

THE INFLUENCE OF MICROHABITAT CHARACTERISTICS ON HABITAT USE
AND BEHAVIOUR OF VERVET MONKEYS (*CHLOROCEBUS PYGERYTHRUS*) IN
A HUMAN-MODIFIED LANDSCAPE

MELISSA MARTINS

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Abstract

As human encroachment on wildlife habitat continues, it is imperative to understand the spatial habitat requirements of species living within modified environments. One species that lives in human-modified environments is the vervet monkey (*Chlorocebus pygerythrus*). The aim of this study was to investigate what features of the microhabitat impact vervet monkey habitat and behavioural use in a human-modified environment. I used a five-year data set (2016-2020) that followed a standardized 15-minute scan sampling protocol collecting behavioural and location data on three groups of vervet monkeys at Lake Nabugabo, Uganda. The results showed habitat use, feeding, resting, and social grooming exhibited a weak relationship with areas close to buildings, kitchens, and the forest edge, but far from crops, roads, and paths. These findings suggest interesting links among behaviour, space use, perceived risks and benefits. This research highlights the trade-offs associated with landscape use by vervets within human encroachment constraints.

Keywords

Primates, microhabitat variables, human-modified landscape, habitat use, behavioural use, GPS, NDVI

Dedications

This work is dedicated to the best study partner, Frank (my cat), who without his constant presence, cuddles, and support, I would not have had the motivation to continue working through Covid-19. I also want to thank the people in my life (you know who you are) whose constant voice of support and acknowledgment got me through the hardest parts of this program, when my own voice wanted to give up. Lastly, I want to dedicate this work to myself. I am incredibly proud of my perseverance and adaptability. Although this program did not play out how I had imagined, I am impressed by my final thesis and the work that went into getting here.

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1 | Introduction

How an animal uses its environment is an integral aspect of animal ecology. Studying habitat use provides insight into species' basic ecological needs, which can be used to create successful conservation plans. Two ecological needs that animals must take into consideration when choosing and using a habitat are: resource acquisition (e.g., food availability; Cowlshaw 1997; Fortin and Fortin 2009; Hebblewhite and Merrill 2009; Willems and Hill 2009; Chapman et al. 2012; Teichroeb and Sicotte 2012; Adams and Teichroeb 2020) and safety (e.g., predator avoidance; Cowlshaw 1997; Enstam and Isbell 2004; Thomson et al. 2006; Fortin and Fortin 2009; Hebblewhite and Merrill 2009; Willems and Hill 2009; Teichroeb and Sicotte 2012; Campos and Fedigan 2014; Coleman and Hill 2014; Adams and Teichroeb 2020). Generally speaking, animals who eat the most nutritious foods have higher overall fitness (Chapman et al. 2012), whereas predation pressure generally has direct costs in the form of mortality and/or indirect costs to individual fitness from using behaviours to reduce mortality risk (Coleman and Hill 2014). Thus, while food availability is an important choice in determining habitat use (Langvatn and Hanley 2013), a trade-off can exist between predation risk and food acquisition (Cowlshaw 1997; Ferguson et al. 1988; Fortin and Fortin 2009). This trade-off can be so influential that prey species feed in sub-optimal foraging habitats to reduce predation risk (i.e., minimize costs and benefits) or feed in optimal foraging habitat despite high predation risk (i.e., maximize costs and benefits; Cowlshaw 1997).

The need to balance foraging costs and benefits is an integral part of optimal foraging theory (MacArthur and Pianka 1966), which states that natural selection favours animals whose behavioural strategies maximize their net caloric energy intake per unit time spent foraging. Optimal foraging theory predicts that an animal must balance the costs and benefits of different

foraging opportunities, ideally by maximizing the benefits while minimizing the costs (MacArthur and Pianka 1966). However, optimal foraging theory can be negatively impacted by factors such as predation risk or competition for resources, that may force some animals to opt for an energy maximizing strategy, while others opt for a time minimizing strategy (MacArthur and Pianka 1966; Pyke et al. 1977). Ideally, an individual would want to consume the highest value food resource in the least amount of time and under the least amount of predation pressure or competition.

Animals may rely on the physical features of their environment to make decisions about food resources and safety in habitat selection. With an increase in human encroachment on natural habitats from urbanization and industrialization, many animals must now consider human disturbance as a feature of their habitat. Land-use changes and resulting human encroachment of animal-habitat have led to an increasing number of species inhabiting human-modified landscapes, which often consist of a mosaic of natural and anthropic land cover (Galán-Acedo et al. 2019). This encroachment on animals' native habitats is often associated with increased human population, small and large-scale agriculture, and logging (Galán-Acedo et al. 2019). While populations of species with short generation times may be able to quickly adapt to such environmental changes, long-lived animals with slow generation times may experience population declines if they lack sufficient behavioural flexibility to cope with human-induced habitat loss, degradation, and fragmentation (Johns and Skorupa 1987; Weisenseel et al. 1993; Cowlshaw 1999; Schwitzer et al. 2011). As the human population and thus human encroachment continues to grow, it is important that the ability of animals to successfully co-inhabit these human-modified environments is studied. This will contribute to a further understanding of how anthropogenic change impacts animal habitat selection.

Certain species are well-adapted to using habitats in or around human-modified environments because they have life-history traits that enable them to adjust to human-induced stressors and/or they have the ability to modify their behaviours (Ditchkoff et al. 2006). Among primates, six key ecological traits have been found to be associated with adaptability: a diet not dominated by fruit (with dietary flexibility), use of multiple vegetation types, semi-terrestrial locomotion, frequent use of cheek pouches, large and variable home ranges, and variable group size (Albert et al. 2014). One primate that has all these traits is the vervet monkey (*Chlorocebus pygerythrus*), and perhaps not surprisingly, it has been recorded living successfully in human-modified environments (Chapman et al. 2016; Thatcher et al. 2020). Vervet monkeys are found within the forests, savannas, and shrublands of the southeastern region of Africa, ranging between Ethiopia and South Africa, including the countries of Botswana, Burundi, Eswatini, Kenya, Malawi, Mozambique, Rwanda, Somalia, Tanzania, Uganda, Zambia, and Zimbabwe (Butynski and de Jong 2019). They are semi-terrestrial/semi-arboreal cercopithecines that have an omnivorous diet composed largely of fruit (50% ripe, and 17.9% unripe; Chapman et al. 2016), but also feed on flowers, leaves, and insects (Struhsaker 1967; Melnick 1987; Ditchkoff et al. 2006). Even though a large component of their diet is fruit, vervets have a dietary flexibility that allows them to adapt their diet according to resource availability (Albert et al. 2014). Their generalist diet and high degree of terrestriality facilitate access to anthropogenic food resources via crop foraging, “stealing” (foraging on human foods that are not in/on crop land), or provisioning (public food handouts). While beneficial to vervets, crop foraging and “stealing” are not desirable from a human perspective and can often lead to human-monkey conflict. Such conflict is often associated with chasing, scaring, rock throwing or placing snares, traps, or poison bait from humans or chasing, scaring, barking, or biting by dogs (Naughton-Treves 1998;

Chapman et al. 2016; Thatcher et al. 2019b). Although the IUCN classifies vervets as Least Concern, their global population trend is decreasing, and they are at a risk of local extinction (Butynski and de Jong 2019). The main threats to the species are human-caused habitat degradation, fragmentation, and destruction, combined with human-monkey conflict (Butynski and de Jong 2019). The combination of being perceived by humans as “pests” and human encroachment on their habitat may ultimately cause a great risk to long-term species survival. Thus, it is critical to understand vervet habitat use in human-modified environments. In this thesis, I examined the habitat attributes of a human-modified landscape in Uganda to better understand what characteristics predict the habitat selection and behaviour of a long-lived mammal, the vervet monkey.

Habitat selection can be examined at different scales. Characteristics of the macrohabitat are present at broad spatial scales, and include characteristics such as the different types of landscapes within a larger geographic region (e.g., old-growth forest, human settlements, water bodies, or clear-cut forest; Block and Brennan 1993; Michalski and Peres 2005). At finer spatial scales, microhabitat characteristics may include how a patch of land is composed of different tree species, levels of forest canopy coverage, or patch distance to the nearest town or forest edge (Block and Brennan 1993; Michalski and Peres 2005; Herrera et al. 2011; Akers et al. 2013; Farris et al. 2014; Patterson et al. 2018; Sodik et al. 2019; Thatcher et al. 2019a). Macrohabitat characteristics are often used to predict the distribution and abundance of populations and species as a whole, while microhabitat characteristics are finer-scale environmental features that can be used as predictive cues for behavioural responses of social groups or individual animals (Block and Brennan 1993).

My research focused on the microhabitat characteristics that influence habitat use and behaviour, including potential trade-offs between food availability and safety as hypothesized by optimal foraging theory. The variables I have chosen for this study can be loosely categorized by their benefits, costs, and potential trade-offs, and include: 1) distance to water, 2) within forest cover (yes/no), 3) Normalized Difference Vegetation Index (NDVI), 4) distance to nearest buildings (kitchens, accommodations, and other buildings), 5) distance to nearest crop, 6) distance to the nearest forest edge, and 7) distance to nearest road or path.

Generally speaking, animals will benefit from using habitats that are in close proximity to important resources. Water is a necessary resource for all living organisms. Some animals may access water by drinking infrequently but opportunistically from waterholes, streams, and rain puddles; in urban habitats, Chacma baboons (*Papio ursinus*) have even been observed drinking from swimming pools instead of using a known waterhole (Hoffman and O’Riain 2011). In contrast, some animals seem to require drinking daily, like the savannah-woodland living vervets in the Segera Range, Kenya, where all known vervet groups have access to a river within their home range (Isbell et al. 2004). Other species like black howler monkeys (*Alouatta pigra*) obtain most of their water requirements from the consumption of water-rich foods like new leaves and fruit (Dias et al. 2014). However, individuals spent more time drinking from water sources in habitats with higher maximum temperatures and periods with high consumption of low water-content foods such as mature leaves (Dias et al. 2014).

Habitat attributes like forest canopy coverage provide benefits to animals in the form of both food availability and safety. Increased forest canopy coverage may be positively associated with food abundance, since leafless trees have less vegetation and are thus less likely to produce fruits (Kim and Riondato 2016). Positive relationships have been detected between the amount of

leaves in the canopy and fruit production (McCarthy and Quinn 1992; Strum 2010). Ideally, an animal would thus choose to use a habitat within the forest coverage due to the potential of natural food resources, assuming it is a relatively safe environment free of immediate threats (Sodik et al. 2019). Forest canopy coverage can also provide camouflage from predators and protection from the weather elements including sun, rain, wind, or storms (Herrera et al. 2011; Sousa et al. 2014). High temperatures and intense sunlight can cause an individual to prioritize resting in the shade of the forest canopy over feeding or active movements like playing (McFarland et al. 2014). At Nabugabo specifically, this may be contributing to the reason the vervets don't need to drink a lot of water. Bolen and Robinson (2003) state that food and shelter/cover are two basic and essential habitat requirements. The tree canopy provides and fulfills these two habitat elements; food providing nutrients and energy, while simultaneously providing shelter and protection from extreme weather and predators (Bolen and Robinson 2003). Vervet monkeys in South Africa (Patterson et al. 2018), javan slow lorises (*Nycticebus javanicus*; Sodik et al. 2019), and Geoffroy's tamarins (*Saguinus geoffroyi*; Kim and Riondato 2016) all use areas with higher forest canopy coverage because it provides camouflage from predators, increased food abundance, and protection from extreme weather. Herrera et al. (2011) encountered three species of lemurs more frequently in areas with 1) greater forest canopy coverage likely associated with increased camouflage from aerial predators, and 2) low understory cover, which the authors attributed to greater understory visibility that allows the lemurs to monitor their surroundings for terrestrial predators (Herrera et al. 2011). These examples showcase the positive interaction between food in high canopy coverage areas and increased safety.

Vegetation biomass or plant productivity is an essential variable for predicting habitat use and potential foraging opportunities (Pettorelli et al. 2011). One method to remotely measure primary plant productivity of an area is by calculating the NDVI, which can be quantified from high spatial resolution satellite imagery (Rouse et al. 1973; Tucker 1979). NDVI has been used to study the home range patterns of vervet monkeys at the Lajuma Research Centre in the western part of the Soutpansberg Mountain range, South Africa (Willems et al. 2009). The results showed that monthly NDVI values positively correlated to leaf cover and food availability. The authors found that range use could be expressed in terms of NDVI, where NDVI signifies a behavioural response to food availability. Time spent on the ground increased with group size but decreased linearly with monthly NDVI, indicating that predation risk tolerance changes in response to leaf cover and thus visibility within the habitat (Willems et al. 2009).

An important food source for animals living in human-modified landscapes may be anthropogenic foods. While the benefits of these may be high, due to their clustering and potentially nutritious foods found in buildings and croplands, accessing such foods may be risky (potential human-monkey conflict). Anthropogenic food proxies included in this study are distance to nearest buildings and crops. Omnivorous species like baboons and vervet monkeys have adjusted to living near tourist-lodges and buildings with kitchens because they get access to additional food resources via public food handouts, “stealing”, or garbage dump foraging (Brennan et al. 1985; Strum 2010; Chapman et al. 2016). Although proximity to buildings like kitchens or tourist accommodations are good opportunities for additional feeding sources, they can also pose a risk due to the potential of human-wildlife conflict. When comparing buildings like tourist accommodations to buildings owned by local people, a difference may be seen in

monkeys perceived risk and thus the use of habitat close to these buildings. Locals (often farmers) in Kenya (Brennan et al. 1985; Wallace and Hill 2012), St. Kitts (Dore et al. 2018), Cameroon (Kavanagh 1980), and Uganda (Saj et al. 2001) have reportedly perceived vervets as pests mainly due to crop foraging and stealing (Else 1991). The vervets may have learned that the humans near these locations have a negative perception of them that results in a greater risk to steal or forage near their houses. Whereas near tourist accommodations, the perceived risk may be less due to the tourist perception of vervets. Tourists are more likely to see vervets as exciting and thus may be more likely to give food handouts or to not react as negatively to stealing (Brennan et al. 1985; Chapman et al. 2016; Thatcher et al. 2019b).

Individuals that have learned to successfully forage on crops have gained the benefit of an additional food source but are at the risk of human-wildlife conflict (high benefit, high risk; Hoffman and O’Riain 2011; Chapman et al. 2016;). Although Cancelliere et al. (2018) found that crops at Lake Nabugabo, Uganda were not more nutritionally valuable than naturally occurring foods for the vervet monkeys, they provide a benefit of accessibility since they are highly spatially clustered which reduces the amount of energy an individual expends to forage, whereas naturally occurring food tends to be more spread out, requiring more energy to forage (Cancelliere et al. 2018). An interesting trade-off exists between access to anthropogenic crop foraging and the risk of human-monkey conflict. Monkeys will have to decide if foraging from crops is worth the potentially dangerous dog or human interaction.

Close proximity to the forest edge habitat also has associated benefits and risks. Sometimes the habitat outside the forest boundary might alter these benefits and risks, especially when dealing with human influence. Japanese macaques (*Macaca fuscata*) have been found to use forest edges more frequently when there is a decline in naturally produced food resources in

the forest and an increase in food resources due to agriculturalization, specifically when the forest-edge borders cropland (Ebihara and Takatsuki 2021). Vervets, unlike many primates, can be found in savannah-woodland ecosystems, choosing to use open areas, along the forest edge, and within the forest, speaking to their adaptability to successfully live in such contrasting environments (Jaffe and Isbell 2009). Many anthropogenic features can be found on the outside of the forest edge, including crops, buildings, roads, and any associated human/dog interaction. The use of forest edge habitat may depend on the vervet monkeys' perceived risk of the potential human conflict/interaction that may occur on the other side of the edge (Mormile and Hill 2017). For example, if the forest edge borders a tourist location compared to a crop, it may be expected to see more use along the edge that borders the tourist location due to the higher potential for food handouts (high benefit, low risk; Brennan et al. 1985). Compared to near crops where locals may view the vervets as pests and will send dogs or chase the vervets themselves (high benefit, high risk; Mormile and Hill 2017).

Finally, while some features of the environment have both risks and benefits, others such as roads and paths mainly pose risks. Roads are a known source of danger to wildlife. Cunneyworth and Duke (2020) studied collision rates for vervets (*Chlorocebus pygerythrus hilgerti*), baboons (*Papio cynocephalus cynocephalus*), Angolan colobus (*Colobus angolensis*), and Sykes's monkeys (*Cercopithecus mitis albogularis*), along a road in Kenya and found that vehicle collisions were the most common anthropogenic cause of injury and death, where 83% of collisions led to the death of the monkey.

The three groups of vervet monkeys studied live in a human-modified environment on the shores of Lake Nabugabo, Uganda. The majority of the lake is surrounded by dense wetland (Chapman et al. 2003), but the west side of the lake consists of a human modified landscape

which includes a matrix of grasslands, patches of forest, areas with natural regenerating vegetation, farm fields, and a few buildings including tourist accommodations (Chapman et al. 2016). The vervets' diet consists of ripe fruit, unripe fruit, flowers, mature leaves, young leaves, and insects (Chapman et al. 2016). In addition, the vervets are known to occasionally forage from crops, steal from kitchens, and accept tourist food handouts (Chapman et al. 2016). There are known human-monkey conflicts in the form of humans chasing, scaring, rock throwing, and setting traps, and dogs chasing, barking, and biting the vervets (Chapman et al. 2016). Living in this human-modified environment makes these three groups of vervets a good choice to study.

The aims of this research were two-fold. First, based on optimal foraging theory, I hypothesized that vervet monkeys will use microhabitats that maximize access to food resources and safety while minimizing predation risk and human-wildlife conflict (Figure 1). Specifically, I predict that:

1a) vervet habitat use will have a **strong negative relationship** with areas **close to** high plant productivity, as quantified by NDVI (i.e., values closer to one) and within forest coverage because these areas have low risks and high benefits. Otherwise stated, habitat use will increase as the distance to areas with NDVI values near one and forest coverage decreases (use closer to).¹

¹ Note: in order to visually compare results within a single figure, NDVI and forest coverage are represented as distances in my predictions. True Prediction: Habitat use will have a **strong positive relationship** with high plant productivity, as quantified by NDVI (i.e., values closer to one) and within forest coverage because these areas are hypothesized to have low risks and high benefits. Otherwise stated, habitat use will increase as NDVI values increase closer to one and within forest coverage increases. Modified Prediction represented as distances: See 1a above. Explanation: Although these predictions are presented differently (one as a distance to high NDVI quadrats and the other as NDVI values of a given quadrat) they are predicting the same relationship, which is that habitat use will increase with NDVI values near one and within forest coverage. Stating the predictions as distances allow it to be comparable with the other predictions/variables and allow representation within one figure. Without this modification in the prediction the figure would not work with all variables included as the stated relationships would be in opposite directions. For example: If low risk and high benefit category was changed to a positive relationship as dictated by the true prediction for 1a, this would mean that the high risk and low benefit category must change to a negative relationship (since these are opposite categories). That would mean variables characterized as high risk and low benefit such as distance to roads would have a negative instead of positive relationship; i.e., habitat use would be close to roads, which is not my predicted relationship. Therefore, representing prediction 1a as distances allow for visual comparison within the single figure.

1b) vervet habitat use will have a weak negative relationship with distance to crops, kitchens, and forest edge because there are high risks and high benefits. Otherwise stated, habitat use will slightly increase as the distance to crops, kitchens, and the forest edge decrease (use closer to).

1c) vervets habitat use will have a weak positive relationship with distance to water and accommodations because there are low risks and low benefits. Otherwise stated, habitat use will slightly increase as distance to water and accommodation increases (use far from).

1d) vervets habitat use will have a strong positive relationship with distance to other buildings, roads and paths because there are high risks and low benefits. Otherwise stated, habitat use will increase as distance to other buildings, roads, and paths increase (use far from).

Secondly, I hypothesized that microhabitat variables impact vervet behaviour in different parts of the habitat, in that vervets will feed in high benefit (e.g., high food availability) areas and will rest and engage in social behaviours in low risk (e.g., low conflict) areas. Specifically, I predict that:

2a) feeding behaviours will increase with high plant productivity, as quantified by NDVI values closer to one, presence within forest cover, as the distance to crops, kitchens, and the forest edge decreases (feeding close to), as the distance to roads, paths, accommodations, and other buildings increase (feeding far from), and will not be affected by distance to water. These relationships are predicted because I expect feeding to occur in high benefit areas with access to resources, and may start in high risk areas but then move to a safer area.

2b) resting behaviours will increase with high plant productivity, as quantified by NDVI values closer to one, presence within forest cover, as the distance to crops, roads, paths, kitchens, accommodations, other buildings, and the forest edge increases (resting far from), and will not be

affected by distance to water. These relationships are predicted because I expect resting to occur in a low risk area with no conflict and a high benefit area in terms of safety and camouflage.

2c) social grooming behaviours will increase with high plant productivity, as quantified by NDVI values closer to one, presence within forest cover, as the distance to crops, roads, paths, kitchens, accommodations, other buildings, and the forest edge increases (social grooming far from), and will not be affected by distance to water. These relationships are predicted because I expect social grooming to occur in a low risk area with no conflict and a high benefit area in terms of safety and camouflage.

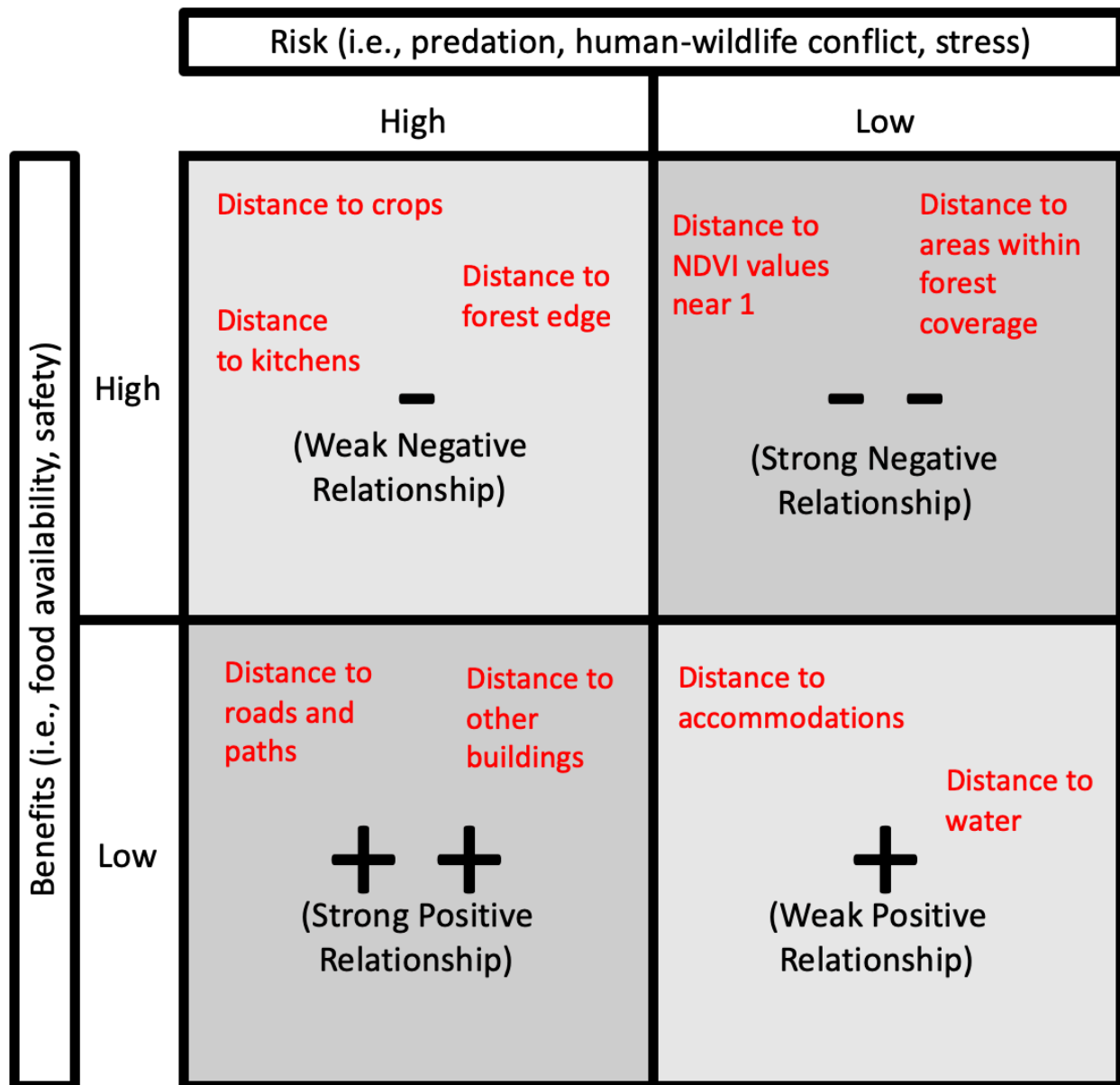


Figure 1. Following hypothesis one, this figure summarizes the predicted relationship of vervet monkey's microhabitat use at Lake Nabugabo, Uganda based on benefits and risks, according to the optimal foraging theory. Note that in order for comparability within one figure, NDVI and forest coverage are represented as distances.

2 | Materials and Methods

2.1 | Study Site and Subjects

Three study groups of vervet monkeys reside on the shores of Lake Nabugabo, Masaka District, in southwestern Uganda. Lake Nabugabo (8.2×5 km) lies at an elevation of 1136 m and is a satellite lake to Lake Victoria (Chapman et al. 2016), formerly a bay of Lake Victoria until approximately 5000 years ago when Lake Nabugabo became isolated by an extensive swamp and sandbar (Stager et al. 2005). The majority of the lake is now surrounded by dense wetland (Chapman et al. 2003), but the west side of the lake consists of a human-modified landscape which includes a matrix of grasslands, patches of forest, areas with natural regenerating vegetation, farm fields, and a few buildings (Figure 2; Chapman et al. 2016). Two wetter seasons occur from March to May and November to December, interspersed with two drier seasons from December to February and May to October (Chapman et al. 2016). There are very few non-human predators of primates at Nabugabo, but there are crowned-hawk eagles (*Stephanoaetus coronatus*), venomous and constricting snakes (e.g., *Dendroaspis polylepis*, *Dispholidus typus*, *Python sebae*), and domestic dogs (Teichroeb et al. 2015; Adams and Teichroeb 2020). Crowned-hawk eagles are rarely seen in the area but have targeted black-and-white colobus monkeys (Adams and Teichroeb 2020). Snakes are observed a bit more frequently (approximately once every two months), and pythons have been observed to kill vervet monkeys at Nabugabo (E. Smeltzer *pers. comm.*), but the primary non-human predator is the domestic dog (Teichroeb et al. 2015; Adams and Teichroeb 2020). Humans also pose a risk to the vervets in the form of chasing, scaring, rock throwing or placing snares, traps, or poison bait (Chapman et al. 2016).

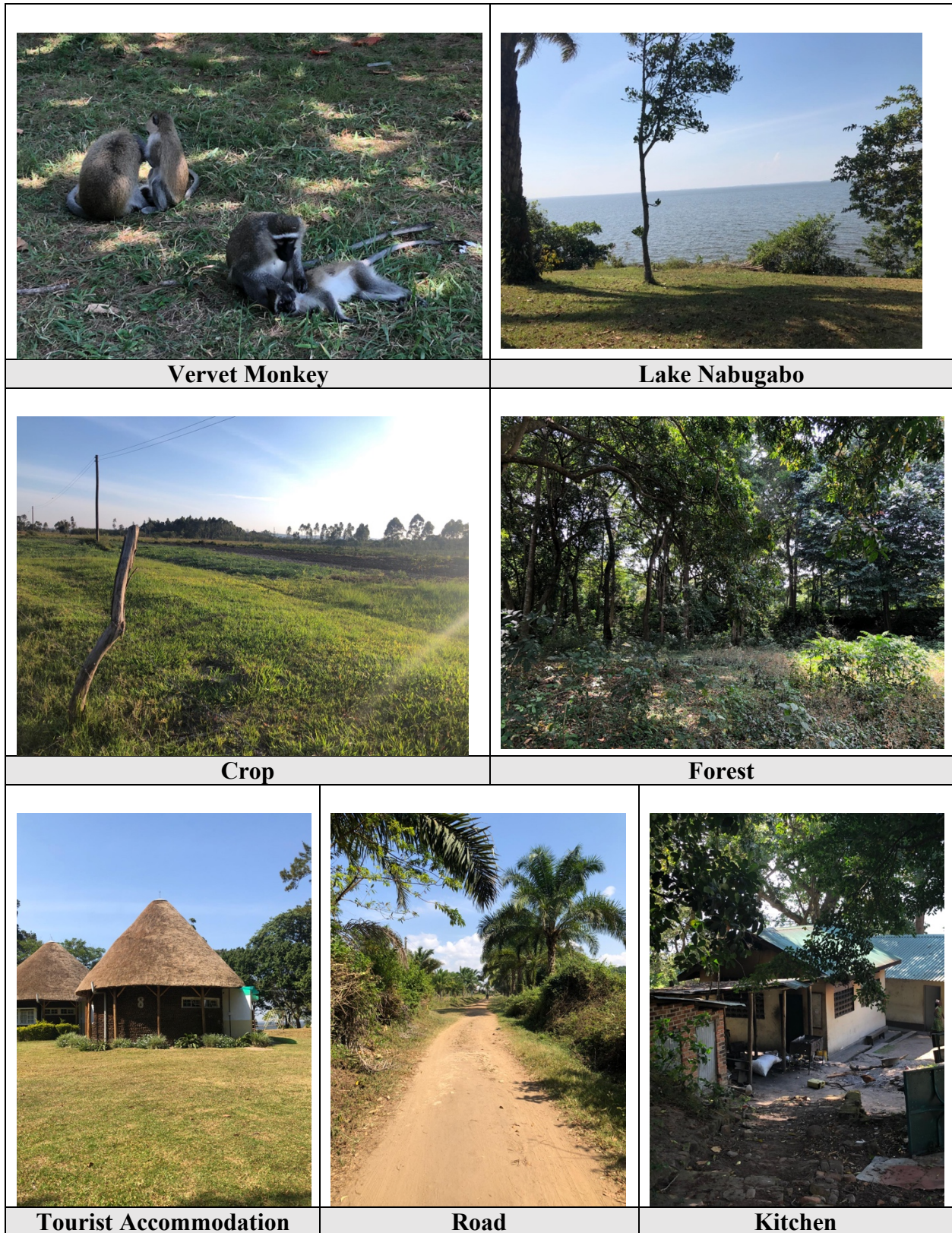


Figure 2. Pictures from in and around the field site at Lake Nabugabo, Uganda. Photos taken by PhD student Simran Prasad.

The three groups of habituated vervet monkeys living at Lake Nabugabo were the subjects for this study; Matovu (M) group, Holiday Center (HC) group, and Kasozi (KS) group. M group was the first group studied starting in 2011, and then in early 2016 HC and KS groups were added to the long-term study groups. All three groups were included in the analyses using the long-term data from 2016-2020. From past research, the only approximate home range known is M group, spanning an area of ~11.6 ha (Chapman et al. 2016). As of January 2022, M group has a total of 51 individuals, HC group was composed of 25 individuals, and KS group at a total of 32 individuals (Table 1). Throughout the years the groups have been under observation, and their composition has changed due to births, dispersals, disappearances (unknown causes), and deaths by predators such as snakes, birds, dogs, and humans.

Group:	M	HC	KS
Adult Females:	14	10	10
Adult Males:	1	2	4
Subadult Females:	2	1	0
Subadult Males:	1	1	1
Juvenile Females:	6	2	2
Juvenile Males:	11	5	6
Unknown Juveniles:	13	4	9
Infants:	3	0	0
Total Individuals:	51	25	32

Table 1. Group composition of the three groups of vervet monkeys (M, HC, KS) living at Lake Nabugabo Uganda as of January 2022.

2.2 | *Data Collection*

2.2.1 | *Behavioural and location data*

The study relied on a long-term behavioural and location dataset of the three groups of vervets at Lake Nabugabo, Uganda. All three groups were monitored on a weekly rotation between M, HC, and KS for a three-week period. Two groups were followed simultaneously by different members of the field research team, followed by one week without data collection. A group would be studied for one week, and each day the field research team collected scan samples (Altmann 1974) on five individuals at 15-minute intervals, recording each individual's general activity (e.g., resting, foraging, moving, grooming) and their nearest neighbours. For each scan sample, location was simultaneously recorded using a grid quadrat system overlaid on Google Earth images of the appropriate area (Figure 3; Chapman et al. 2016). There were three different Google Earth images reflecting the approximate home ranges of the three vervet monkey groups. The Google Earth images were of a high enough spatial resolution (approximately <1 m) to accurately identify unique habitat features (e.g., individual trees, buildings) known to the observer, and thus an accurate location was recorded. Each quadrat is approximately 36 m × 36 m or 1296 m² (Chapman et al. 2016).

For the purpose of this study, I focused on three key behavioural categories: feeding, resting, and social grooming (combination of receiving groom and giving groom). Feeding was defined as an individual manipulating and/or ingesting food (Struhsaker 1967). Resting was defined as an individual sitting in a relaxed (i.e., non-vigilant) manner; they may also be lying on their side or straddling a tree branch (Struhsaker 1967). Social grooming was defined as an individual receiving or giving grooming, itself defined as individual combing through their fur using their fingers and/or mouth, and may place foreign particles in their mouth; grooming may

also be accompanied by lip-smacking or teeth chattering (Struhsaker 1967). To quantify the intensity of quadrat use (habitat use), I calculated the sum of all behaviours (which is also the total number of times a quadrat has been observed in use) found in a single quadrat that was recorded in the scan dataset. To estimate the intensity of behavioural use occurring within a given quadrat, I calculated the independent sum of each behaviour of interest (feeding, resting, social grooming) in a given quadrat. This was calculated per group (three times; M, HC, KS groups) and per year (five times; 2016-2020). Using ArcMap, I created choropleth maps (Dent 1990) that showcase the intensity of quadrat use in regards to overall habitat use and for each behaviour. I used the Jenks Natural Breaks algorithm (Jenks 1967) to automatically assign five breaks/categories of intensity use for each map.

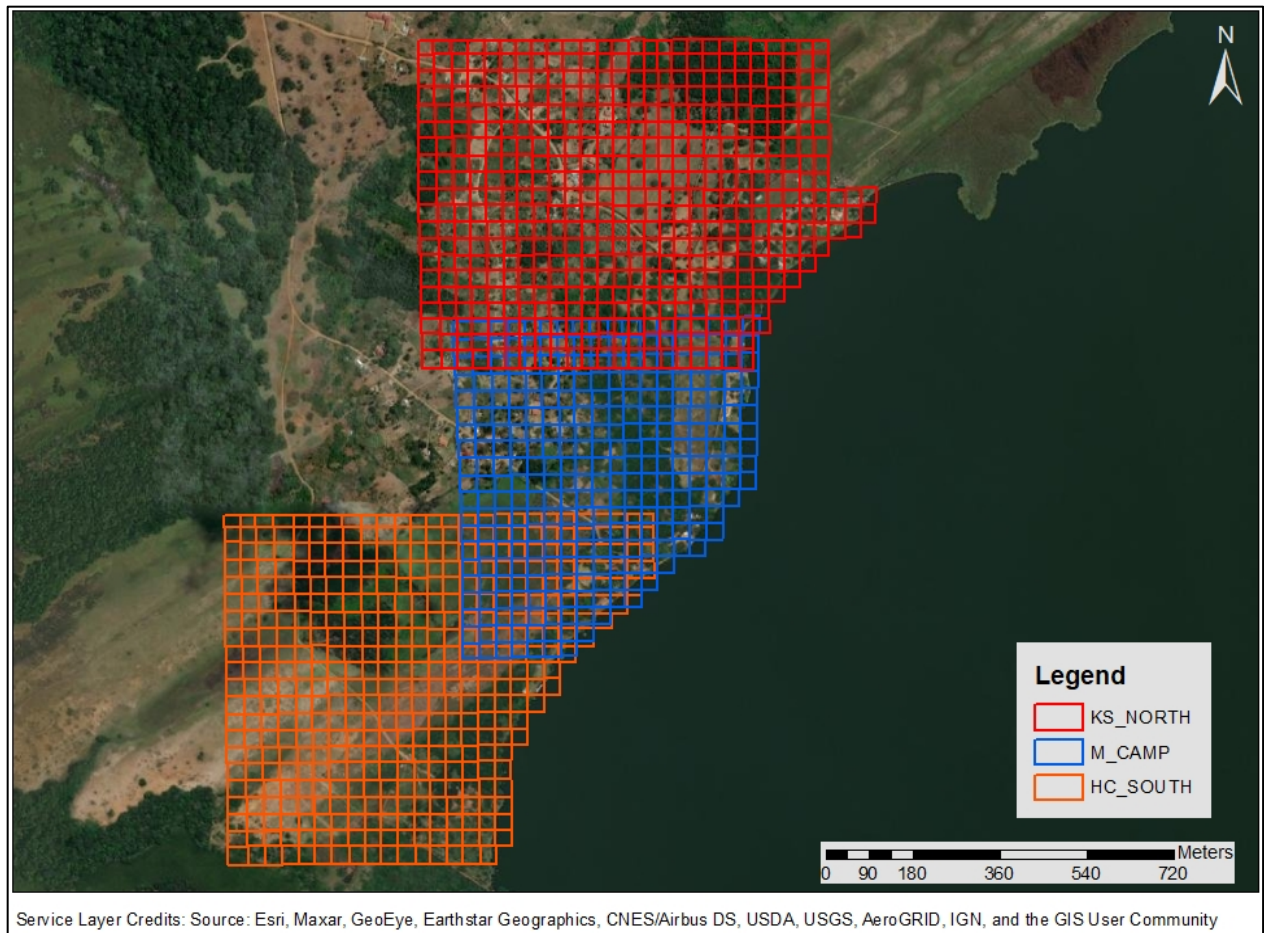


Figure 3. Digitized version of the three maps used to represent the approximate home range area of three vervet monkey groups living at Lake Nabugabo: KS group in red, M group in blue, and HC group in orange. Bottom left corner of each map is the 0,0 point and one unit of the georeferenced image (36 m) is equal to 1 cm.

2.2.2 | *Microhabitat data*

The three Google Earth images with the overlaid grid quadrat system were georeferenced into ArcMap (ESRI Version 10.8), where the origin of the coordinates was identical to the hand-drawn grid on the original Google Earth images (Figure 3). Three shapefile layers were created where each hand drawn quadrat on the original map was converted into a polygon. The centroid (centre point) of each polygon quadrat was identified in ArcMap, and a point shapefile was created for each map. The map for M group is located between HC (southwest of M) and KS (north of M) group maps, such that the top and bottom of the M group map overlaps slightly with both HC and KS group maps (Figure 3). To ensure there were not multiple quadrats and centroids representing the same landscape features, I converted all quadrats and centroids from the overlapping portions of KS and HC to the equivalent quadrat and centroid on M map. Since I was interested in the intensity of use/habitat use, I only included quadrats that appeared in at least one scan sample. While the absence of use can also be informative, quadrats without at least one scan were excluded as it does not necessarily indicate that vervets did not use that quadrat, but rather that our study groups did not. The sample size for number of quadrats for each group is $n = 196$ for M, $n = 248$ for HC, and $n = 304$ for KS. For each quadrat, I calculated NDVI (a measure of vegetation biomass), distance to nearest road and path, kitchen, accommodation, other building, water, forest edge, and crop, as well as inside or outside of forest cover.

2.2.2.3 | *Normalized Difference Vegetation Index (NDVI)*

To calculate the NDVI, European Space Agency Sentinel-2 satellite imagery (10 m spatial resolution in the visible and near-infrared bands) was sourced from Google Earth Engine (Gorelick et al. 2017). Since the quadrat size in this study is $36 \text{ m} \times 36 \text{ m}$, the higher spatial resolution of Sentinel-2 imagery (compared to 30 m Landsat, for example) allows for more

accurate calculating of average quadrat NDVI. Sentinel-2 bands 2 (blue), 3 (green), 4 (red/R), and 8 (near-infrared/NIR) were used to create true colour images and calculate NDVI. One cloud-free satellite image of the study area was found per year (2016-2020) and to limit the effects of seasonal variation on NDVI, images were selected for each year that were within the same two-month period (January and February). Sentinel-2 imagery collected before 2018 has not been corrected to surface reflectance. Therefore, a sensor invariant atmospheric correction algorithm (SIAC) was used in Google Earth Engine to convert the cloud-free Sentinel-2 imagery for each year (2016-2020) to surface reflectance (Yin et al. 2019). Although images from post-2018 have atmospherically corrected versions already, the same SIAC process to top-of-atmosphere reflectance images from all years was applied to ensure consistency through time. The 2016 image had some geo-registration errors (i.e., image not perfectly aligned), but this was corrected with manual adjustment to spatially align it with more recent years.

All atmospherically corrected Sentinel-2 images were then converted to NDVI, which was calculated in ArcMap using the raster calculator and the following formula (float allows for decimal outputs):

$$\text{EQ1a: } \quad \text{NDVI} = (\text{Float}(\text{band8}) - (\text{Float}(\text{band4}))) / (\text{Float}(\text{band8}) + \text{Float}(\text{band4}))$$

OR

$$\text{EQ1b: } \quad \text{NDVI} = (\text{NIR} - \text{R}) / (\text{NIR} + \text{R})$$

NIR and R represent the near-infrared and red spectral wavelength bands collected by a remote sensor (Rouse et al. 1973; Tucker 1979). Healthy green leaves absorb solar radiation strongly in the Red spectral regions but reflect radiation strongly in the near-infrared. The differential reflectance in these wavelength regions results in green leaves outputting positive NDVI values closer to one. Bare soil, clouds, snow, and impervious surfaces output NDVI values close to

zero, while water exhibits negative NDVI values (Neigh et al. 2008). Once NDVI is calculated for each raster cell, the average value across each year for each the 36 m × 36 m quadrats was calculated.

2.2.2.4 | *Distance Features*

Since Google Earth Pro had the most up-to-date high spatial resolution (<1 m) imagery of the field site at Lake Nabugabo, Uganda, it was used to create the digitized version of the desired distance features. Lines were manually drawn to represent all the roads and paths. A road was defined as anything that was at least one car wide (two cars could fit if they go over the side of the road) and where cars, boda bodas (motorcycles), bicycles, and pedestrians pass occasionally. A path was defined as a repetitively used trail at least one person wide but insufficiently wide for a car, mainly used by pedestrians, bicycles, or boda bodas. Polygons of existing buildings, the Lake Nabugabo, forest patches, and crops were created by digitizing on top of the imagery provided by Google Earth Pro. Buildings were classified by type: kitchen, accommodations, and other buildings (from now on referred to as just “buildings”; e.g., homes, outhouses, animal pens). Kitchens were defined as buildings in which food was prepared and/or stored; kitchens may or may not be attached to accommodations, which were defined as buildings that house sleeping quarters for tourists, researchers, or non-locals in which there is a likelihood that food was present and/or food handouts may be given to the vervet monkeys. The building category consisted of buildings that were known to be neither kitchens nor accommodations. While buildings may have had kitchens and food in them, local knowledge indicates that they were most likely houses where food handouts were unlikely (though stealing by the vervets was still possible at a higher risk of conflict). The only water polygon was Lake Nabugabo on the East edge of the village. The forest patches were digitized based on the Google Earth Pro imagery.

Crop polygons were identified in one of two ways: 1) the field research team walked around the perimeter of all known crop gardens while taking GPS points that were digitized into polygons by uploading the points and tracing their path, or 2) visually identified on the map by the field research team, digitized, and then uploaded to ArcMap. I then created an appropriate shapefile (line feature class or polygon feature class) for each of these six features of interest (roads, paths, buildings, water, forest edge, and crops).

All relevant shapefiles were imported into ArcMap. From the centroid of each quadrat, the distance to the nearest feature of interest was calculated using the Near tool. The distances measured (in meters) were: distance to road, distance to path, distance to kitchen, distance to accommodation, distance to building, distance to water, distance to forest edge, and distance to crop edge. When taking distance measurements for a polygon shapefile, any point within the polygon is 0 m, which makes sense for crops or buildings (when a centroid is inside a crop or building the distance is 0 m). However, for distance to forest edge, I wanted the distance from the edge (positive value) regardless of whether a centroid is inside the forest or outside the forest. Changing the shapefile into a line feature class allowed distances to be calculated on both sides of the forest edge. Afterwards, I created a new variable called Forest cover. Forest cover was a categorical variable which stated yes if a quadrat centroid is within the forest edge boundary line (i.e., inside the forest) or stating no if a quadrat centroid is outside the forest edge boundary line (i.e., outside the forest).

2.3 | *Statistical analysis*

Spatial autocorrelation tests were run in ArcMap using Moran's I on all dependent variables (habitat use, feeding, resting, social grooming). All dependent variables were found to be spatially autocorrelated with Moran's I values above zero, signifying clustering of similar

values. This means the vervets' habitat use, feeding, resting, and social grooming behaviours are all clustered around certain areas.

In R, a correlation matrix was used to see if any independent variables (NDVI, forest cover, and distance to the following features: building, kitchen, accommodation, crop, road, path, water, and forest edge) were correlated. The correlation matrix (Table 2) indicated that distance to kitchen was highly correlated ($r > 0.6$) with both distance to accommodation ($r = 0.7352$) and distance to water ($r = 0.6183$); in addition, distance to accommodation was highly correlated with both distance to water ($r = 0.8976$) and distance to path ($r = 0.6480$). Using $r > 0.6$ as the cut-off is a conservative threshold for collinearity that gives a relatively good confidence that collinearity among predictors is not affecting the results (Dormann et al. 2013). Since including these correlated values in a model would result in multicollinearity, I opted to remove both distance to water and to accommodation since 1) they were correlated with each other and with distance to kitchens and paths (for accommodations), and 2) keeping distance to kitchen within the model, allows the potential difference in vervet habitat use and behaviour use close to kitchens versus buildings to be studied. Known kitchens typically are found at tourist locations and were categorized as high risk, high benefit (due to the potential of food handouts, stealing, and lower-staked human conflict), whereas buildings typically belong to local people who view the vervets as pests and categorized as high risk, low benefit (due to greater perceived chance of high-stake human conflict). Therefore, the final eight independent variables used in the models are: NDVI, forest cover, and distance to nearest: building, kitchen, crop, road, path, and forest edge.

Since my data were non-normally distributed, right-skewed, and over dispersed count data, I chose to use a negative binomial generalized linear mixed effect model (Lindén and

Mäntyniemi 2011). Within each model, group, year, and landscape type (to account for spatial autocorrelation) were used as random effects. Landscape type was a categorical variable created strictly to use as a random effect to help account for some spatial autocorrelation (Dormann et al. 2007). It states which one of six landscape categories: cropland, forest, village (where local people live), waterfront (edge of lake), field (open area with no trees or buildings), or tourist (where the tourist accommodations and known kitchens exist). Each quadrat was individually analysed to determine which landscape type they best suited. If there were multiple landscape types present in a quadrat, I categorized landscape type based on visual assessment of which one was taking up 50% or more of the quadrat. All eight independent variables were included as fixed effects. To find the best model, I conducted an automated model selection process (package MuMIn, function dredge) and selected the best model using the corrected Akaike Information Criterion (AICc). There were four sets of models run under these criteria for each of the four dependent variables: habitat use, feeding, resting, and social grooming (all previously defined prior).

All statistical analyses, unless otherwise stated above, were conducted using the statistical programming software R (version 3.6.2)(R Core Team 2020) with a significance level set to $\alpha \leq 0.05$. All means are reported \pm standard error (SE) unless otherwise indicated.

	NDVI	Forest Cover	Building	Kitchen	Accom	Crop	Road	Path	Water	Forest Edge
NDVI	1.0000	-0.5963	0.0025	0.0835	0.1122	-0.1256	0.0442	0.0605	0.0943	-0.0727
Forest Cover		1.0000	-0.0470	-0.0105	-0.0018	0.1116	0.0357	-0.0049	0.0398	0.1527
Building			1.0000	0.0884	-0.1142	0.2251	0.3354	0.1628	-0.2749	-0.1091
Kitchen				1.0000	0.7352	-0.0904	0.5651	0.5943	0.6183	0.1585
Accom					1.0000	-0.2590	0.2338	0.6480	0.8976	0.3244
Crop						1.0000	0.3951	-0.1542	-0.3022	-0.0118
Road							1.0000	0.0729	0.1439	0.0882
Path								1.0000	0.5554	0.1544
Water									1.0000	0.3592
Forest Edge										1.0000

Table 2. Correlation matrix showcasing the correlation coefficients (r) of all independent variables: NDVI, forest cover, distance to: building, kitchen, accommodation (Accom), crop, road, path, water, and forest edge. The bolded values showcase the highly correlated variables ($r > 0.6$) of distance to kitchen with both accommodation and water, and distance to accommodation with both water and path.

3 | Results

The total number of individual vervet monkey observations throughout the five years was 114,402. Feeding made up 28.86% ($n = 33\,021$), resting made up 12.16% ($n = 13\,908$), and social grooming made up 8.52% ($n = 9744$) of all the observations across the five years.

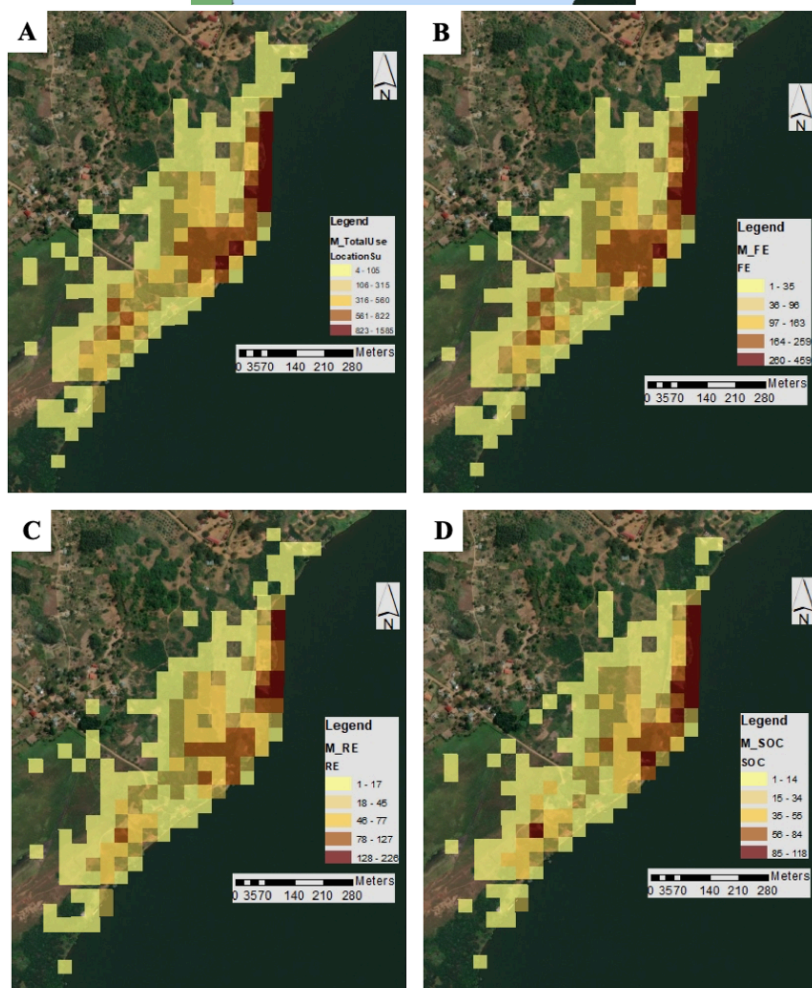
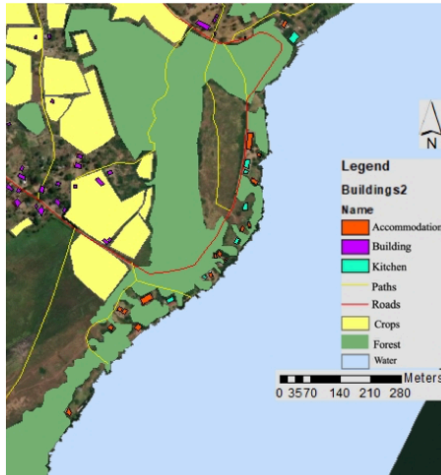
Over the five-year period, M group used an area of 0.2540 km^2 (or 25.10 ha; $n = 196$ quadrats used), HC group used an area of 0.3214 km^2 (or 32.14 ha; $n = 248$ quadrats used), and KS group used an area of 0.3940 km^2 (or 39.40 ha; $n = 304$ quadrats used). Average values of quadrat use for each group and each dependent variable can be seen in Table 3. The quadrat use intensity maps for all three groups indicate that overall habitat use and each behavioural use occurred in similar areas (Figure 4 for M, 5 for HC, and 6 for KS). The intensity maps show that for all three groups areas close to open fields/pastures and to buildings were used less, whereas those within the forest or close to the forest edge by the water's edge, by the research station, and/or by an accommodation/tourist location were used more.

Vervet monkey habitat use and all three behavioural use (feeding, resting, and social grooming) was best explained by a model including additive effects of distance to buildings, kitchens, crops, roads, paths, and the forest edge (excluding paths for the three behaviour models; Table 4; Figure A1 and A2 in Appendix A). Vervet monkeys were more likely to use and perform feeding, resting, and social grooming in habitats close to buildings, kitchens and the forest edge and far from crops, roads, and paths (excluding paths for the three behaviour models). Note that a negative relationship indicates overall use and behavioural use close to the variable and a positive relationship indicates overall use and behavioural use far from the variable. For a list of competing models (falling $< 2 \Delta\text{AIC}$ of top models) see Tables A1-A4 in

Appendix A. All competing models for each of the four models consist of the top models' variables and an assortment of combinations of NDVI, forest cover, and distance to path.

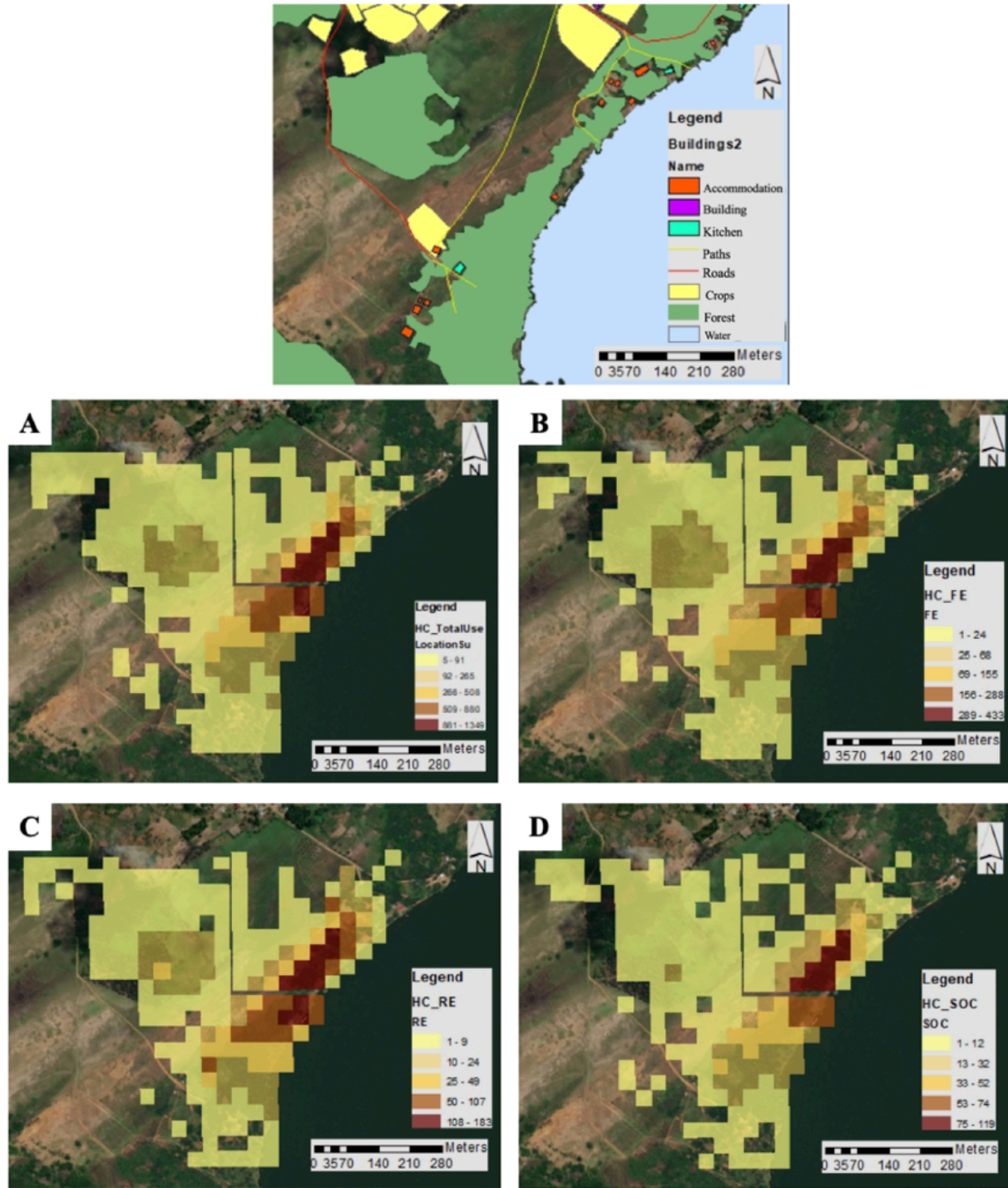
		M	HC	KS
Average overall quadrat/habitat use (measured as the total number of observations recorded in a quadrat)	Mean \pm SE	241.16 \pm 22.12	146.83 \pm 16.91	101.06 \pm 7.45
	Range of observations	4 to 1585	5 to 1349	4 to 743
	Associated Intensity Map	Figure 4A	Figure 5A	Figure 6A
Average feeding quadrat use	Mean \pm SE	69.76 \pm 6.48	43.40 \pm 5.26	28.24 \pm 2.13
	Range of observations	1 to 459	5 to 1349	1 to 210
	Associated Intensity Map	Figure 4B	Figure 5B	Figure 6B
Average resting quadrat use	Mean \pm SE	29.22 \pm 2.75	18.48 \pm 2.17	11.84 \pm 0.90
	Range of observations	1 to 226	1 to 183	1 to 87
	Associated Intensity Map	Figure 4C	Figure 5C	Figure 6C
Average social grooming quadrat use	Mean \pm SE	21.16 \pm 1.97	12.02 \pm 1.35	8.61 \pm 0.62
	Range of observations	1 to 118	1 to 119	1 to 57
	Associated Intensity Map	Figure 4D	Figure 5D	Figure 6D

Table 3. Average values of quadrat use for each group of vervet monkeys (M, HC, KS) and each dependent variable (overall habitat use, feeding, resting, and social grooming).



Service Layer Credits: Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 4. Intensity use maps for: **A)** overall habitat usage (LocationSu), **B)** feeding (FE), **C)** resting (RE), and **D)** social grooming (SOC) behaviours of Matovu (M) vervet monkey group living at Lake Nabugabo, Uganda from 2016-2020. Each quadrat is approximately 36 m × 36 m and the intensity of the colour indicates the intensity of grid cell use or behavioural use. The map on the left illustrates the underlying matrix of habitat features measured in this study.



Service Layer Credits: Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 5. Intensity use maps for: **A)** overall habitat usage (LocationSu), **B)** feeding (FE), **C)** resting (RE), and **D)** social grooming (SOC) behaviours of Holiday Center (HC) vervet monkey group living at Lake Nabugabo, Uganda from 2016-2020. Each quadrat is approximately 36 m × 36 m and the intensity of the colour indicates the intensity of grid cell use or behavioural use. The map on the left illustrates the underlying matrix of habitat features measured in this study.

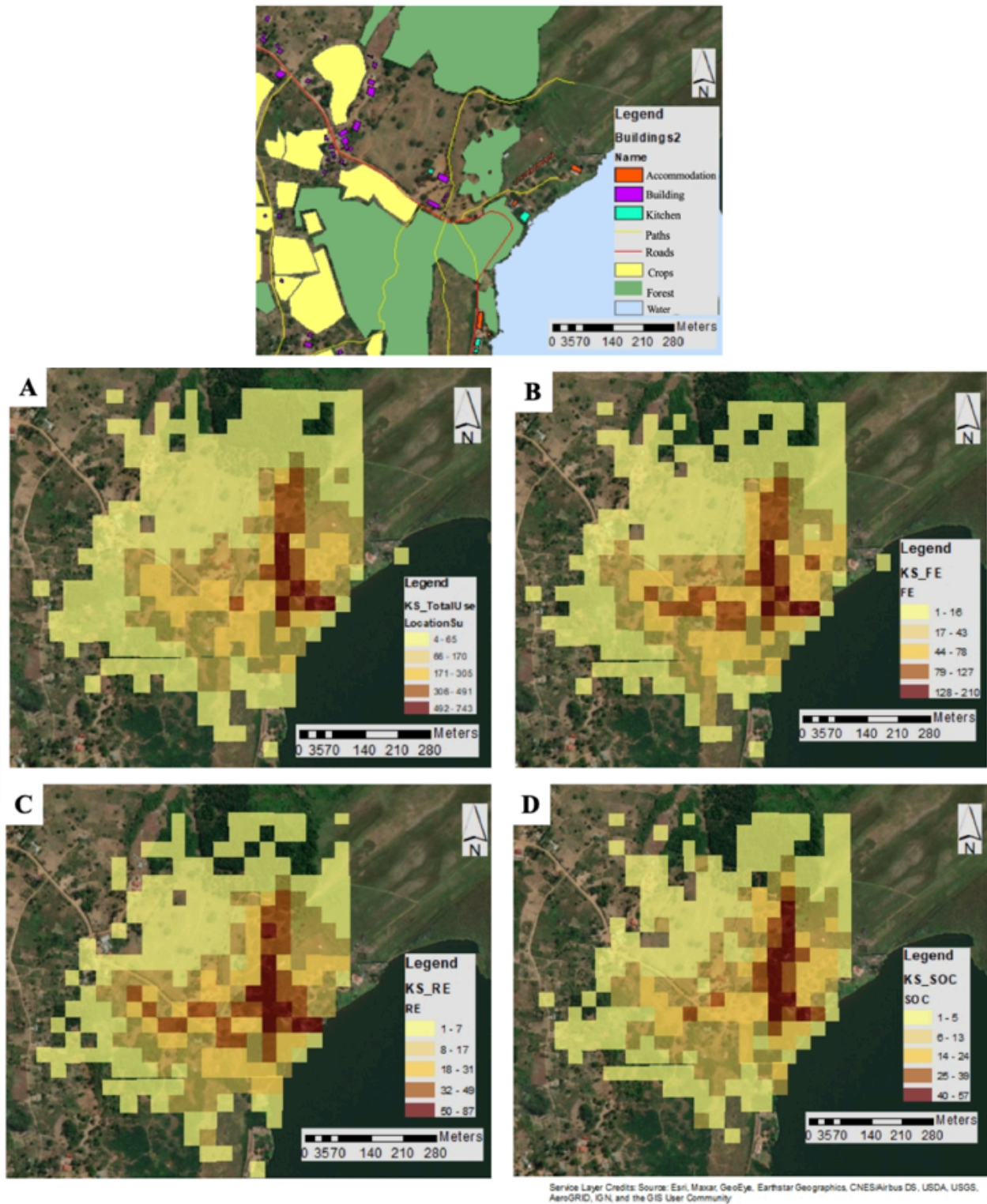


Figure 6. Intensity use maps for: **A)** overall habitat usage (LocationSu), **B)** feeding (FE), **C)** resting (RE), and **D)** social grooming (SOC) behaviours of Kasozi (KS) vervet monkey group living at Lake Nabugabo, Uganda from 2016-2020. Each quadrat is approximately 36 m × 36 m and the intensity of the colour indicates the intensity of grid cell use or behavioural use. The map on the left illustrates the underlying matrix of habitat features measured in this study.

Dependent Variables	Independent Variables	df	LogLik	AICc	Δ AICc	weight	Estimate	Std. Error	Z Value	P(> z)	GLMM R ² m	GLMM R ² c	Prediction Supported?
Habitat Use	(Intercept)	11	-10429.49	2088.1	0.00	0.401	4.9940	0.4460	11.197	All variables have a p value of:	0.3321	0.6180	n/a
	D to building						-0.0040	0.0003	-13.866				No
	D to kitchen						-0.0057	0.0004	-13.445				Yes
	D to crop						0.0038	0.0003	11.203				No
	D to road						0.0018	0.0004	4.613				No
	D to path						0.0011	0.0005	2.264				No
	D to forest edge						-0.0105	0.0008	-13.940				Yes
Feeding	(Intercept)	10	-7685.953	15392.0	0.00	0.312	3.9260	0.5157	7.613		0.3366	0.6421	n/a
	D to building						-0.0044	0.0003	-14.190				No
	D to kitchen						-0.0060	0.0004	-15.871				Yes
	D to crop						0.0041	0.0004	10.805				Yes
	D to road						0.0019	0.0004	4.893				No
	D to forest edge						-0.0109	0.0009	-12.782				Yes
	(Intercept)	10	-6011.804	12043.7	1.14	0.188	2.9242	0.4363	6.702		0.2926	0.5326	n/a
Resting	D to building						-0.0037	0.0003	-11.124				No
	D to kitchen						-0.00516	0.0004	-12.544				No
	D to crop						0.0035	0.0004	8.641				No
	D to road						0.00167	0.0004	3.977				Yes
	D to forest edge						-0.0112	0.0010	-11.607				Yes
	(Intercept)	10	-5365.084	10750.3	1.55	0.137	2.2341	0.3800	5.879		0.2678	0.4823	n/a
	Social Grooming	D to building						-0.0029	0.0003	-9.313			
D to kitchen							-0.0047	0.0004	-11.682				No
D to crop							0.0037	0.0004	9.511				No
D to road							0.0019	0.0004	4.518				Yes
	D to forest edge						-0.0098	0.0009	-10.378				Yes

Table 4. Factors influencing habitat use and behaviours of vervet monkeys in a human-modified environment at Lake Nabugabo, Uganda. Model based information: “D to” = Distance to associated independent variable, df = degrees of freedom; LogLik = Log likelihood; AICc = Akaike Information Criterion; Δ AICc = Delta Akaike Information Criterion; weight = Akaike weight; GLMM R²m = marginal R² (variance explained by fixed effects) and GLMM R²c = conditional R² (variance explained by the entire model, both fixed and random effects) both described by Nakagawa and Schielzeth (2013); P values significant ≤ 0.05 marked with *. Every top model has a competing model within $< 2 \Delta$ AIC; see Tables A1-A4 in Appendix A for a list of competing models.

4 | Discussion

Contrary to one of my predictions, vervets did not exhibit a strong use for areas classified as high benefit and low risk in terms of foraging (high plant productivity (NDVI) and forest cover). Instead, vervets' overall habitat use exhibited a weak relationship with areas that were close to buildings, kitchens, and the forest edge, but far from crops, roads, and paths. With the exception of distance to paths, vervets feeding, resting, and social grooming behaviours followed the same trend as overall habitat use (Table 5). The resulting weak negative relationship of distance to buildings, kitchens and the forest edge with overall habitat use and use for feeding, resting, and social grooming indicates that these areas are considered as high benefit and high risk. Whereas distance to crops, roads, and paths were found to have a weak positive relationship with overall habitat use and use for feeding, resting, and social grooming (excluding paths for the three behaviours) classifying them in the low benefit, low risk category (Figure 7). These findings suggest some interesting but unexpected links among behaviour, space use, perceived risk (predation, human-monkey conflict), and perceived benefits (resource acquisition).

Dependent Variable	Independent Variable	Predicted Strength and/or Direction of Relationship	Predicted: Use Close or Far	Prediction Supported	Result Strength and Direction of Relationship	Result: Use Close or Far
Habitat Use	D to Forest Edge	Weak Negative	Close	Yes	Weak Negative	Close
	D to Building	Strong Positive	Far	No	Weak Negative	Close
	D to Kitchen	Weak Negative	Close	Yes	Weak Negative	Close
	D to Crop	Weak Negative	Close	No	Weak Positive	Far
	D to Road	Strong Positive	Far	No*	Weak Positive	Far
	D to Path	Strong Positive	Far	No*	Weak Positive	Far
Feeding	D to Forest Edge	Negative	Close	Yes	Weak Negative	Close
	D to Building	Positive	Far	No	Weak Negative	Close
	D to Kitchen	Negative	Close	Yes	Weak Negative	Close
	D to Crop	Negative	Close	No	Weak Positive	Far
	D to Road	Negative	Far	Yes	Weak Positive	Far
Resting	D to Forest Edge	Negative	Far	No	Weak Negative	Close
	D to Building	Negative	Far	No	Weak Negative	Close
	D to Kitchen	Negative	Far	No	Weak Negative	Close
	D to Crop	Negative	Far	Yes	Weak Positive	Far
	D to Road	Negative	Far	Yes	Weak Positive	Far
Social Grooming	D to Forest Edge	Negative	Far	No	Weak Negative	Close
	D to Building	Negative	Far	No	Weak Negative	Close
	D to Kitchen	Negative	Far	No	Weak Negative	Close
	D to Crop	Negative	Far	Yes	Weak Positive	Far
	D to Road	Negative	Far	Yes	Weak Positive	Far

Table 5. Original predictions compared to the results from the models. Rows highlighted green indicate predictions that are supported by the findings in this paper. Within the Prediction Supported column, No's marked with a * indicate a support for the direction of relationship but not the strength (which changes the benefit and risk category the variable falls within). Table based information: "D to" = Distance to associated independent variable.

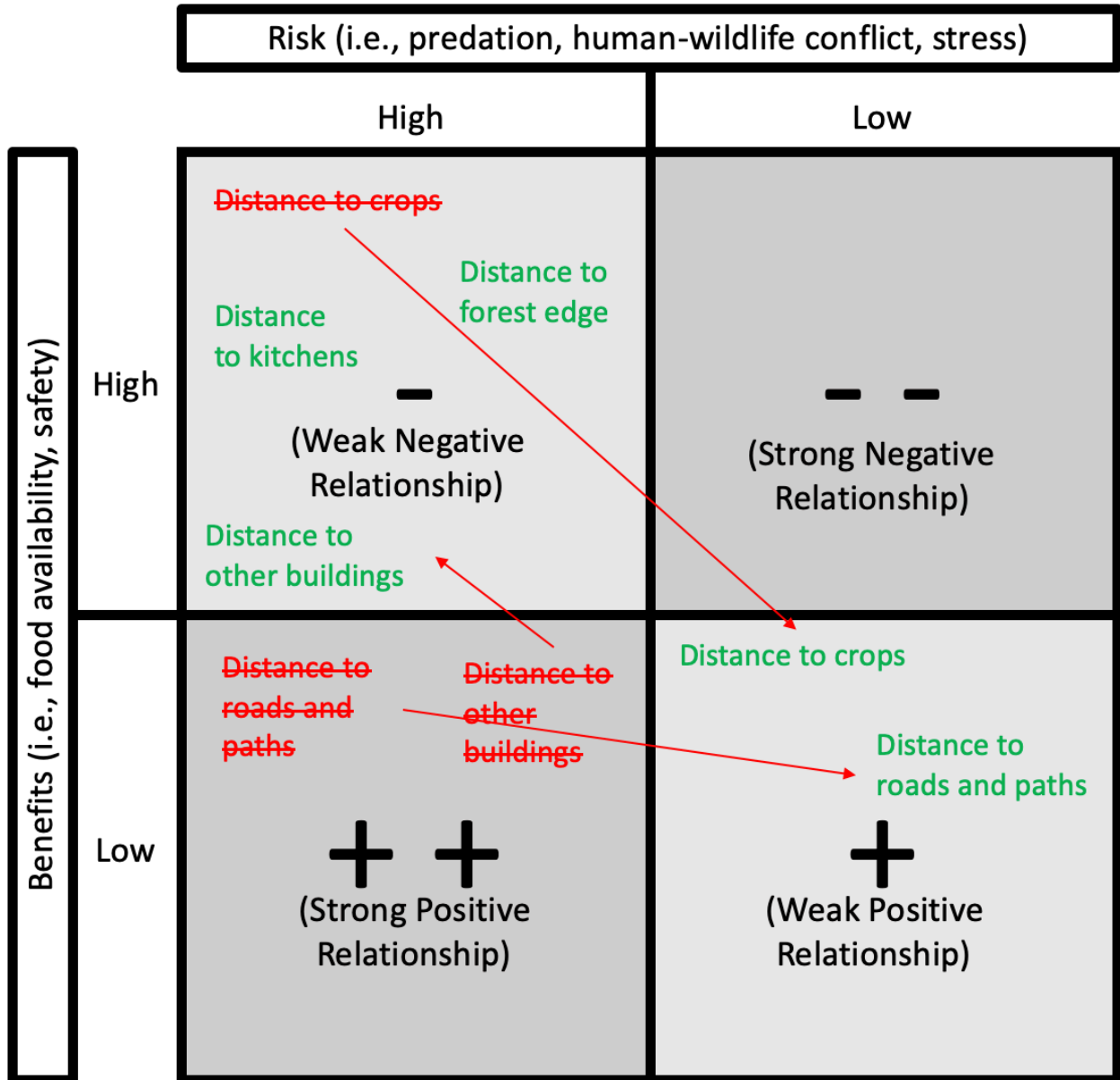


Figure 7. Results from the habitat use negative binomial generalized linear mixed effect model visually displaying the results on the hypothesis one graphic.

None of the results indicated a strong use for areas I originally hypothesized would be classified as high benefit, low risk or low benefit, high risk. This is unexpected because in theory, if an area has high benefits but low risks it would be an ideal habitat choice and if an area has low benefits but high risks it would be an ideal habitat to avoid. Since Lake Nabugabo is a human-modified environment, the results may suggest that this human encroachment has created few areas that are high in naturally occurring benefits that are not impacted by human presence/conflict. It also suggests that at Lake Nabugabo high risk areas are only coupled with high beneficial areas, forcing the vervets to make decisions on if the risk is worth the potential reward. Alternatively, it could suggest there may be an interaction effect between one or more of my predictor variables within a given quadrat. Potentially a high benefit/low risk variable may be co-occurring with a low benefit/high risk variable and this interaction between variables may be why none of the originally labelled high benefit/low risk variables are present in the final models.

The results did showcase a weak negative relationship with distance to forest edge, buildings, and kitchens. These fall within the high benefit, high risk category, where overall habitat use, feeding, resting, and social grooming are occurring close to these three features. Generally speaking, in areas of high benefit and high risk, an individual will have to weigh the pros and cons and decide based on the perceived risk if the benefit is worth it. This result suggests a deviation from the optimal foraging strategy, where an animal will choose to feed in the optimal foraging habitat despite the high predation risk (i.e., maximize costs and benefits; Cowlshaw 1997). Optimal foraging can be negatively impacted by factors such as predation risk and human conflict that may force an animal to select the energetically most efficient food option found in a high risk area (MacArthur and Pianka 1966; Pyke et al. 1977).

Starting off with distance to the forest edge, my original predictions are supported that vervets use habitats and perform feeding close to the forest edge. My predictions for resting and social grooming were not supported, but the results also show a use close to the forest edge. Forest edge thus falls in the high benefit, high risk category. Forest edge habitat has both benefits and risks, but these can potentially be altered depending on what is on the other side of the edge. When looking at the Nabugabo population of vervets, the most intense use is seen in areas next to tourist locations, the research station, and kitchens, but typically these areas are also bordering a forest. This can explain why the model shows a tendency for habitat use close to the forest edge. In this case, the forest edge provides a safe area where the vervets can either stay within the coverage of the trees (providing safety in the form of camouflage from predators/humans/dogs and protection from weather elements) and perform behaviours like feeding, resting, and social grooming (Kim and Riondato 2016; Patterson et al. 2018). Simultaneously, the openness on the other side of the forest edge allows the vervets to stay vigilant of their surroundings for predators (and/or human-monkey conflict) and look for opportunities to steal or be given food-handouts (Patterson et al. 2018). That said, neither NDVI nor forest cover variables significantly improved any of the models fits. This indicates that for the Nabugabo population, forest edge habitat is more important than forest cover and that NDVI is either not a good indicator of primary productivity here or primary productivity is not a good predictor for habitat use (or both). Alternatively, NDVI may be a good indicator of primary productivity but that productivity may not be a good estimator of food availability for these omnivorous but highly frugivorous vervets, and therefore not a good predictor of habitat use. However, both NDVI and forest cover did actually fall $> 2.0 \Delta AICc$ for many of the other competing models (see Tables A1-A4 in Appendix A), which may indicate some support for an

effect of these variables. Vervets' extraordinary flexibility, adaptability, and opportunistic behaviour allow them to use and thrive in forest edge habitats (Ukizintambara 2010). Brennan et al. (1985) found that vervet densities were higher on the forest edge near tourist-lodges than anywhere else in Amboseli National Park in Kenya. These previous reports are consistent with my findings that the Nabugabo vervets tend to use habitat near the forest edge next to kitchens, often associated with tourist locations, compared to within dense forests. In terms of NDVI, perhaps the scale at which I measured NDVI was too broad on a temporal scale (i.e., quantified based on a single photograph per year). NDVI has been successfully used to predict the range use of vervets on a monthly scale at the Lajuma Research Centre in the western part of the Soutpansberg Mountain range, South Africa (Willems et al. 2009), but perhaps my average annual measure failed to capture its potential importance. It should also be noted that NDVI does not quantify vertical structure (e.g., understory, crops, upper canopy). Future studies can look into additional remotely sourced variables such as Leaf Area Index (LAI), which captures the total area of leaves (the surfaces which interface with the atmosphere) relative to a unit of ground area (Zheng and Moskal 2009) in order to characterize the canopy complexity.

Originally, I predicted that distance to buildings would have a strong positive relationship with habitat use, such that individuals would avoid these areas of potential low benefits and high risk. The results indicated a weak negative relationship within the high benefit, high risk category, representing habitat use and feeding, resting, and social grooming use close to buildings (which disagrees with all of the predictions). An interesting contrast is seen between all models and the intensity maps. From the intensity maps, it appears that areas close to buildings are used less frequently, yet the model results indicate a tendency for the vervets to use areas close to buildings. Interestingly, when you look at the intensity maps you can see that there are

considerably more of these less frequently used quadrats close to buildings (the light-yellow quadrats) compared to the fewer number of intensely used quadrats (the darker brown quadrats) far from the buildings. This could signify that although preference in habitat use may be for areas far from buildings, the vervets willingly venture close to buildings for a reason. Although I originally predicted that vervets would use habitats far from buildings due to the high risk and low benefits, the results suggest that there are potential high benefits near buildings which may at times outweigh the high risk. The potential benefit gained from proximity to buildings is resource acquisition such as stealing or crop foraging (Brennan et al. 1985; Chapman et al. 2016), and the risk is human-monkey conflict (human chasing, dog barking/biting; Chapman et al. 2016). I also predicted that closer distances to buildings will decrease feeding, resting, and social grooming, which is the opposite of what was found. Once again, there are conflicting results between the intensity maps and all the models. This indicates that although vervets may prefer to intensely perform feeding, resting, and social grooming away from buildings, there are still a larger number of less frequented quadrats closer to buildings. These quadrats could provide enough of a “safe” space for the vervets to simultaneously perform these behaviours while also being vigilant of their surroundings for humans, dogs, or potential opportunities to steal/crop forage, but not safe enough to stay around for long. This is similar to Cañadas Santiago et al. (2019), who found that vigilance in howler monkeys increased as encounters with humans increased. The authors suggest that howlers altered their behaviour based on the different types of anthropogenic disturbances, and the intensity of their response was coupled with the perceived risk of the human encounter. In this study, the vervets may be staying vigilant of their surroundings and may modulate behaviours (rest, groom, feed, steal, or run away) based on the perceived risk of the human reactions. There could also be an important naturally

occurring food resource near the edge of the forest by the buildings/village attracting the vervets there. Akers et al. (2013) found that Western hoolock gibbons (*Hoolock hoolock*) would typically avoid forest edge habitat that was near houses, but due to the high abundance of important food sources in that area, they were forced to visit from time to time. This could be a similar situation in Nabugabo, but unfortunately, a limitation of this study is the lack of data on naturally occurring food sources as a predictor. Another possible explanation for this contrast is that there are certain limitations for the field assistants when following the vervets. Due to fencing, impenetrable forest or swamp areas, or ethical considerations of collecting data while vervets forage on crops, there are some areas where the vervets are less observable and the field assistants are unable to follow them. This could potentially explain the less intense use of space shown in the intensity maps close to buildings, due to the inability to record data in/near these locations. Alternatively, the models did not include any interaction effect between predictor variables. There could be an unknown interaction between buildings and one or more other variables which could potentially explain this contradiction between the intensity maps and the model.

Lastly for the high benefit and high risk category, the prediction that vervets would use areas close to kitchens was supported by the negative relationship between both habitat use and the behaviours with distance to kitchens. Originally the opposite relationship was predicted for resting and social grooming to kitchens, but the result is as previously stated. That said, the weak relationship suggests that the vervets perceive areas near kitchens as high benefit and high risk. Vervets have been observed stealing from kitchens or foraging in garbage dumps (Brennan et al. 1985; Chapman et al. 2016). Known kitchens at Nabugabo are either in the tourist locations or the research station. Both the intensity maps and the modeling indicated a tendency for the

vervets to choose areas close to kitchens (including tourist destinations and the research station). Although there is still the risk of human-monkey conflict, it appears as though the benefits of being close to kitchens (food handouts from tourists, stealing from kitchens, or garbage dump foraging; Brennan et al. 1985) outweigh the risks. The difference between the kitchens' and the buildings' intensity map hot spots may be due to risk perception. In some areas, local people see the vervets as pests (Else 1991) and the vervets may perceive a greater risk to steal or forage near their houses (and yet they still take the risk; Chapman et al. 2016). Whereas near kitchens, the perceived risk may be less due to the tourists' and researchers' perception of the vervets. Tourists have been seen giving food handouts and not reacting negatively to garbage dump foraging which suggests that there is a greater potential for positive interactions (Brennan et al. 1985; Chapman et al. 2016) and researchers act impartial as not to impact results of data collection (neutral interaction). The vervets may have learned this potential difference in risk thus explaining the intense use near these locations compared to buildings. Therefore, the results of the present study indicate that, similar to other wildlife (Visser et al. 2016; Bötsch et al. 2018; Cañadas Santiago et al. 2019), vervets may adjust their behaviour to different forms of anthropogenic disturbances.

The results also showcased that overall habitat use and feeding, resting, and social grooming had a weak tendency to occur far from crops, roads, and paths. This weak avoidance suggests that the vervets consider these areas as low benefit, low risk. It has been suggested that this trade-off of benefits and risks can draw species to feed in sub-optimal foraging habitats to reduce the predation risk (i.e., minimize costs and benefits; Cowlshaw 1997). But, at Lake Nabugabo, the opposite is seen, where vervets use habitats far from areas with low benefits and low risks potentially indicating that the low predation risk is not worth suboptimal resources or

safety. As previously explained, the results suggest that vervets use habitats close to features that may have high benefits and high risks.

The original prediction for habitat use and feeding use was close to crops falling in the high benefit, high risk category, but the results contradict this. The results agree with my predictions for resting and social grooming; stating that habitat use, feeding, resting, and social grooming all tend to occur far from crops. This classifies distance to crops in the low benefit, low risk category. Crop foraging allows species to supplement their natural diet with additional anthropogenic food sources, but from a human perspective there are high risks associated with it. Vervets at Nabugabo are known to occasionally forage on crops and the locals at Nabugabo often act negatively towards the vervets by throwing rocks, setting poison traps, or sending their dogs to bark or bite the vervet monkeys, which suggests the locals view the vervets as pests (Chapman et al. 2016), and potentially why the results suggest habitat use far from crops. At other places where vervets are found local people are observed using a variety of tactics (a form of human-monkey conflict) to dissuade vervets from foraging on their crops. This can include humans running, screaming, throwing rocks, waving brooms or sticks, dogs chasing, barking, biting, or worse humans setting poison trap baits (Naughton-Treves 1998; Thatcher et al. 2019b). Successful feeding on crops would be hindered by human-monkey conflict and resting and social grooming behaviours typically occur in areas of perceived safety, such as within forest cover or at the forest edge (Patterson et al. 2018). The results suggest feeding, resting, and social grooming have a weak tendency to occur far from crops and close to the forest edge agreeing slightly with the idea that these behaviours would occur in a safer environment. In addition, due to the lack of seasonal natural food fluctuations at Nabugabo, the vervets are not put in a position of nutritional stress seasonally (Schwegel et al. 2022), and therefore do not heavily rely on crops

for food. Also, crops do not provide any nutritional benefit over naturally occurring food resources (Cancelliere et al. 2018), meaning crops can be classified as a low benefit. Interestingly, as mentioned, vervets at Nabugabo do occasionally choose to forage on crops, which suggests that the vervets' risk perception of crop foraging may not be as high as originally hypothesized (or as perceived by a human). The crops may just be a convenient enough resources to occasionally spend minimal time (i.e. using less energy) searching for a lower valued food resources (MacArthur and Pianka 1966). But, typically the vervets will choose habitats far from crops. It may also depend on how far the crop is from a perceived safe area such as the forest edge. Mamo et al. (2021), found that crop foraging by olive baboons (*Papio anubis*), vervet monkeys, bush pigs (*Potamocheirus larvatus*), and crested porcupines (*Hystrix cristata*) decreased in frequency as the distance from the forest edge increased. Similarly, they found that higher amounts of damage in maize fields were correlated with close distances to forests compared to intermediate or far from forest edges. Showcasing that perhaps the crops at Nabugabo are not close enough to forest cover to attempt to forage from frequently.

The last feature to fall in the low benefit, low risk category is distance to roads and paths. The original prediction stated that habitat use would have a strong relationship to be far from roads and paths, categorizing it as low benefit, high risk. The direction of this relationship was correct but it is a weak relationship, thus falling in the low benefit, low risk category. My behaviour predictions were supported stating that resting, feeding, and social grooming tend to occur far from roads. At first, I predicted the vervets would avoid areas near roads and paths due to the high risks surrounding them which involve human traffic via car, motorcycle, bike, or walking. But the low risk category would infer that the roads and paths present at Nabugabo are not as much of a deterrent as I originally thought. Since the community around Lake Nabugabo

is not very large, the traffic may not be very impactful or regular, thus a low risk to the vervets. In addition, these areas do not typically provide any benefit to the vervets. By using areas far from roads and paths, it allows the vervets to prevent any potentially dangerous situations, like vehicle collisions, from occurring (even if it's not very likely at this location; Cunneyworth and Duke 2020), but also allow the vervets to focus on choosing habitats that provide benefits.

It is also interesting to note that, specific to Nabugabo, the tourist locations, research station, and thus kitchens border the lake, and there is a trend based on the intensity maps for at least two of Nabugabo's groups (M and HC) to have the most intense use in these areas. There may be a cumulative benefit of the landscape in this area. The forest provides camouflage which allows the vervets to be under the safety of cover from predators or humans/dogs and protection from the weather elements (Herrera et al. 2011; Sousa et al. 2014). The forest may also be providing naturally occurring food sources that encourage feeding behaviour (Kim and Riondato 2016). Vervet monkeys, Javan slow loris', and Geoffroy's tamarins all used areas with higher forest canopy coverage because it provided camouflage from predators, increased food abundance, and protection from extreme weather (Kim and Riondato 2016; Patterson et al. 2018; Sodik et al. 2019). It's also interesting to note that the vervets in KwaZulu-Natal, South Africa were found resting close to raptor nests (a potential predator) because raptor nests were correlated with high canopy cover, which helps to conceal the troop (Patterson et al. 2018). This showcases that often vervets will use habitats that have both benefits and risks. The water bordering one side may also be acting as a safety feature because they do not have to be cautious of the water (as it does not hold any risk). This means that the vervets do not have to be as vigilant of their surroundings on the water side. In addition, the water may also provide a potential resource (Isbell et al. 2004). Although at Nabugabo the vervets are not seen drinking

from the lake often, the lake still provides a potential water source if needed. Both these features may allow the vervets to feel a higher degree of safety in this area and thus explain the high number of feeding, resting, and social grooming occurring in these areas. Typically, behaviours were seen being performed when the vervets were in a relaxed state and far from any potential stressors (Cowlshaw 1997). Lastly, close proximity to kitchens provides an additional opportunity to acquire food resources (and thus promote feeding behaviours). Thatcher et al. (2019a), found that vervet monkey social behaviour increased as positive human incidents (human food consumption) increased. They attributed this increase in social behaviours to having access to high value food items (human-food), which meant less time spent foraging (for natural occurring food) and thus more time available for social behaviours. Similarly, Patterson et al. (2018) also found that resting and social grooming by vervets occurred after consuming provisioned food (food provided from humans). They suggest that a regular supply of provisioned food provides more energy to meet metabolic demands compared to wild foods. This agrees with Jaman and Huffman (2013), who found that access to provisioned foods for rhesus macaques (*Macaca mulatta*) was related to an increase in resting, feeding, and grooming behaviours not only because the provisioned food provides more energy, but they do so with a smaller amount of food and in a shorter amount of time than wild plant foods. This means the monkeys are expending less energy and time foraging and thus have more time to perform other behaviours.

One limitation of this study was that although Group was accounted for as a random effect in the models, proximity to another group during observations could have an effect on habitat use and behaviour (intergroup competition). It is known that KS group's southern range overlaps with M group's northern range, and that HC group's northern range overlaps with M

group's southern range, thus, there could easily be an effect of group territories. If both groups are within these overlapped areas of their territories, they will face off and chase each other until one group scares the other away. Though both groups use the same area, it is rarely at the same time. Therefore, since M group is between two groups, theoretically, KS and HC may be impacting M group's habitat use and behaviour (and vice versa). There is also at least one other group not studied to the west of HC, so any intergroup competition doesn't just relate to these three study groups. Intergroup competition can cause a deviation from optimal foraging especially if one group is monopolizing specific high value habitat or specific high value resources, thus potentially forcing another group to find a substitution. Future studies should document proximity of other groups during observations. Future research can also collect more detailed microhabitat data, including canopy cover, understory cover, human-monkey interaction, dog-monkey interaction, predator data, natural food data, and crop foraging data. The models in this study were limited to the information I could source or create remotely, and therefore there could be other underlying variables contributing to habitat use and behavioural use in these populations of vervets.

5 | Conclusion

In conclusion, this study suggests that the greatest influence on vervet monkey's microhabitat use at Lake Nabugabo, Uganda were benefits in the form of resource availability and perceived risk in the form of human-monkey conflict. The ability of the vervets to use habitats and perform certain behaviours in certain areas more often than others showcases their ability to adapt to anthropogenic pressure. This bodes well for the species' continual long-term survival as habitat areas are frequently coming under an increasing amount of anthropogenic pressure and change. Understanding what features of the landscape these primates use, will help land planners and developers to better understand the habitat requirements needed to successfully co-inhabit with this species. This research highlights the value of wildlife spatial ecology studies in providing mechanisms for identifying priority management and conservation efforts for wildlife at the highly complex human-wildlife interface. I recommend consideration of the protection of indigenous flora when building in human-modified environments, as well as ensuring ample distance from known forest patches which are home to primates when planning and/or building roads, paths, or crops. Research and recommendations like this are important for urban planners and policy makers, allowing the persistence and growth of wildlife communities within the constraints of human encroachment, especially considering Lake Nabugabo is recognized by RAMSAR for its biodiversity and is thus an important site to conserve (Ramsar Convention Secretariat 2021). Understanding vervet monkey spatial ecology within a human-modified landscape also contributes to determining ways in which human-monkey conflict can be mitigated and/or managed sustainably.

6 | References

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Appendix A

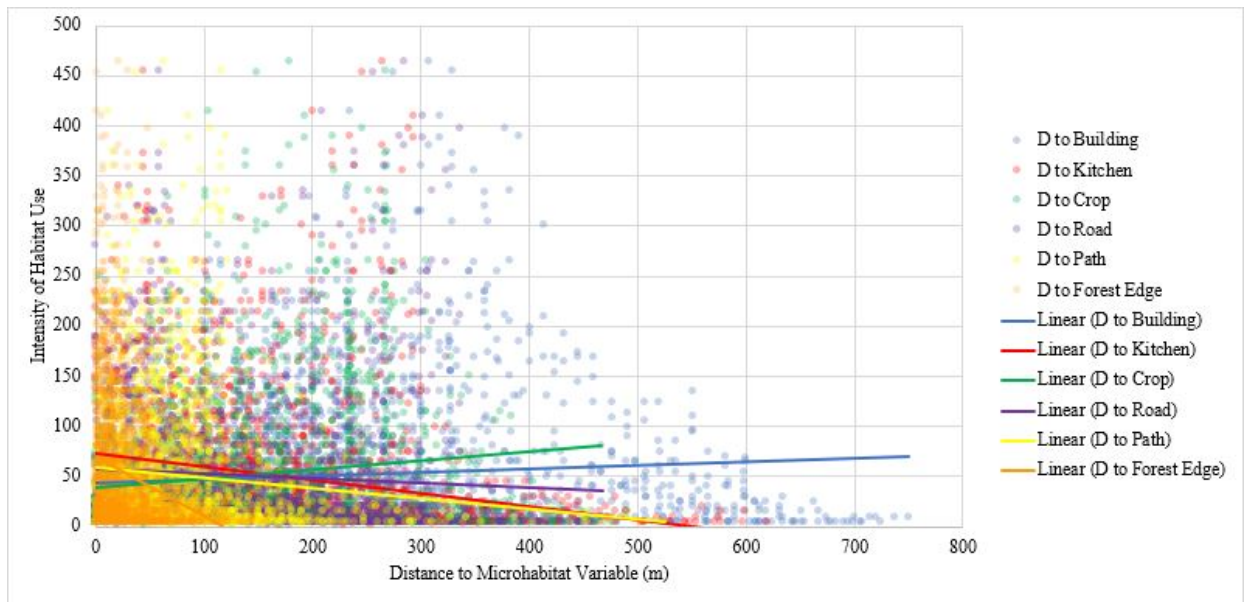


Figure A1. Graph showcasing the overall intensity of habitat use (combination of M, HC, and KS groups) with the distance to the significant microhabitat variables (m). Trendlines show a relatively weak relationship between most variables and intensity. Note that trendlines for distance to building, road, and path show the opposite relationship to the models (but both are weak relationships). Legend based information: “D to” = Distance to associated microhabitat variable.

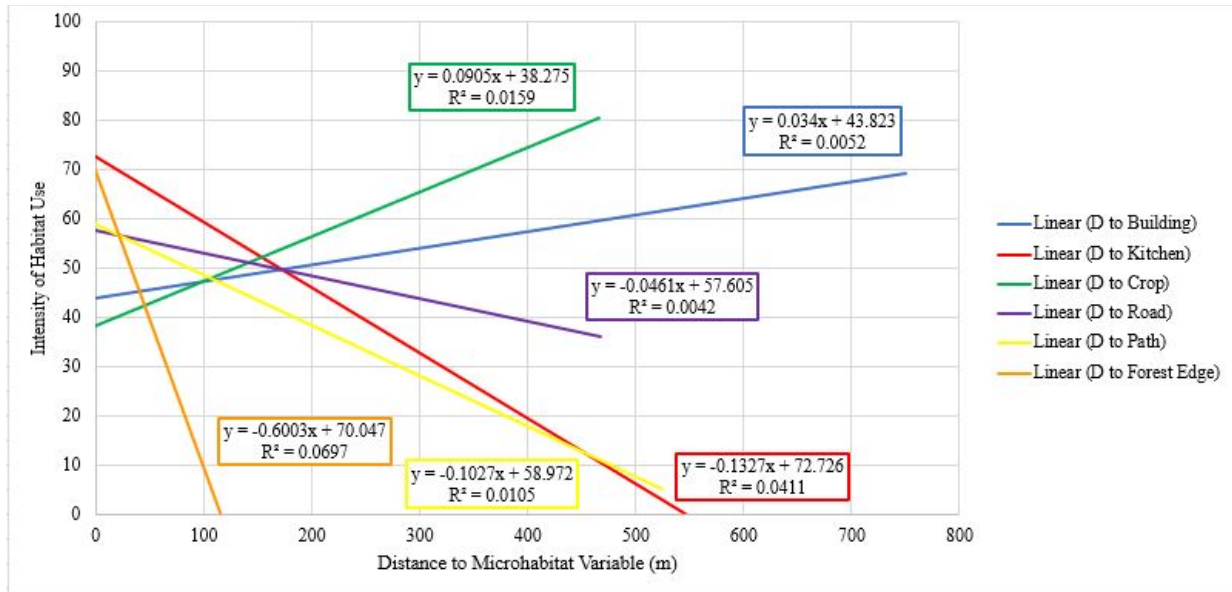


Figure A2. Graph showcasing the overall intensity of habitat use (combination of M, HC, and KS groups) with the distance to the significant microhabitat variables (m). The data points are removed from this graph in order to zoom into the trendlines and provide equations of each line. Trendlines show a relatively weak relationship between most variables and intensity. Note that trendlines for distance to building, road, and path show the opposite relationship to the models (but both are relatively weak relationships). Legend based information: “D to” = Distance to associated microhabitat variable.

Dependent Variables	Independent Variables	df	LogLik	AICc	Δ AICc	weight
Habitat Use model 1 (top model)	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge	11	-10429.49	20881.1	0.00	0.401
Habitat Use model 2	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge Forest cover	12	-10429.19	20882.5	1.41	0.198
Habitat Use model 3	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge NDVI	12	-10429.48	20883.1	2.01	0.147

Table A1. List of competing models (falling within $< 2 \Delta$ AIC of top model) for factors influencing habitat use of vervet monkeys in a human-modified environment at Lake Nabugabo, Uganda. Model based information: “D to” = Distance to associated independent variable, df = degrees of freedom; LogLik = Log likelihood; AICc = Akaike Information Criterion; Δ AICc = Delta Akaike Information Criterion; weight = Akaike weight. Top model highlighted in yellow.

Dependent Variables	Independent Variables	df	LogLik	AICc	Δ AICc	weight
Feeding model 1 (top model)	(Intercept) D to building D to kitchen D to crop D to road D to forest edge	10	-7685.953	15392.0	0.00	0.312
Feeding model 2	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge	11	-7685.566	15393.3	1.25	0.167
Feeding model 3	(Intercept) D to building D to kitchen D to crop D to road D to forest edge Forest cover	11	-7685.608	15393.3	1.33	0.160
Feeding model 4	(Intercept) D to building D to kitchen D to crop D to road D to forest edge NDVI	11	-7685.902	15393.5	1.92	0.120

Table A2. List of competing models (falling within $< 2 \Delta$ AIC of top model) for factors influencing feeding behaviour of vervet monkeys in a human-modified environment at Lake Nabugabo, Uganda. Model based information: “D to” = Distance to associated independent variable, df = degrees of freedom; LogLik = Log likelihood; AICc = Akaike Information Criterion; Δ AICc = Delta Akaike Information Criterion; weight = Akaike weight. Top model highlighted in yellow.

Dependent Variables	Independent Variables	df	LogLik	AICc	Δ AICc	weight
Resting model 1 (top model)	(Intercept) D to building D to kitchen D to crop D to road D to forest edge	10	-6011.804	12043.7	1.14	0.188
Resting model 2	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge	11	-6010.223	12042.6	0.00	0.333
Resting model 3	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge Forest cover	12	-6010.149	12044.4	1.87	0.131
Resting model 4	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge NDVI	12	-6010.199	12044.5	1.97	0.124

Table A3. List of competing models (falling within $< 2 \Delta$ AIC of top model) for factors influencing resting behaviour of vervet monkeys in a human-modified environment at Lake Nabugabo, Uganda. Model based information: “D to” = Distance to associated independent variable, df = degrees of freedom; LogLik = Log likelihood; AICc = Akaike Information Criterion; Δ AICc = Delta Akaike Information Criterion; weight = Akaike weight. Top model highlighted in yellow.

Dependent Variables	Independent Variables	df	LogLik	AICc	Δ AICc	weight
Social grooming model 1 (top model)	(Intercept) D to building D to kitchen D to crop D to road D to forest edge	10	-5365.084	10750.3	1.55	0.137
Social grooming model 2	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge	11	-5363.301	10748.7	0.00	0.297
Social grooming model 3	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge NDVI	12	-5362.794	10749.7	1.01	0.179
Social grooming model 4	(Intercept) D to building D to kitchen D to crop D to road D to path D to forest edge Forest cover	12	-5363.024	10750.2	1.47	0.143

Table A4. List of competing models (falling $< 2 \Delta$ AIC of top model) for factors influencing social grooming behaviour of vervet monkeys in a human-modified environment at Lake Nabugabo, Uganda. Model based information: “D to” = Distance to associated independent variable, df = degrees of freedom; LogLik = Log likelihood; AICc = Akaike Information Criterion; Δ AICc = Delta Akaike Information Criterion; weight = Akaike weight. Top model highlighted in yellow.