	*Strongyloides fuelleborni*	Vervet	Feces	PQ786131
VT44	*Strongyloides fuelleborni*	Vervet	Feces	PQ786133
VT68	*Strongyloides fuelleborni*	Vervet	Feces	PQ786132
G2	*Cryptosporidium ubiquitum*	Goat	Feces	PQ786274
P4	*Cryptosporidium scrofarum*	Pig	Feces	PQ786275
C2	*Cryptosporidium andersoni*	Cow	Feces	PQ786276
D4	*Cryptosporidium andersoni*	Dog	Feces	PQ786277
D17	*Cryptosporidium canis*	Dog	Feces	PQ786278
VT8	*Giardia intestinalis*	Vervet	Feces	PQ789835
D8	*Giardia intestinalis*	Dog	Feces	PQ789836
H11	*Giardia intestinalis*	Human	Latrine feces	PQ789837
H12	*Enterocytozoon bieneusi*	Human	Latrine feces	PQ791792
H18	*Enterocytozoon bieneusi*	Human	Latrine feces	PQ791793
VT61	*Microsporidia* sp.	Vervet	Feces	PQ791794

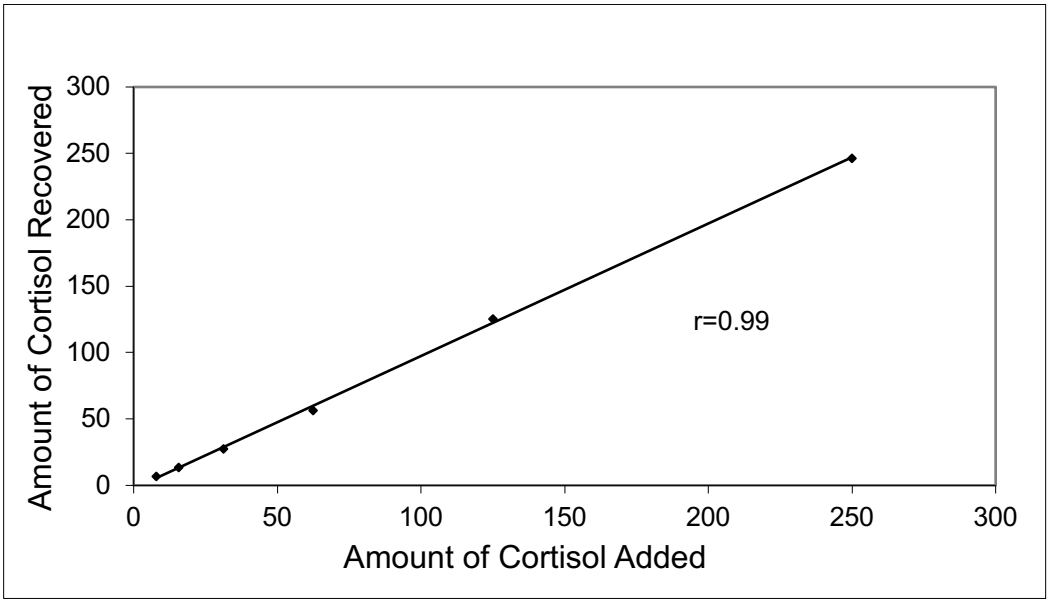
APPENDIX C

Appendix C1: Percentage of scans spent in each category of behaviours by males, females, and females with infants of vervet monkeys at Lake Nabugabo, Uganda, from June-December 2014 and 2015. *AFI = Adult female with infant.

Year	Phase	Sex	No. of scans	Total no. of scans	Moving	Feeding	Grooming	Resting
2014	Pre-deworming (June)	Male	293	1178	20%	36%	6%	20%
		Female	791					
		AFI*	94					
2014	Post-deworming (July)	Male	335	1431	22%	32%	6%	20%
		Female	880					
		AFI*	216					
2014	Early reinfection (Aug.)	Male	125	535	16%	31%	8%	24%
		Female	321					
		AFI*	89					
2014	Late reinfection (Sept. - Dec.)	Male	183	692	18%	33%	14%	16%
		Female	883					
		AFI*	458					
2015	June	Male	220	854	19%	30%	13%	15%
		Female	466					
		AFI*	168					
2015	July	Male	252	852	18%	33%	12%	14%
		Female	438					
		AFI*	162					
2015	Aug.	Male	219	692	18%	33%	14%	16%
		Female	345					
		AFI*	128					
2015	Sept. - Dec.	Male	1017	2932	16%	35%	13%	15%
		Female	1439					
		AFI*	476					



Appendix C2. Vervet monkey (*Chlorocebus pygerythrus*) fecal cortisol parallelism (t=0.69, p=0.51, df=7).

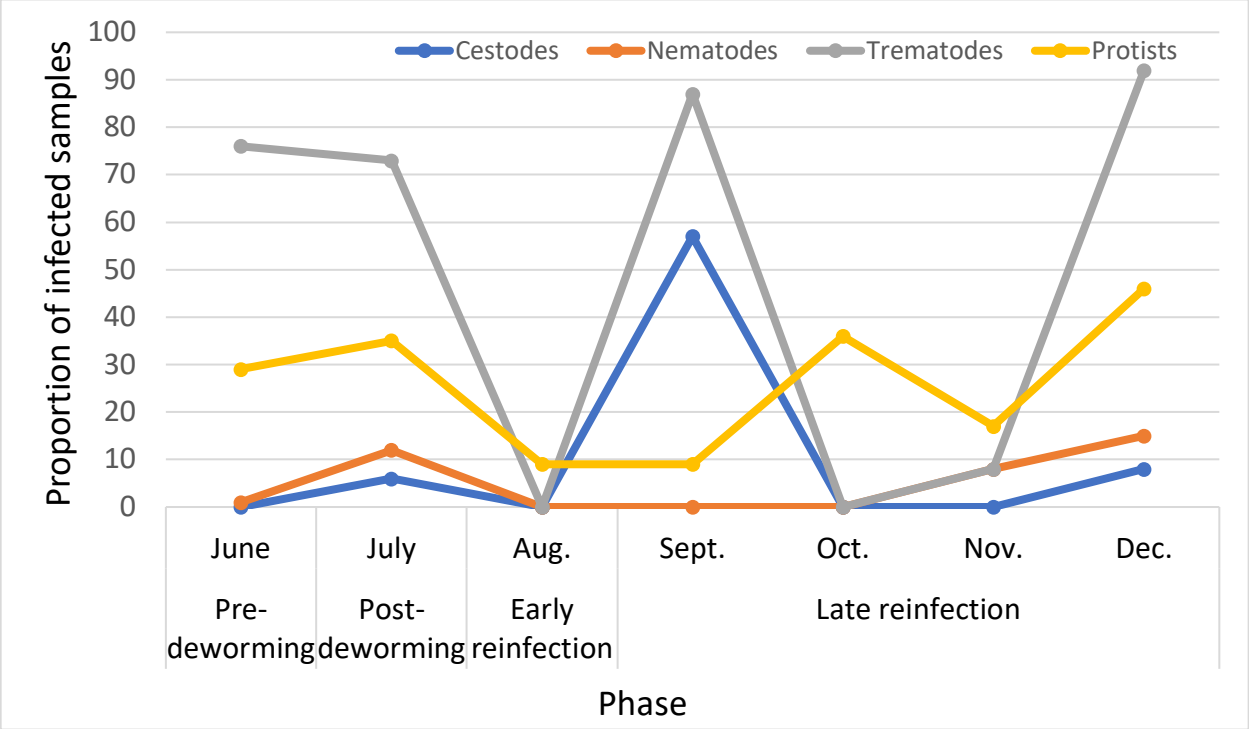


Appendix C3: Vervet monkey (*Chlorocebus pygerythrus*) fecal recovery of standard hormone added to a pooled fecal extract and the amount of cortisol recovered was correlated with the amount added.

Appendix C4: Parasite taxa, number of parasites found, and prevalence of parasite. Summary of parasite taxa, and their prevalence from 19 adult vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda from June-December 2014. Prevalence is calculated as the number of individuals infected with a given parasite taxon, divided by the total number of individuals sampled.

Parasites	Taxon	No. positive samples (individuals)	Prevalence	Route of transmission
Trematodes	*Schistosoma* spp.	1(1)	5.3%	Direct contact[1]
	Trematode (unidentified)	125(17)	89.5%	-
Cestodes	Cestode (unidentified)	17 (13)	68.4%	-
Nematodes	*Ascaris* spp.	1 (1)	5.3%	Feco-oral route[2]
	Strongyloides spp.	5 (5)	26.3%	Soil[3]
	Strongyle	2 (2)	10.5%	Soil[4]
	Trichostrongylus spp.	2 (2)	10.5%	Feco-oral route[5]
	Trichuris spp.	2 (2)	10.5%	Oral route[5]
Protists	*Amoeba* spp.	5 (5)	26.3%	-
	Coccidian oocysts	16 (10)	52.6%	-
	Cryptosporidium spp.	2 (2)	10.5%	Feco-oral route and direct contact[6]
	Entamoeba coli	13 (8)	42.1%	Oral route[5]
	Entamoeba hartmanni	1 (1)	5.3%	Oral route[5]
	Entamoeba histolytica	5 (5)	26.3%	Oral route[5]
	Giardia spp.	1 (1)	5.3%	Feco-oral route[7]
	Iodamoeba spp.	16 (7)	36.8%	Feco-oral route[8]
	Unidentified	3 (3)	15.8%	-

[1] Corachan. 2002. Schistosomiasis and International Travel. *Clin Infect Dis* 35: 446-50. [2] Asaolu & Ofoezie. 2019. Ascaris spp. In: Water and Sanitation for the 21st Century: Health and Microbiological Aspects of Excreta and Wastewater Management (Global Water Pathogen Project). Michigan State University. [3] Hasegawa et al. 2016. Strongyloides infections of humans and great apes in Dzanga-Sangha Protected Areas, Central African Republic and in degraded forest fragments in Bulindi, Uganda. *Parasitol Int* 65:367–70. [4] Ghai et al. 2014. Nodule Worm Infection in Humans and Wild Primates in Uganda: Cryptic Species in a Newly Identified Region of Human Transmission. *PLoS Negl Trop Dis* 8:39. [5] Boundenga et al. 2018. Diversity and prevalence of gastrointestinal parasites in two wild Galago species in Gabon. *Infect Genet Evol*. 63:249–56. [6] Feng et al. 2018 Genetic Diversity and Population Structure of Cryptosporidium. *Trends in Parasitol* 38: 997–1011. [7] Kramer et al. 2009 Treatment of Giardiasis in Common Marmosets (*Callithrix jacchus*) with Tinidazole. *Comp Med* 59:174–9. [8] Issa RM. 2014 Non-pathogenic protozoa. *Int J Pharm Pharm Sci 6* (suppl 40):30-40.



Appendix C5: Proportion of fecal samples infected with parasites**.** Proportion of vervet monkey fecal samples infected with different parasite taxa (trematodes, cestodes, nematodes, & protists) during each study phase at Lake Nabugabo, Uganda, from June – December 2014

Appendix C6: Parasite and fecal glucocorticoid metabolites (fGC) data. Summary of parasite data and number of samples assayed for fGC from fecal samples collected from 19 adults in one group of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda between June-December 2014. *AFI = Adult female with infant

Phase	**Month**	**Sex**	**No. of individuals**	**% infected individuals**	**No. of samples**	**No. of positive samples**	**% positive samples**		**No. of samples assayed for fGC**
Pre-deworming	June	Male	6	100%	29	23	79%	80.55%	22
		Female	10	100%	37	29	78%		37
		AFI*	1	100%	6	6	100%		6
Post-deworming	July	Male	4	100%	11	10	91%	88.23%	7
		Female	10	100%	31	27	87%		23
		AFI*	2	100%	9	8	89%		7
Early reinfection	August	Male	5	20%	10	1	10%	9.38%	6
		Female	10	10%	19	2	11%		16
		AFI*	2	0%	3	0	0%		2
Late reinfection	September	Male	3	100%	5	5	100%	100%	2
		Female	8	100%	14	14	100%		14
		AFI*	2	100%	4	4	100%		2
	October	Male	2	100%	3	2	67%	45.45%	2
		Female	9	33%	13	4	31%		10
		AFI*	3	100%	6	4	67%		3
	November	Male	3	0%	3	0	0%	25%	2
		Female	6	50%	6	3	50%		5
		AFI*	3	0%	3	0	0%		3
	December	Male	2	100%	2	2	100%	92.31%	1
		Female	4	75%	4	3	75%		4
		AFI*	7	100%	7	7	100%		6
	Total				**225**	**154**			**180**

Appendix C7: Model averaged parameter estimates for the top models for mean fecal glucocorticoid metabolites (fGC) outcome. The table shows relative importance (∑), regression coefficient (b), unconditional standard error (SE), and 95% confidence interval (CI) for b. Statistically significant predictors are in bold.

Outcome	**Predictors/Levels**	∑	***b***	**SE**	**95% CI for *b***
fGC	Phase_Pre-deworming	1.00	-1.71	3.33	-8.28 to 4.86
	Phase_Early reinfection		**13.07**	**3.67**	**5.83 to 20.30**
	Phase_Late reinfection		**19.74**	**2.47**	**14.86 to 24.61**
	Lagged MPSR	0.90	2.58	1.64	-0.67 to 5.82
	Sex_Male	0.86	-1.23	2.17	-5.52 to 3.05
	Sex_AFI		0.98	2.19	-3.36 to 5.32

Appendix C8: Model averaged parameter estimates for the top models for behavioral outcomes. The table contains relative importance (∑), regression coefficient (b), Unconditional standard error (SE) and 95% confidence interval (CI) for b. Statistically significant predictors are in bold.

Outcomes	**Predictors/levels**	∑	***b***	**SE**	**95% CI for *b***
Proportion of moving scans	Phase_Pre-deworming	1.00	0.04	0.16	-0.28 to 0.37
	Phase_Early reinfection		-0.21	0.19	-0.58 to 0.17
	Phase_Late reinfection		**-0.34**	**0.13**	**-0.58 to -0.08**
	MPSR	0.79	-0.10	0.07	-0.24 to 0.04
	Mean fGC	0.34	0.02	0.04	-0.06 to 0.10
	Sex_Male	0.32	0.02	0.09	-0.15 to 0.20
	Sex_AFI		-0.07	0.12	-0.31 to 0.17
Proportion of feeding scans	Phase_Pre-deworming	0.63	0.09	0.10	-0.11 to 0.28
	Phase_Early reinfection		-0.01	0.09	-0.21 to 0.18
	Phase_Late reinfection		-0.09	0.11	-0.31 to 0.11
	MPSR	0.30	0.01	0.02	-0.05 to 0.06
	Mean fGC	0.64	-0.06	0.06	-0.17 to 0.06
	Sex_Male	1.00	-0.15	0.08	-0.31 to 0.02
	Sex_AFI		**-0.38**	**0.091**	**-0.56 to -0.18**
Proportion of grooming scans	Phase_Pre-deworming	1.00	-0.02	0.20	-0.42 to 0.38
	Phase_Early reinfection		0.28	0.23	-0.17 to 0.73
	Phase_Late reinfection		**1.39**	**0.15**	**1.11 to 1.69**
	MPSR	0.40	0.03	0.05	-0.08 to 0.15
	Mean fGC	0.25	0.01	0.03	-0.05 to 0.06
	Sex_Male	1.00	**-2.44**	**0.34**	**-3.13 to -1.75**
	Sex_AFI		-0.08	0.13	-0.35 to 0.18
Proportion of resting scans	Phase_Pre-deworming	1.00	-0.08	0.14	-0.35 to 0.19
	Phase_Early reinfection		0.17	0.16	-0.14 to 0.48
	Phase_Late reinfection		**-0.71**	**0.13**	**-0.96 to -0.45**
	MPSR	0.37	0.03	0.05	-0.07 to 0.12
	Mean fGC	0.36	-0.03	0.05	-0.13 to 0.08
	Sex_Male	0.17	0.03	0.09	-0.15 to 0.21

	Sex_AFI		0.01	0.06	-0.11 to 0.14

Appendix C9: Results of ANOVA following generalized linear models (GLMs) for the behavioural outcome variables across months during the non-experimental year (2015) in vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda. Predictors include month (June – December), and sex. The outcome variables include proportion of moving, feeding, grooming, and resting scans.

Outcomes	**Predictors**	**Chisq**	**df**	**p-value**
Proportion of moving scans	Month	7.28	3	0.06
	Sex	3.57	2	0.18
Proportion of feeding scans	Month	6.95	3	0.07
	Sex	1.09	2	0.58
Proportion of grooming scans	Month	3.46	3	0.34
	Sex	188.36	2	<0.05*
Proportion of resting scans	Month	0.97	3	0.81
	Sex	2.59	2	0.27