# Sitatunga population ecology and habitat use in central Uganda

by

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# Abstract

Effective wildlife management involves understanding the population status and habitat of the species in question, as well as human interests in management decisions. Human dimensions are complicated - African wildlife topics often spark international interest in addition to local concerns. Most African countries surpass those in the global north in the amount of habitat under protection and funds allocated to conservation. Trophy hunting, while controversial, provides much needed conservation funds and provides incentives for local communities to conserve wildlife and habitat. Due to the various human interests involved, the African Wildlife Consultative Forum (AWCF) acts to bring stakeholders together to address emerging issues and collaborate on solutions. As an initiative based in Africa, AWCF positions Africans to take the lead in conserving their resources.

Sitatunga is a wetland-dependent antelope species endemic to sub-Saharan Africa. Due to the difficulty of working in papyrus marshes, information about sitatunga populations and habitat use are sparse and often conflicting. Adult male sitatungas are sought by trophy hunters, thereby providing an incentive to conserve wetlands. Nevertheless, wetlands are decreasing in Uganda, spurring concerns of barriers to dispersal. I used spatial mark-recapture methods and the time in front of the camera (TIFC) method to estimate density of sitatunga in the Mayanja River area of central Uganda. I used 29 camera traps and observation platforms in and around the wetlands, observing openings in the papyrus. I recorded over 900 encounters with sitatunga during the study. The analysis shows that sitatunga are heterogeneous in terms of movement, with one group moving 25 times farther than the other group. The estimated population density declines over the three years of the study, from 22 / km of river (95% CI 17 – 26) to 7 / km of river (95% CI 4 – 9). The results also show that TIFC density estimates are comparable to those from spatial capture-recapture methods, reinforcing the estimates of density. Since TIFC does not have the same assumptions that spatial methods do, TIFC will be useful for species that do not conform to spatial mark-recapture model requirements. Population genetics can reveal additional information about the sitatunga population viability and habitat connectivity, so I analyzed DNA samples from adult male sitatunga. Results show that this population is not reproductively isolated, indicating wetland connectivity at a larger scale.

Using camera traps, I analyzed space use of the ungulate assemblage in the study area, which included domestic cattle. I placed cameras in forests, shoreline wetlands, and interior wetlands. I compared the proportion of days with a detection of the species in three habitat types between different hydrologic conditions in the river – high, normal, and low water. Sitatunga are unique in the ungulate community in that they use remote wetlands consistently, regardless of water level. In the forest habitat, all species except sitatunga and warthog show an increase in the proportion of days with a detection over time, regardless of water levels. Even though the intensity of use of forests increases for most species, I expect that dietary and temporal activity differences allow for coexistence in this community, including the novel competitor.

Sitatunga move more than predicted, have high habitat connectivity, and high fidelity to wetland vegetation. Taking these results together, I suggest that this population of sitatunga is not in decline as density results indicate. Instead, sitatunga are relocating activity centers to areas outside my trapping array or to closed papyrus, where I am unable to detect them. Population density and genetic mixing indicate that this population of sitatunga is secure and there is no conservation concern, although clearly wetlands must be conserved to ensure population persistence.

# Preface

This thesis is original work by Camille Holbrook Warbington. Field methods were performed in accordance with the Canadian Council on Animal Care guidelines, and approved by the University of Alberta BioSciences Animal Care and Use Committee (Protocol # AUP 00001399).

The literature review in chapter 2 is original work by C. H. Warbington. Dr. Mark S. Boyce provided feedback on writing.

David Huggard and Marcus Becker of the Alberta Biodiversity Monitoring Institute (ABMI) provided guidance on the TIFC method in chapter 3. C. H. Warbington designed and implemented the field work, performed statistical analysis, and wrote the text. Megan Brownlee processed some of the data and performed initial TIFC calculation. M. S. Boyce provided input and feedback during the field work, analysis, and writing.

The sample analysis for chapter 4 was performed by Wildlife Genetics International. Dr. David Paetkau provided initial interpretations of the results. C. H. Warbington designed and implemented the field work, performed statistical analysis, and wrote the text. Dr. Mark S. Boyce provided input and feedback during the field work, statistical analysis, and writing.

For chapter 5, C. H. Warbington designed and implemented the field work, performed statistical analysis, and wrote the text. Unpublished data from a manuscript by Jocelyn Chui is included in the discussion section. M. S. Boyce provided input and feedback during the field work, statistical analysis, and writing.

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# Chapter 1

## 1 General Introduction

The International Union for the Conservation of Nature (IUCN) maintains the Red List of Threatened Species (https://www.iucnredlist.org/about/background-history). Assigning a species to a threat status category includes assessment of extent and quality of habitat and population size (IUCN Species Survival Commission 2012). However, the IUCN acknowledges that uncertainty exists in these assessments, and the uncertainty can include lack of knowledge (IUCN Species Survival Commission 2012). Other than Red List status, lack of data affects general management of wildlife populations. If data are sparse, management decisions can rely on opinion or intuition, which can be misleading (Bunnefeld and Milner-Gulland 2016). Using sparse data in management is a widespread concern – only one of every 200 harvested species is monitored (Kindsvater et al. 2018). The only solution to this issue is to collect more high-quality data, to benefit conservation and management.

In addition to analyzing populations and habitats, managers also must consider human dimensions of wildlife conservation. An axiom in wildlife management places human interests as an equal consideration to wildlife populations and habitats (Anderson 1999); indeed, these three factors are interrelated and inextricable from each other. Over the next 50 years, major risks to biodiversity include human population growth and development in the tropics, which invokes all three concerns (Tilman et al. 2017). While human population growth does have detrimental effects on wildlife populations and habitats (Laurance and Useche 2009; Di Marco et al. 2018), wildlife also can negatively affect human well-being, including affecting attitudes towards conservation (Dunham et al. 2010; Dickman et al. 2011; Barua et al. 2013). To complicate things further, humans living far away from the wildlife in question can have an interest in conservation activities, possibly in disagreement with local people (Dickman et al. 2011). In some cases, these far-removed people cannot be ignored, because they provide much-needed conservation dollars (Lindsey et al. 2017; Tilman et al. 2017; Lindsey et al. 2018). Thus, for effective conservation in the tropics, the attitudes and expectations of all interest groups must be considered.

The sitatunga (*Tragelaphus spekii*) is a wetland-specialist African antelope (May and Lindholm 2013). Sitatunga live in dense wetland habitats – meaning that they are both difficult to observe (May and Lindholm 2013; Andama 2019) and that their habitats are under threat from human development (Namaalwa et al. 2013; Barakagira and de Wit 2017; Mwanjalolo et al. 2018). Even though they are listed as Least Concern by the IUCN, there is conflicting information about habitat use, density, and movement (Owen 1970; Manning 1983; Ross 1992; Beudels-Jamar et al. 1997). Despite the uncertainty, in 2008 the Uganda Wildlife Authority authorized a sitatunga hunt (Andama 2019). While recent studies attempted to estimate sitatunga density in Uganda, they have relied on techniques that do not work well in East African wetlands (Owen 1970; Beudels-Jamar et al. 1997; Kumanya and Amanya 2016; Andama 2019). Updated scientific data regarding habitat use and connectivity, community dynamics, and population density will improve management and ensure the hunt is sustainable (IUCN 2012).

Clearly human attitudes and opinions factor heavily into wildlife management, possibly nowhere more so than in Africa. In Chapter 2, I provide an overview of challenges to wildlife conservation in Africa, with emphasis on a collaborative environment fostered by the African Wildlife Consultative Forum (AWCF). I describe how the AWCF identified wildlife management issues affecting conservation in Africa, focusing on human dimensions, which include international interest regarding sustainable use of wildlife. This chapter also addresses the costs associated with conservation, both in terms of money and opportunity costs to local people. The remainder of my chapters concentrate on sitatunga ecology in central Uganda, especially population density and habitats. This chapter on the AWCF will be submitted for publication in *Conservation Biology.*

Estimating density and abundance is important for conservation decision making (Mills 2007; Craigie et al. 2010; Hopcraft 2016). Recent advances in statistical methods for modelling population density can provide better population density estimates for sitatunga than those reported previously (Efford and Fewster 2013; Augustine et al. 2018; Nakashima et al. 2018). In Chapter 3, I explore using camera traps and spatially explicit capture recapture (SECR) models to provide sitatunga density estimates particular to central Uganda. I also assess an emerging method - time in front of the camera - to elucidate if it is a more effective means for estimating density of sitatunga and other habitat specialist species. Chapter 3 will be submitted to *Oryx* for publication.

Because sitatunga rely on wetlands, and wetlands are under stress from development caused by human population growth, sitatunga populations may be fragmented and isolated from each other (East 1998; Silvius et al. 2000; Hoban et al. 2013). In my fourth chapter, I use population genetic methods to discern the connectivity of sitatunga subpopulations in terms of expected and observed heterozygosity, inbreeding coefficient, and effective population size. I also evaluate whether existing microsatellite loci developed for other species can amplify and show variation in sitatunga, thereby identifying loci for use in sitatunga populations in other parts of their range. This chapter will be submitted to *Conservation Genetics*.

In addition to sitatunga, wetlands and adjacent habitats support other herbivores, such as hippopotamus (*Hippopotamus amphibious*) and bushbuck (*Tragelaphus scriptus*) (Kingdon and Hoffman 2013; May and Lindholm 2013; Rich et al. 2016). Human developments in central Uganda mean native herbivores are adapting to land clearing, increased fire frequency, and a novel competitor in domestic cattle (*Bos taurus*) (Ogutu et al. 2016; Mwanjalolo et al. 2018). Wetlands also are affected by climate change, meaning water provisioning is variable and unpredictable (Tockner and Stanford 2002; Erwin 2009; Engelbrecht et al. 2015). In Chapter 5, I examine habitat use and community dynamics in the Mayanja River area relative to how space use by the species in the herbivore assemblage changes over time and with hydrologic conditions in the river. Chapter 5 will be divided into two manuscripts: the dynamics of the ungulate community in forests will be submitted to *The African Journal of Ecology*, and a paper focusing on sitatunga and cattle will be submitted to *Wetlands*. Finally, my sixth chapter serves to synthesize the information gained from this research project, and I also provide suggestions for future research and management of sitatunga.

# Chapter 2

## 2 African Wildlife Consultative Forum: a grassroots initiative for wildlife conservation

### 2.1 Introduction

In 2015, an American dentist became internet infamous when he killed an African lion (*Panthera leo*) in Zimbabwe during a trophy hunt (Capecchi and Rogers 2015). In the ensuing weeks, trophy hunting in Africa was criticized and debated on social and traditional media, leading to proposed importation bans of hunting trophies to the European Union (EU) (International Union for the Conservation of Nature (IUCN) 2016). Concerns regarding trophy hunting extended to academia as well – articles in scholarly journals addressed the ethics and economic contributions of trophy hunting to wildlife conservation, and whether wildlife management is benefited by hunting dollars (Fischer et al. 2015; Batavia et al. 2018). Pursuant to this outcry, there are questions about the use of trophy hunting in conservation of biodiversity in Africa, in terms of ethics, efficacy, and revenue.

Trophy hunting is defined as a hunting experience to take one or more individuals of a certain species with specific desired characteristics (IUCN 2016). In response to the proposed restrictions on trophy hunting in the EU, the IUCN's Sustainable Use and Livelihoods specialist group (SULi) published a briefing paper aimed at helping decision makers to understand the issues behind trophy hunting before making blanket bans or other constraints (IUCN 2016). In their paper, SULi indicates that trophy hunting can play an important role by providing benefits for wildlife and people, while acknowledging that some hunting programs have room for improvement (2016). These improvements include reaching requirements set out as best practices in the IUCN Species Survival Commission's (SSC) "Guiding Principles on Trophy Hunting as a Tool for Creating Conservation Incentives" (IUCN 2012). The IUCN's (2016) SULi states,

> "(t)here are important roles for many hunting stakeholders in improving standards, including importing countries, donors, national regulators and managers, community organizations, researchers, conservation organizations, and the hunting industry and hunter associations…"

For over 15 years, the African Wildlife Consultative Forum (AWCF) has performed this role, bringing together a group of stakeholders from trophy hunting countries in Africa to discuss African wildlife conservation issues and to coordinate responses to current events (https://www.awcfinfo.org/). As an initiative based in Africa, AWCF is uniquely positioned to address conservation in the face of conflicting issues and changing pressures on natural systems.

To highlight the significance of trophy hunting in Africa, and how the AWCF is poised to facilitate positive influences of trophy hunting, we must understand the context and issues facing biodiversity conservation across the continent. In this paper, I address three conservation challenges – humans, land management, and funding – and how the AWCF indicates that trophy hunting can positively influence all three in Africa.  Due to international scrutiny focused on trophy hunting and conservation in Africa, a closer examination of these challenges will illuminate the importance of incorporating multiple strategies in biodiversity conservation in a rapidly changing world.

## 2.2 Challenge One: Human dimensions of wildlife conservation

Across the globe, 70% of megafauna species are in decline, with the majority of species facing habitat loss as well as exploitation for meat and body parts (Hoffmann et al.

2010; Tilman et al. 2017; Ripple et al. 2019). Documenting such declines is frustrated by deficient data; one estimate is that only one of every 200 harvested wildlife species is monitored (Kindsvater et al. 2018). The mere presence of humans and associated land conversion is correlated with increased extinction risk, and is more predictive than life history or climate variables (Di Marco et al. 2018). Even within protected areas, there is a positive relationship between human populations and species extinction rates (Brashares et al. 2001). Vulnerable species in the tropics are likely to be negatively affected by multiple human-caused factors, and the combinations act synergistically on the affected species – causing more harm in conjunction than individually (Laurance and Useche 2009). Human activity also has indirect effects on wildlife, influencing habitat use and behaviour, such as causing wildlife to adopt more nocturnal activity (Averbeck et al. 2012; Gaynor et al. 2018; Ehlers Smith et al. 2019). Because human population in sub-Saharan Africa is projected to increase, proactive approaches to safeguard biodiversity are necessary to ensure wildlife persistence (Tilman et al. 2017).

The opposite is also true - living alongside wildlife has negative consequences on humans, including conflict between wildlife and agriculture, such as crop-raiding or livestock depredation (O’Connell-Rodwell et al. 2000; Gadd 2005; Rust et al. 2016; Mhuriro-Mashapa et al. 2018; Gebresenbet et al. 2018), and even human fatalities (Dunham et al. 2010). While direct economic losses are obvious, the subtle, indirect costs of living with wildlife, in terms of opportunity cost, diminished psycho-social wellbeing, and disruption of food security due to wildlife threats are often driving negative attitudes of local people towards conservation (Dickman et al. 2011; Barua et al. 2013; Blair and Meredith

2018). Exacerbating these attitudes is that traditional wildlife management is sometimes detached from the concerns and experiences of local people (Barua et al. 2013).

To facilitate coexistence between humans and wildlife, managers can target the behaviour of wildlife or encourage human efforts to conserve. Management interventions vary widely and include implementing deterrents, such as fencing, or direct control, such as hunting (Mhuriro-Mashapa et al. 2018; Ochieng et al. 2018). Managers must take care in implementing interventions, because the solution to one problem can cause problems in other areas. For example, attempts to deter crop-raiding elephants (*Loxodonta africana*) by installing electric fences can restrict access to grazing areas for pastoralists (Blair and Meredith 2018). Furthermore, managers must monitor interventions to ensure that the desired outcome is achieved, and be willing to innovate novel solutions to conservation challenges (Sutherland and Wordley 2017; van Eeden et al. 2018). Similarly, expectations of local communities must be addressed to ensure that management goals align with community goals. In Uganda, local pastoralists were unsatisfied with a trophy-hunting enterprise because the community wanted to reduce the population of wildlife that they viewed as pests, while wildlife managers intended the scheme to reduce poaching (Ochieng et al. 2018). This example demonstrates that even when the management target is wildlife populations or behavior, the attitudes and desires of the humans involved, including local community members and wildlife managers, must be considered.

Local communities vary in cultural identity, norms, and values. These differences lead to differing land uses, attitudes towards wildlife, and motivations, even in neighboring communities. Two culturally different communities in Ethiopia experiencing similar losses of livestock to lions differed in their attitudes towards wildlife (Gebresenbet et al. 2018).

This means that managers must take care in assigning generalizations to wildlife issues that might alienate or further marginalize minority or other groups (Thakadu 2005).

To counteract negative consequences associated with living alongside wildlife and to encourage conservation of wildlife and habitats, many countries have implemented some type of compensation or shared-benefits program. These programs vary from direct payments for losses to revenue-sharing schemes from photographic tourism, trophy hunting, and/or national park gate fees (Archabald and Naughton-Treves 2001; Dickman et al. 2011; Ochieng et al. 2018). As with any management intervention, there are complicating factors to each type of program. In the case of payments for losses due to wildlife, the compensation can act as a moral hazard, meaning that compensation decreases the incentive to reduce hazards to agriculture such that poor husbandry of herds or crops remains a problem (Dickman et al. 2011; Bauer et al. 2017). Managing iconic African species such as elephant or lion is further complicated by global interest in their status, leading to a market failure – when the object of interest is globally valuable but not valued locally (Dickman et al. 2011). In the case of lions, a high external value (more valuable globally) of a lion can be translated into local payments to encourage coexistence, thereby involving distant human stakeholders in the management process (Dickman et al. 2011).

Compensation and government-based management interventions are not enough for local people to support conservation. If management is not sensitive to the attitudes and needs of the local community, interventions can lead to a perception that wildlife only benefits the country or outfitters, leading to a loss of support for management institutions (Gillingham and Lee 1999; Noga et al. 2018). To counteract the disconnect between management goals and local needs, many countries in Africa have implemented community-based natural resource management (CBNRM) programs to encourage local communities to conserve and benefit from natural resources (Gibson and Marks 1995; Gillingham and Lee 1999; Pienaar et al. 2013; Ochieng et al. 2018). Effective CBNRM involves delegation of some management decisions to local communities, often in conjunction with a non-governmental organization in a supporting role (Gruber 2011; Naidoo et al. 2016; Mariki 2018). In this way, cultural and economic needs of local communities can be directly affected by the management decisions, and local people have a voice in the process. CBNRM benefits arise from revenue generation, which can involve consumptive and non-consumptive wildlife tourism, or sale of products such as timber (Gruber 2011; Naidoo et al. 2016). Benefits of CBNRM programs must outweigh the costs of conservation, requiring a consistent revenue stream (Thakadu 2005; Gruber 2011; Mbaiwa 2017).

In some countries, there are national CBNRM-support organizations, such as the Namibian Association of Community-Based Natural Resource Management Organisations (NACSO). Stakeholders have different perspectives and expertise that can positively affect conservation outcomes in which they have a vested interest (Sterling et al. 2017). These NGOs and government representatives are some of the delegates to the AWCF, giving them opportunity to discuss challenges in community engagement, human-wildlife conflict, and other issues pertinent to involving local people in conservation. Likewise, AWCF countries considering CBNRM initiatives can learn from established programs, thereby building capacity and exchanging knowledge. Stakeholder engagement through the AWCF is instrumental in addressing the anthropogenic conservation challenges in Africa.

## 2.3 Challenge Two: The Role of Protected Areas in wildlife conservation

Lands encompassed in official protected areas (PAs) often are perceived as important contributions to conservation (Chardonnet 2019). However, lands labelled as PAs are not always effective in the conservation of biodiversity, nor are they automatically safe from degradation and human effects. The efficacy of PAs for biodiversity conservation is disappointing because conservation values of sites selected from PAs were actually lower than those selected from the world at random (Brum et al. 2017). A review of PAs in Africa shows similar alarming results, with a decline in population size for 69 species between 1970 and 2005 (Craigie et al. 2010). In West Africa, an analysis of species extinction risk in nature reserves showed observed extinction rates of large mammals were on average 28 times higher than predicted by species-area models; the variation was best explained by human population presence (Brashares et al. 2001). This result is especially concerning, because almost one third of PAs in Africa are under intense human pressure (Jones et al. 2018). Perhaps it is not surprising, then, that the IUCN Program on African Protected Areas and Conservation (Papaco) recently reported that "(t)he results of protected areas in terms of conservation are very uneven in Africa, in general poor, and studies on biodiversity carried out in recent years show a sharp decline…" (Chardonnet 2019). These results suggest that for effective biodiversity conservation in Africa, we need to consider non-traditional conservation areas while reforming the management of official protected areas.

Again, issues involving PA management involve local communities and economic opportunity. Living near a PA can afford greater access to resources and employment opportunity, but also increased risk, or perception of risk, from wildlife (MacKenzie et al. 2017). PA conflicts in developing countries are often driven by livelihoods, thus many communities are more supportive of the PA if conflict with wildlife is low (MacKenzie et al. 2017; Soliku and Schraml 2018). Other than conflict with wildlife, indigenous people can feel alienated by management of a PA, leading to questions about fairness (Newmark and Hough 2000; Blaustein 2007). If local communities were displaced to create the PA, resentments can carry over to management agencies that restrict access to cultural sites or resources (Thondhlana and Cundill 2017). PAs can intrude into ancestral traditions, and there can be the perception that wealthy tourists get preferential treatment (Newmark and Hough 2000; Blaustein 2007). In Africa, people surrounding PAs experienced more displacement, more conflict, and less empowerment than other regions (Oldekop et al. 2016). In addition to conservation of biodiversity, a major goal of PAs should be to conserve cultural values, thus preserving the relationship between indigenous people and endemic resources (Dudley 2013).

Areas that do not fit the IUCN definition of protected area still can contribute to conservation (Borrini-Feyerabend et al. 2013; Dudley 2013; Chardonnet 2019). Indeed, conservation will need to use highly modified, human-dominated landscapes in the future (Kueffer and Kaiser-Bunbury 2014; Chardonnet 2019; Clements et al. 2019). In addition to traditional conservation strategies, options include creation of artificial habitats, embracing novel ecosystems, and promoting biodiversity in altered landscapes (Kueffer and Kaiser-Bunbury 2014). These options may not be applicable for preservation of all species; however, they represent the type of flexibility and landscape-level approaches that managers might need to address modern conservation issues. Alternative management strategies, in the form of CBNRM and privately owned nature conservancies, are already increasing the amount of land under some type of conservation, even if not recognized as part of the PA network (Borrini-Feyerabend et al. 2013; Dudley 2013). A study in the Cape Floristic Region found high potential for private conservancies to increase the diversity of protected species and populations (Clements et al. 2019). In comparison to cattle ranching, privately owned conservancies and game ranches in South Africa protect multiple biomes and species that would otherwise be eliminated (Langholz and Kerley 2006; Pienaar et al. 2017). However, private conservancies have the same risk of alienating local communities as government agencies when management decisions affect the risk of wildlife conflict (Mhuriro-Mashapa et al. 2018). In the future, the IUCN and Convention on Biological Diversity foresees conservation necessarily taking place outside of recognized PAs, thus supporting that "other effective area-based conservation measures," such as a private conservancy, should be pursued (Borrini-Feyerabend et al. 2013).

AWCF is uniquely positioned to aid in conservation support by bringing together private conservancy owners, government managers, CBNRM associations, and other land managers. With delegates from the public and private sector, representing interests of local communities living with wildlife as well as wildlife businesses, the AWCF discusses best practices, human-wildlife coexistence, and international policies that affect hunting and wildlife management across Africa.

## 2.4 Challenge Three: Conservation Funding

If wildlife is to pay for its own conservation, then revenue comes from tourism – both consumptive (hunting) and non-consumptive (photographic) (Chardonnet 2019). Both of these activities are expected to contribute to conservation and sustainable development, naturally with varying results.

Photographic tourism often is perceived as a way for PAs in economically developing locations to enhance funding available for conservation (Blaustein 2007; Drumm 2008). However, there are negative consequences to increased tourism. Increasing tourism to sensitive PAs can lead to loss of biodiversity, resource decline, and a decrease in visitor experience - resulting in less tourism dollars in the future (Drumm 2008). Photographic tourists typically want to see iconic or rare animals in undisturbed nature, meaning devoid of human structures and activities (Chardonnet 2019). In contrast, hunting tourists are willing to spend time in areas without a high density of wildlife or undisturbed scenery, and in areas with high human and livestock presence, stressing the potential for hunting to generate conservation revenues in areas that other tourists would avoid (Lindsey et al. 2006). In terms of conservation, these two activities are complementary in that they bring conservation to a diversity of landscapes, both in undisturbed (usually PAs) and in human-altered locations (CBNRM). Hunting tourism has the added benefit of being funded by the hunters, without support from donors or government commitment (UICN/PACO 2009). In this way, hunting has the potential to bring conservation to areas outside of CBNRM areas. Recent reports indicate that trophy hunting is in decline in parts of Africa, as evidenced by a decrease in land designated for hunting in Tanzania and based on a decline in the number of hunters in Namibia (Chardonnet 2019). The uncertainty of hunting revenue stresses the need to diversify and expand financial portfolios for conservation areas, and have all types of revenue generation as options (Emerton et al. 2009).

High-end tourism development in the Okavango and Chobe regions of Botswana is biased towards foreign companies (Mbaiwa 2017). Further, over 70% of the revenue generated is sent to parent companies outside of Botswana, while poverty levels increased in local districts (Mbaiwa 2017). Conditions such as these understandably lead to questions about fairness and equitable treatment of local people (Blaustein 2007). In contrast to non-consumptive tourism, over 76% of hunting revenue remained in the country (Mbaiwa 2018). In Botswana, consumptive wildlife tourism generates 7.5 times more revenue than non-consumptive tourism, illustrating the local importance of hunting to economic development. During a trophy-hunting ban in Botswana, revenue shortfalls led to reduction in benefits to local communities, increased negative attitudes towards conservation by local communities, and an increase in poaching (Mbaiwa 2018). A simulated hunting ban in Namibia significantly reduced the number of CBNRM conservancies that could cover operating costs, while the effects of a photographic tourism ban did not have as severe an effect (Naidoo et al. 2016). These results stress that flexibility in terms of revenue-generating activities are imperative for persistence of CBNRM initiatives.

Budget for management is a key component of conservation area effectiveness, regardless of governance type (Chardonnet 2019; Adams et al. 2019). Estimated costs of effective conservation in Africa such as border protection and poaching patrols range from \$700 – 2000 USD per $km^2$ per year (Lindsey et al. 2018; Chardonnet 2019). In 2009, the IUCN estimated that hunting economic returns per $km^2$ were \$110 USD, far below these estimated costs (UICN/PACO 2009). Even in the PA network, revenues fall short of management costs, leading to deficits of over \$ 1 billion USD per year for PAs with lions (Lindsey et al. 2018). Perhaps it is surprising then that 70% of African countries are above-average performers in biodiversity conservation, while 25% of European countries are major underperformers (Lindsey et al. 2017). Developed countries pay a small fraction of the finances needed for PAs, while poor, rural, and forest-dependent groups bear the opportunity costs without meaningful compensation (Kashwan 2017). Conservation of megafauna impose huge costs to the countries in which they reside (Lindsey et al. 2017). Given that many African wildlife species are globally valuable, and that African countries are already ahead in terms of conservation performance, foreign investments to African conservation should be normalized as part of international development (Dickman et al. 2011; Lindsey et al. 2017; Tilman et al. 2017; Lindsey et al. 2018). Options vary widely and include establishing trust funds to fund PA management, or debt-for-nature schemes which exchange debt alleviation for conservation investment (Lindsey et al. 2018). Due to the benefits human receive from nature and that investment in conservation is more profitable than the cost of repairing environmental damage, the implementation of proactive payments to African conservation are long overdue (Balmford et al. 2002; UICN/PACO 2009).

Funding for protected areas is fundamentally linked to management and sustainable development – once again showing that conservation is an inherently human activity. The AWCF brings together delegates from NGOs, governments, science, community development, and other interest groups to collaborate on conservation issues, including trophy hunting. By working inside Africa alongside wildlife managers, scientists, community groups, and donors, the AWCF is positioned to address conservation challenges, including affecting change in perception of trophy hunting and its role in conservation. In 2018 the 16th meeting of the AWCF in Kampala, Uganda featured a discussion about the negative connotations of the term "trophy hunting" and suggestions for best practices in sharing hunting information on social media. This discussion topic emphasizes the ability of the AWCF to be proactive about controversy and to promote collaboration between interest groups. Until the high external value of iconic African species is realized, and developed counties pay their share of conservation costs, African wildlife management groups require the flexibility to raise funds by consumptive and non-consumptive means; the AWCF remains a vital part of conservation planning and capacity building.

## 2.5 Conclusion

Conservation in Africa is challenging due to global perceptions of wildlife management, land-use pressures, and funding shortfalls. Even though conservation across the continent shows inconsistent results, there are numerous options to change attitudes in local populations, place more land under conservation management, and diversify funding options to improve management. Although difficult, there is potential to translate the global value of African wildlife species to a local value, thereby encouraging local people to conserve. By opening a dialog between conservation stakeholders, AWCF offers a way to identify areas needing improvement and exchange knowledge about effective strategies between countries. By improving collaboration and capacity building, Africans are building the future of conservation in Africa and identifying appropriate strategies to do so.

# Chapter 3

## 3 Population density of sitatunga in riverine wetland habitats

### 3.1 Introduction

Knowledge of animal populations is fundamental in effective wildlife management, thus estimating density is a primary concern (Mills 2007; Craigie et al. 2010; Strampelli et al. 2018). Monitoring is even more important for hunted populations, to set effective quotas and recognize trends (IUCN Sustainable Use and Livelihoods Specialist Group 2016; Bunnefeld and Milner-Gulland 2016). One estimate states that only one of every 200 harvested species are monitored (Kindsvater et al. 2018). Addressing the dearth of data will require techniques tailored to the population of interest in terms of habitat and basic ecology of the species.

Sitatunga (*Tragelaphus spekii*) is an antelope species endemic to sub-Saharan Africa, and is one of the least known African large antelopes (May and Lindholm 2013; Andama 2019). Trophy hunters prize sitatunga for their spiral horns, but robust density estimates remain elusive (Owen 1970; Ross 1992; Beudels-Jamar et al. 1997; May and Lindholm 2002; Andama 2019). The lack of reliable density estimates is due, in part, to the dense vegetation in the marshes where they live. Sitatunga are wetland specialists, and are strongly associated with permanent wetlands (Owen 1970; Games 1983; Manning 1983; May and Lindholm 2013; Chapter 5). According to May and Lindholm (2013), there are three subspecies of sitatunga: the forest sitatunga in Central and West Africa (*T.s. gratus*); the East African sitatunga, found in the Lake Victoria basin (*T.s. spekii*); and the Zambezi sitatunga, found from Zambia south and west to Namibia (*T.s. selousi*). Of the three, forest sitatunga have markedly different habitats and patterns of use of wetlands than the other two subspecies and will not be considered here (May and Lindholm 2013; Manguette et al. 2016;

Brichieri-Colombi et al. 2017). The other two subspecies, East African and Zambezi sitatunga, inhabit wetlands of similar vegetation type, but the wetlands in the range of Zambezi sitatunga are affected by strong wet season – dry season changes in wetland quality and extent (Owen 1970; Games 1983; May and Lindholm 2002; Warbington, Pers. Obs.). Most wetlands in eastern and southern Africa are densely vegetated and often dominated by papyrus (*Cyperus papyrus*), which grows in dense stands up to 5 m tall (Games 1983; Jones and Muthuri 1985; Andama 2019). Papyrus makes traditional population survey techniques difficult, and often leads to incomplete or conflicting information (Owen 1970; Williamson 1986; East 1999; Jachmann 2002; Mugerwa et al. 2012).

Traditional aerial and ground survey methods provide the previous estimates of sitatunga density and movement. Densities of East African and Zambezi sitatunga vary from 0.5 to 57 / km$^2$, and movement estimates from 100 m – 6 mi (9.6 km) (Games 1983; Manning 1983; Ross 1992; Beudels-Jamar et al. 1997; Table 3.1). Two home range estimates for Zambezi sitatunga in Zambia agree that home ranges are small and overlap (Manning 1983; May and Lindholm 2002; Table 3.1); one movement estimate for East African sitatunga found observations were always within 500 m of the first sighting (Owen 1970; Caro et al. 1998). However, May and Lindholm (2002) report that there are two distinct home range areas for Zambezi sitatunga, one for the wet season and one for the dry; and the wet season range often included multiple activity centres. Likewise, published density estimates for East African sitatunga include two extremes (0.05 – 55 / km$^2$) (Owen 1970; Beudels-Jamar et al. 1997; Caro et al. 1998). The wide range of estimates in the literature suggest that population estimates may be location-specific and not generalizable.

Recent advances in density estimation could provide a solution for animal species difficult to monitor with traditional methods. Using camera traps and spatially explicit models of density are becoming more user-friendly and applicable to a wide range of scenarios (Bowkett et al. 2008; Trolle et al. 2008; Amin et al. 2016; Apps and McNutt 2018b; Agha et al. 2018). Recently, the maximum likelihood (ML) spatially explicit capture-recapture (SECR) and Bayesian spatial capture-recapture (SCR) estimators have expanded to include a variety of options that users can tailor to specific situations (Borchers and Efford 2008; Royle et al. 2014a). In General, SECR and SCR methods consist of a hierarchical model, with a model for detection informing a point-process model for the distribution of home range centres in state space (Borchers and Efford 2008; Royle et al. 2009). Detection functions are described by $g_0$, or the probability of detecting an animal on a single occasion if the trap is located directly on the animal's activity centre, and $\sigma$, the scale factor for the detection function that is also an indication of home range size (Royle et al. 2009; Efford and Fewster 2013)[1]. Bayesian methods use prior information, MCMC simulation, and data augmentation to estimate model parameters and density (Royle et al. 2009; Gopalaswamy et al. 2012). For sitatunga in Uganda, the primary challenges to density estimation using spatial methods include habitat configuration and individual identifiability. To evaluate which spatial density estimation method is useful for sitatunga, I evaluate how SECR and SCR address these challenges.

A common assumption in spatial density models is that animal home ranges are roughly circular (Efford 2019a). From this assumption arises the assumption that animal

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[1] Articles using Bayesian SCR often use notation of $p_0$ instead of $g_0$; $\lambda_0$ is used instead of $g_0$ for models using expected number of detections at the animal's home range centre; for consistency I will use $g_0$ in this paper

movement around their center of activity is not biased in a certain direction, and is Euclidean (Rhodes et al. 2005; Downs and Horner 2007). Euclidean movement assumes symmetrical home ranges, which may be false if animals strongly associate with landscape features (Sutherland et al. 2015). In central Uganda, like many parts of sitatunga range, the habitat consists of riverine wetlands, which are long and narrow in nature. Because sitatunga are wetland specialists, I expect that their centres of activity and primary movement patterns will align with the wetland configuration. This means that sitatunga movement is strongly biased in the direction of the river, thus their home ranges will be elongated and not circular (Jennrich and Turner 1969). When home ranges become asymmetric, abundance calculated using Euclidean distance becomes negatively biased (Sutherland et al. 2015). A key factor in the effectiveness of camera traps for spatial density methods is maximizing recaptures of identifiable individuals (Carter et al. 2019). To achieve this, camera traps also would be biased in the direction of the river, and not across the minor axis of sitatunga movement. An isotropic detection function is not appropriate in this case. Since the trap array and movement are biased in the same direction, the resulting density estimates will be biased in an unpredictable direction  (Efford 2019a). Anisotropic detection functions would improve model performance (Murphy et al. 2016). In addition, using ecological distance for movement rather than Euclidean distance would provide unbiased abundance estimates (Sutherland et al. 2015). For ML implementation, secr is an established R package with multiple written guides on implementation of the model under multiple variations and scenarios (Efford 2019b). Secr has an add-on, secrlinear, that accounts for linear or long and narrow habitats and non-Euclidean movement (Efford 2017; Efford 2019b) [2]. To date, there

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[2] For this paper SECR refers to the ML spatially explicit capture-recapture methodology, and secr refers to the software and code to implement SECR in R

is not an established Bayesian framework that allows for a habitat network and non-Euclidean movement. To implement such a model in SCR would require adaptation of available code, which is not a simple undertaking. If asymmetric home ranges and non-Euclidean movement is an important aspect to consider when estimating density, then the ML estimation is the only available option.

Sitatunga are individually identifiable based upon natural markings and horn shape in males (Owen 1970; Breuer and Ndoundou Hockemba 2008). I use the natural markings on their face and in small areas on their flanks to distinguish between individuals. Identification to individual therefore requires clear images of the head. Due to the rapid growth of papyrus, and the nature of camera trapping research, I expect numerous photographic encounters where the identity of the photographed individual cannot be determined. For ML SECR, only complete identifications are commonly used in the model. This results in discarding encounters with imperfect identification, which can be a substantial proportion of total sample size (Rayan et al. 2012; Strampelli et al. 2018). In addition, reducing the sample to include only identifiable individuals increases bias and reduces precision for the estimated model parameters (Royle et al. 2014a). Uncertain identity encounters also mean that the encounter histories of identifiable animals are incomplete, underestimating the rate of individual encounters (Royle et al. 2014a). Bayesian SCR offers a different option – using the uncertain identifications to probabilistically determine if the unknown encounter is a previously identified individual or if it is an encounter of an unknown animal (Augustine et al. 2019). In cases where encounters cannot be assigned to a known individual, I often can determine the age and/or sex of the sitatunga. SCR models can use Markov Chain Monte Carlo (MCMC) methods to reconstruct capture histories for latent individual identities; using categorical identity covariates and spatial information removes potential bias from density estimates, aids in parameter estimation, and increases precision (Royle et al. 2014a; Augustine et al. 2019; Murphy et al. 2019). Thus Bayesian SCR methods are favorable when using natural marks and data with incomplete identifications to estimate density.

There are other important aspects of Bayesian methods to consider. Current SCR methods use prior information to set up and update the model (Borchers and Efford 2008). SCR users must practice great care when setting prior information, because inappropriate specification, even when using uninformative priors, can lead to inaccurate, imprecise, and incorrect conclusions (Gopalaswamy et al. 2012). Bayesian methods also are complicated in terms of evaluating output, because there are no established model selection criteria for SCR models, whereas ML models can be ranked by multiple methods, such as Akaike's Information Criteria (AIC) (Borchers and Efford 2008; Gopalaswamy et al. 2012). A final consideration is that SECR methods allow $g_0$ and/or $\sigma$ to vary by covariates for time, individual, or location, whereas available SCR code does only in limited cases (Borchers and Efford 2008; Augustine et al. 2019). In a comparison of performance between R packages secr (ML) and Bayesian SPACECAP, Noss et al. (2012) found that secr was more sensitive to few resightings, but outperformed SPACECAP in terms of faster computing times and simpler user specification of input and evaluation of output. SPACECAP performed better than secr for small sample sizes and for rare or elusive species (Noss et al. 2012). Selection of ML or Bayesian spatial density estimation methods relies upon the needs of the user and the complexity of the data.

An alternative to SECR or SCR models of density, the random encounter and staying time (REST) model does not require individual identification nor does it have assumptions about home range (Nakashima et al. 2018). The REST equation for density (*D*) is:

$$\widehat{D} = \frac{E(Y) * E(T)}{sH}$$

where *E(Y)* is the expected number of detections of the species of interest, *E(T)* is the expected staying time, or the amount of time a detected animal remains in the field of view of the camera, *s* is the area of detection, and *H* is the duration of the sampling period (Nakashima et al. 2018). In their paper, Nakashima et al. used video recordings from camera traps to estimate *T* ( 2018). The Alberta Biodiversity Monitoring Institute (ABMI) developed a similar model, time in front of the camera (TIFC), which uses still photography trail cameras to estimate *D* (Huggard 2018). The key difference is the TIFC model uses the total time during the monitoring period that a member of the species is in the field of view (*M*):

$$\widehat{D} = \frac{M}{sH}$$

(Huggard 2018; Nakashima et al. 2018).

There are two major considerations for using TIFC: (1) estimating the camera's effective detection distance (*r)*, and (2) how to account for the probability that the animal(s) left the field of view during the time between photographic events (Huggard 2018). The area surveyed by the camera is directly calculable from the angle of the field of view (*a*) and *r*:

$$s = \pi * r^2 * (\frac{a}{360})$$

(Huggard 2018). Estimation of *r* is critical because underestimating *r* results in overestimating density. Vegetation, animal size, and camera performance all affect *r* estimation, and *r* can change during project duration (Huggard 2018). The other consideration is a by-product of still photography recording an incomplete account of detection duration, instead of a complete record from the time an animal enters the field of view to the time it exits, which is available from video recordings. If an animal stays in the field of view, but does not move enough to trigger a photographic event, then *M* is underestimated by counting only the amount of time in recorded images. Using TIFC also requires that cameras are set to take pictures with no delay between events and are sensitive enough to detect all animals within the field of view. Despite these caveats, if TIFC provides comparable density results to SECR and/or SCR estimates, then this method is a viable alternative for monitoring cryptic species in difficult habitats.

I chose to estimate density of sitatunga using three methods: the maximum likelihood R package secr, the Bayesian R code SPIM (spatial partial identity model), and the TIFC model (Huggard 2018; Augustine and Royle 2019; Murray G. Efford 2019; R core Team 2019). I chose secr because I can specify that the habitat is a network and sitatunga movement is non-Euclidean, but I must discard uncertain identity encounters. I chose SPIM because it uses partial identity information to improve estimation of $g_0$, $\sigma$, and density, but I cannot specify a habitat network or non-Euclidean movement. I used TIFC because it does not require individual identity and it makes no assumptions about home range. I also evaluate the modelling process to determine if these methods can be readily adopted for wildlife management in Uganda. This is the first known attempt to estimate sitatunga density using camera traps and spatial methods.

## 3.2 Study Area

The study area is in the Nakaseke District of central Uganda, 900 – 1000 m above sea level, from 371536 m E, 147039 m N to 379234 m E, 128150 m N (Andama 2019, Figure 3.1). The Mayanja River is part of the Nile watershed. The study area consists of private lands and multiple landowners. Uganda Wildlife Safaris (UWS) operates a hunting concession on these lands; target species include sitatunga, bushbuck (*Tragelaphus scriptus*), waterbuck (*Kobus ellipsiprymnus*), warthog (*Phacochoerus africanus*), bush pig (*Potamochoerus larvatus*), oribi (*Ourebia ourebi*), and bush duiker (*Sylvicapra grimmia*). The Uganda Wildlife Authority has overall management responsibility for wildlife and hunting, but UWS performs some on-site management, such as anti-poaching patrols.

The wetlands consist primarily of papyrus; other sedges and aquatic vegetation also are present, such as water lily (*Nymphaea lotus*) (Andama 2019, Warbington, Pers. Obs.). Forests along the wetland edge include other *Cyperus* spp., *Acacia* spp., and *Lantana* sp. (Andama 2019, Warbington Pers. Obs.).

Average annual rainfall is 1282 mm and average temperature is 22.2 °C ((Climate-data.org 2019). Major human disturbances in the area include charcoal production and livestock grazing (Andama 2019).

## 3.3 Methods

### *3.3.1 Field Methods*

I collected data during three time periods: April – August 2015, May – August 2016, and January – August 2017. I separated the study area wetlands into two segments: Shoreline areas were accessible by foot and River areas accessible by canoe. Machans are raised platforms, placed in trees or free standing, that overlook openings in the papyrus marsh. Undisturbed papyrus can grow in dense stands up to 5 m tall (Jones and Muthuri 1985). To maximize ability to see sitatunga, workers with machetes created openings in the wetland by cutting the papyrus and other vegetation to approximately 20 cm in height. Openings varied in size, but the average size was approximately 800 $m^2$. Each machan may have overlooked multiple openings, and openings could contain open water or aquatic vegetation. Due to the growth rate of papyrus, openings needed to be re-cut approximately every four to six weeks.

I numbered machans and generated a randomized list of Shoreline machans to determine order of visitation. Starting in 2015, I visited the specified Shoreline machan in the hours around dawn (approximately 600 to 900), and dusk (approximately 1600 to 1900) to photograph sitatunga visiting the openings. I used a Canon DSLR camera with a 150 – 600 mm lens. I photographically recorded each sitatunga visiting the opening, attempting to obtain multiple angles of each individual to aid in identification. I recorded any sitatunga sighting, even if I did not obtain usable photographs. I recorded each encounter, noting sex and age if possible.

For River machans, I placed trail cameras in openings created as above. I did not go to these machans as I did for the Shoreline machans due to the danger of encountering hippopotamus on the river in the dark. I used Reconyx HyperFire trail cameras with semi-covert infrared flash for night surveillance (Reconyx®, Holmen, Wisconsin USA). I also placed camera traps in Shoreline wetland areas. Because of reports from local farmers of sitatunga using dry-land habitat, I also placed trail cameras in forested areas, defined as dry-land habitats with a preponderance of woody stems and a continuous canopy at least 3 m in height. I placed forest cameras within 20 m of wetland edge. I attempted to maximize chances of sitatunga encounters by placing cameras in areas with sitatunga sign, such as wildlife trails, bedding areas, or feces (Carter et al. 2019). I placed multiple cameras at most sites attempting to photograph both flanks (Karanth 1995; Sun et al. 2014). I did not use bait. I used some of the camera sites in multiple years of the study, depending on accessibility. I mounted cameras on poles or trees in the area of choice. I programmed the cameras to take a burst of three pictures at any time when triggered by the motion sensor, with no delay between photographic captures. I also programmed the camera to take a picture at noon every day to verify that the camera was still operational. I visited the cameras approximately every four to six weeks to change memory cards, replace batteries, and clear the camera site from vegetation encroachment. Depending on conditions I encountered during maintenance visits, I relocated some cameras to new survey areas. I categorized a trail camera encounter as a photographic set of a sitatunga, with new encounters occurring after a 30 minute period without a detection.

### *3.3.2 Photograph Identification*

I used a three-identifier system to attempt an identification of each sitatunga encounter with a photoset (Foster and Harmsen 2012). Independently, three people examined the photoset of an encounter to determine if the individual had been seen previously to the current event, if it was a new individual, or if it was unidentifiable (U) based upon the images in the photoset. I created a catalogue entry with the date and location of sighting and all usable images for each identified sitatunga. To be marked final, two of the three identifiers would agree with an identification (or U). In cases where the three identifiers could not agree, a fourth person would examine the photoset and catalogue of known individuals to determine a final identification.

In addition to observations, I also included encounters with sitatunga harvested from hunting or those found dead. I recorded date and location of recovery and took pictures of the face and other potentially identifying features to compare to known individuals for inclusion in analysis.

The identifiers classified 2015 and 2016 photosets as a single data set. To simulate new, independent data sets, I classified the 2017 photoset without the catalogue of individuals developed in previous years. Thus, an individual sitatunga could be identified in each year.

I classified sitatunga encounters by date, time, location sex, and age. I defined a lamb (L) as any individual of small body size occurring with an adult female sitatunga. Age of lambs is from birth – 0.5 years. Sex of lambs cannot be easily determined because horn growth does not occur while the lamb is still travelling with its dam. Adult females (F) are reddish brown in colour, lack horns, have a larger body size than lambs, and can occur alone or in groups. I did not assign age groups to female sitatunga due to lack of external signs indicating age. I defined a male sitatunga as any individual with horns. I adapted a chart regarding horn growth in nyala (*Tragelaphus angasii*), a species in the same genus as sitatunga, to aid in classifying age of male sitatunga (Anderson 1986). The youngest age class of male sitatunga (Y) have horns that extend no further than the tips of the ears, forming a V shape. I assume that Y class males are 0.5 to 1.5 years of age. Immature male sitatunga (I) have horns encompassing a V shape then bending towards the midline (spine), with extended, tapered sides. Class I males are approximately 1.5 to 2.5 years of age. Adult male sitatunga (A) horns have a full twist, usually in an hourglass shape, and they are over

2.5 years of age. Whenever possible, I assigned a sex/age category to all sitatunga encounters, even if individual identification was not possible.

Males identified as Y class in 2015 could age to I class in 2016 or 2017. Due to the variety of horn shapes that I recorded, Y class horn growth was unpredictable. Aging male sitatunga to the next age class was difficult, especially if I did not sight them in each year of the study. Due to the potential errors in identification, I modeled each year as separate events in SECR/SCR analyses.

Protocols for animal use were approved by the Animal Care and Use Committee for Biosciences (University of Alberta, Research Ethics Office, protocol AUP00001399). I also obtained permits from the Uganda Wildlife Authority, and the Uganda National Council for Science and Technology, registration number NS 523.

### *3.3.3 Analysis Methods*

#### *3.3.3.1 SECR and SCR Data Preparation*

For both SCR and SECR density estimation, I used both the trail camera data and the photograph data (Gopalaswamy et al. 2012). An occasion is defined as a single day of the study. A session refers to the year I collected the data. I assigned a value of one for a detection of a particular individual at a location and occasion, and a zero if not detected to create capture histories for all identifiable individuals. For multiple detections of the same individual at the same occasion and location, I treated the detection as a single event. For uncertain marked status individuals (UMS), I recorded the location, occasion, and group designation (if possible) of each detection in a separate data file. All calculations performed in R (R Core Team 2019).

#### *3.3.3.2 Bayesian Methods*

I used Bayesian SCR models in the R package SPIM (Augustine and Royle 2019). I created the habitat mask by digitizing a polygon on the study area that included all wetland areas 5 linear km up and downstream from the trapping array. Because I used natural marks, the total number of "marked" individuals is not known; I added individuals to this category as I identified them. Thus, I used the Metropolis-Hastings algorithm, for the combination of unknown marked status (UMS) and marked individuals. I used the identity categories assigned to each encounter to reduce the uncertainty of resolving the identities of UMS individuals (Murphy et al. 2019). For example, a sighting of an UMS I class male could not be a known individual from any other group, Each individual has an identity covariate designating group, 1 = L, 2 = F, 3 = Y, 4 = I, 5 = A. I assigned a zero for identity covariate for any individual where such assignment could not be made. I assumed the distribution of marked individuals across the landscape was spatially uniform. I used uninformative priors for $g_0$, $\sigma$, $\gamma$ (population proportions for the groups), and $\psi$ (probability that a detection history in the augmented data set belongs to a real individual). For $g_0$, I set initial value of 0.025 and tuning parameter of 0.0007. For $\sigma$, I set initial value of 2.8 km and tuning parameter of 0.175. The $\gamma$ initial values were equal between groups (0.2 for each). I used a Poisson observation model, because I can record > 1 observation per detector per occasion. To start, I ran each year of data with 20000 iterations, with 1000 iterations discarded as burn-in; I augmented the data set with 3000 all-zero detection histories for marked individuals and 1000 all zero detection histories for unmarked individuals. I evaluated the results by examining the posterior densities, acceptance rates for $g_0$ and $\sigma$ between 0.2 and 0.4, and the effective sample size of > 400. Depending on the output, I changed the values of burn-in, iterations, or tuning parameters and ran the model again. To estimate density (D), I divided the results for total animals by the size of the habitat mask. For each year's output, I calculated the mode and 95% credibility intervals for the model parameters $g_0$, $\sigma$, and D.

#### *3.3.3.3 Maximum Likelihood Methods*

I used ML SECR models in the R package secr (v. 3.2.1; Efford 2019) and the add-on package secrlinear (v. 1.1.1; Efford 2017). To create the habitat network, I used a shapefile of Uganda rivers to create the habitat mask (Uganda Energy Sector GIS Working Group, 2014). Using ArcGIS, I relocated each camera trap to the nearest point in the center of the Mayanja River. I clipped the rivers file to include any contiguous section of river within 20 km of one of the traps. I used "networkdistance" to restrict animal movement along the habitat network (Efford et al. 2016). I used a half-normal detection function, a binomial observation model, and proximity detector designation, as individuals could appear at multiple traps on an occasion. I developed a set of ten *a priori* models that included possible sources of variation in sitatunga density. Depending on the model, I allowed a combination of $g_0$, D, and $\sigma$ to vary between sessions (years). For some models I also used *hcov*, a hybrid mixture model, which uses a categorical variable for class membership for two or three groups. Models using *hcov* return a value *pmix* to indicate the proportion of the sampled individuals belonging to each group. In some models I also allowed $\sigma$ and $g_0$ to vary by a categorical covariate, *sex.* I ranked models and evaluated them by Akaike's Information Criterion, corrected for small sample sizes (AICc).

#### *3.3.3.4 TIFC Analysis Methods*

I used camera trap data for TIFC density estimation. I calculated *H* by converting the number of days each camera was deployed and functional into seconds. I considered the first and last days of deployment as active for half a day (12 h). I recorded the time duration covered by the images for each encounter, and the length of time between photographic bursts (hereafter gaps). I separated the gaps into three groups: (1) gaps less than 20 s, (2) gaps between 20 – 120 s, and (3) gaps over 120 s. I followed ABMI's gap length protocol as follows: (1) for gaps < 20 s, I assumed the animal did not leave the field of view between photographic events, hence I included the entire gap length in analysis; (2) for gaps 20 – 120 s, I calculated gap-leaving probabilities to prorate the length of the gap that the animal stayed in the field of view, and this calculated amount was included in analysis;  (3) for gaps > 120 s, I assume the animal left the field of view, then returned to trigger the next photographic event, thus I discarded the entire length of these gaps (Huggard 2018). For encounters consisting of a single image, I assigned a time of 1 s, as this is the average amount of time between photos in 3 second bursts.

To calculate gap-leaving probabilities, I evaluated camera trap data of sitatunga from 2018 for strong evidence if sitatunga did or did not leave the field of view during gaps of 20 – 120 seconds. An example of strong evidence of staying is an animal in roughly the same location in the last image of one burst and the first image in the subsequent burst. Evidence of leaving includes the animal's hindquarters in the last image of one burst and the animal's head in the first image of the subsequent burst. Using a binomial model with a logit link, I fit a smoothing spline to the probability of leaving as a function of gap length. For gap lengths in group (2), I calculated the prorated duration of the gap by multiplying the length of the gap to the probability that the animal stayed during a gap interval of that duration and added those seconds to the total.

I evaluated two values for *r,* 7 m and 5 m. I evaluated 7 m because this is the value calculated by ABMI for the effective detection distance of white-tailed deer, a mammal of similar size to sitatunga, in the densest habitat ABMI evaluates (Huggard 2018; M. Becker, Pers. Comm.). Apps and McNutt (2018) tested the performance of Reconyx Hyperfire cameras, and found that animals approaching the camera directly were detected reliably within 5 m of the camera. This finding, coupled with the growth rate of papyrus, justifies testing *r* at 5 m.

I calculated four density estimates for TIFC: an *r* = 5 m using only the time documented in the images (T-1), r = 5 m and including the probabilistically resolved gap lengths (T-2), and both these tests substituting *r* = 7 m (T-3 and T-4). To calculate 95% confidence intervals, I calculated standard error of the samples by jackknifing. I used the SE to calculate 95% confidence intervals in seconds, which I converted to upper and lower density estimates. I used R package bootstrap (v. 2019.6) for jackknife estimation of SE (R Core Team 2019; Tibshirani and Leisch 2019). I used Microsoft Excel for all other calculations.

## 3.4 Results

I used 24 detection locations in 2015, 16 locations in 2016, and 21 locations in 2017. Average spacing between camera traps was 434 m. Total trap extent was 9525 m. I recorded 767 trap days in 2015, 398 in 2016, and 1552 in 2017. I recorded 129 human observation events in 2015, 92 in 2016, and 135 in 2017.

### *3.4.1 Individual Identification*

I recorded 491 encounters with sitatunga in 2015, 170 in 2016, and 298 in 2017 (Table 3.2). Of all encounters, identifiability within a year ranged from 21.8 % to 54.4%

(Table 3.2). I identified 137 unique individuals in 2015, 42 in 2016, and 34 in 2017 (Table 3.3). In both the identifiable and unidentifiable sets, encounters were biased towards male sitatunga (Table 3.3). Trail cameras recorded the most encounters and the majority of unidentifiable encounters (Table 3.2, 3.4). Among all encounters of male sitatunga, adult males accounted for the largest proportion (Table 3.5).

### *3.4.2 Bayesian Analysis*

The habitat mask surrounded an area of 17.4 km$^2$ (Figure 3.2). I did not achieve the target acceptance rates for σ or effective sample size for any year of data using the baseline parameters. I attempted to resolve this by re-running the model with adjusted tuning parameters and/or number of iterations. I re-ran the 2016 data set twice: once with a total of 30000 iterations, and changing tuning parameters for σ to 0.09, and once with 20000 iterations with σ tuning parameter set to 0.2. These adjusted models also failed to reach target acceptance rates for σ or effective sample size. I re-ran the 2015 data with 100,000 iterations with the original tuning parameters. I achieved the target acceptance rate for σ and effective sample size, but the acceptance rates for $g_0$ fell below the target. For 2015, the estimated density is 28 / km$^2$ (95% CI 22 – 34). I present the results of the re-run Bayesian models for 2015 and 2016, and the 2017 results without any adjustment of original parameterization (Table 3.6).

### *3.4.3 Maximum Likelihood Analysis*

To facilitate analysis as a network of habitat and traps, I used ArcGIS to relocate the traps to the nearest location on the center of the river. Relocation distance ranged from 33 to 682 m ($\bar{x}$ = 368 m, Figure 3.3). Of the ten candidate models, each returned an optimization error when including a file for varying effort for each location, session, and occasion. I received the same error when I used the knownmarks = FALSE option in the details specification. As a result, the models omit both options.

I used a network length of 411 km as the habitat mask. According to AICc, the best model allows density, $\sigma$, and $g_0$ to vary by session (year), and additionally $\sigma$ and $g_0$ vary by the hybrid mixture model (Table 3.7). The population consists of 52% class one and 48% class two. The estimated density is 22 / km of river (95% CI 17 – 26) in 2015, 12 / km of river in 2016 (95% CI 9 – 14), and 7 / km of river in 2017 (95% CI 4 – 9). The detection probability for class one is higher (2017: group 1 $g_0 = 0.019$, group 2 $g_0 = 7.9 \times 10^{-4}$), while the movement parameter for class two is higher (2017: group 1 95% CI 22 – 42 m, group 2 95% CI 647 – 1260 m). Across the three years of the study, estimated population density is declining. The 2015 density estimates from secr and SPIM are comparable.

### *3.4.4 TIFC Analysis*

In 2018, I recorded 35 gap lengths from 20 – 120 seconds. Of these instances, 13 individuals definitively left the field of view during the gap (Figure 3.4). The fitted probability model shows the highest probability of leaving occurs at intermediate gap lengths (Figure 3.5). When including probabilistically resolved gap lengths for sitatunga, the total seconds of individuals in the field of view of trail cameras increases by at least 48% (Table 3.8). For Reconyx Hyperfire cameras, $a = 42°$ (Reconyx, Holmen, Wisconsin, USA). The area of detection, $s$, for $r = 5$ m and 7 m, is $9.16 \times 10^{-6}$ km, and $1.08 \times 10^{-5}$ km respectively. Density estimates from TIFC are higher when using $r = 5$ (T-1 and T-2), and when including resolved gap lengths (T-2 and T-4, Figure 3.6). For 2015, estimated density from TIFC range from 11 (95% CI 9 – 12, T-4) to 30 (95% CI 27 – 33, T-2; Table 3.9). Density estimates from TIFC are comparable to estimates from SECR and SPIM (Figure 3.6).

## 3.5 Discussion

This study is the first to estimate density of sitatunga using camera traps. I used both spatial density methods and a novel model, TIFC, which have comparable results. SECR analysis provides an estimation of sitatunga movement, which is much longer than previously reported for East African sitatunga (Owen 1970). TIFC shows promise for density estimation without requiring individual identification or assumptions about home range. Used in conjunction, spatial density models and TIFC provide population and movement information for a cryptic animal in dense habitats.

SECR and SCR analysis estimates for movement and home range size of Mayanja River sitatunga are larger than expected, being over 1 km for some individuals. The SECR best model shows two classes in the hybrid mixture, with $\sigma$ for group B over 25 times larger than group A. I suggest that group A consists of females, lambs and Y class males, and group B is I and A class males. I frequently observed female sitatunga with and without lambs in the same locations, while adult males ranged widely across the study area (C. Warbington, Pers. Obs.). The group configuration I suggest would align with previous studies indicating that home ranges are small and overlap (May and Lindholm 2002), and that males move more than females as is typical among mammals (Manning 1983). These results indicate that sitatunga movement is heterogeneous between groups, illustrating the usefulness of estimating multiple detection function parameters as is possible with secr.

In addition to elucidating sitatunga movement, my results suggest that sitatunga density is declining over the study period. Other than an actual decline, there are several possible reasons why these results arose. First, the wetland conditions in the study area varied extensively from year to year, which likely affected movement and density estimation.

During 2016, there was a prolonged flood, and in early 2017 there was an extreme drought and bushfires within the wetland. In studies of Zambezi sitatunga, movement changed dramatically between wet and dry seasons, with wetter conditions leading to smaller home ranges (May and Lindholm 2013). In addition, as wetland conditions change the Zambezi sitatunga move up to 12 km to new areas (May and Lindholm 2002). Zambezi sitatunga space use also changes after wildfires, including moving to burned areas to exploit new plant growth (Manning 1983; Ross 1992; May and Lindholm 2002). In another study, I detected that sitatunga decreased their use of dry-land habitats over time, possibly in response to disturbance by cattle and human encroachment (Chapter 5). Second, I placed my camera traps in artificial openings in the wetlands, where cameras and human observers can see sitatunga. The sitatunga may be using the closed papyrus, but I would be unable to detect them. Thus, the changes in habitat conditions or disturbance, coupled with higher than expected movement, could compel sitatunga to relocate to less disturbed areas outside of my trapping array, or to using closed papyrus instead of openings. Instead of an overall population decline, my results could be interpreted as evidence that East African sitatunga in the Mayanja River are more transient and have multiple home range centres in response to water level changes in the wetland, much like the Zambezi sitatunga (Ross 1992; May and Lindholm 2002).

I used three techniques in this study to estimate density of sitatunga. As expected, each method has advantages and drawbacks. The spatial density methods work best when the trapping array is related to the movement of the study species. Specific suggestions for study design are placing two camera traps per home range, or a trap spacing of 2 * $\sigma$ (Royle et al. 2014b; Sun et al. 2014; Milleret et al. 2018). Due to the heterogeneity between the two groups of sitatunga, a larger trapping area might have produced better results. SPIM does not currently allow for estimation of multiple $g_0$ or $\sigma$, offering instead a single estimation of detection function parameters and the proportion of the population that belong to each identity group. This is a major drawback for using SPIM to estimate density for sitatunga and other heterogeneous populations. Density estimation with secr and secrlinear works well for species with long and narrow habitat and movement or detection heterogeneity, but I was unable to use data from UMS encounters. TIFC density estimation requires careful calculation of the effective area of detection, as illustrated by my results. Similarly, whether an animal is likely to leave the area of detection during gaps between photographic bursts is probably species-specific, although advancements in video surveillance of wildlife could eliminate this consideration. Overall, there are a variety of density estimation methods from camera trap data that managers can tailor to the ecology of the species of interest, even if movement is unknown or for unmarked populations.

In this study I show that TIFC provides comparable density estimates to spatial methods. TIFC provides another technique for wildlife managers, especially for unmarked species and dense habitats. TIFC has no underlying assumptions about home range or movement, thus is also useful for data deficient species. For East African sitatunga in Uganda, spatial density models reveal that this population includes two highly heterogeneous groups, in terms of detection probability and movement. My results indicate that both TIFC and spatial density models provide useful information for wildlife management, and that camera traps are a valuable tool for monitoring species when other methods fail.

**Table 3.1.** Published results of density, home range size, movement, and sex ratio for sitatunga in East and Southern Africa

| Location | Subspecies | Authors | Year | Method | Density | Home Range | Movement | Sex Ratio (m:f) |
|---|---|---|---|---|---|---|---|---|
| Saiwa swamp, Kenya | East African | Owen, R | 1970 | Boat and shoreline observations | 7.3 / linear km, or 55 / $km^2$ | -- | 500 m † | -- |
| Akagera, Rwanda | East African | Beudels-Jamar et al. | 1997 | Boat survey | 37 - 57 / $km^2$ | -- | -- | -- |
| Game Areas, Tanzania | East African | Caro, T et al. | 1998 | Aerial Survey | 0.05 - 0.12 / $km^2$ | -- | -- | -- |
| Mayanja River, Uganda | East African | Andama, E | 2018 | Boat and ground Transects | 12 / $km^2$ | -- | -- | -- |
| Okavango Delta, Botswana | Zambezi | Games, I | 1983 | Aerial Survey | 234 ± 138 / 300 $km^2$ or 0.78 / $km^2$ | -- | 100 m † | 1 : 2.5 |
| Bangweulu Swamp, Zambia | Zambezi | Manning, IPA | 1983 | Boat observations | 10 - 20 / $km^2$ | Males: 0.363 $km^2$, Females: 0.176 $km^2$ ‡‡ | 6 miles‡ | 1 : 1 |
| Okavango Delta, Botswana | Zambezi | Ross, K | 1992 | Boat observations | 0.5 / $km^2$ | -- | * | -- |
| Busanga, Zambia | Zambezi | May, J and Lindholm, R | 2002 | Aerial Survey | 0.11 - 0.13 / $km^2$ | 0.09 - 11.8 $km^2$ in dry season; 0.6 $km^2$ wet season †† | †† | 1 : 2 |

† Sitatunga were always resighted within this distance of original sighting location

‡ One male was tracked over this distance

‡‡ Home ranges overlap extensively

* Obvious expansion of movement in response to flooding, but unclear if it is dispersal, migration, or home range expansion

**Table 3.2.** Encounters of sitatunga on the Mayanja River of central Uganda by year, type of observation, identifiability, and the proportion of encounters that are unidentifiable.

| Year | Human observer | Trail Camera | Mortality | Total | Identifiable | Unidentifiable | Proportion Unidentifiable |
|---|---|---|---|---|---|---|---|
| 2015 | 215 | 269 | 7 | 491 | 267 | 224 | 0.456 |
| 2016 | 68 | 99 | 3 | 170 | 73 | 97 | 0.571 |
| 2017 | 37 | 253 | 8 | 298 | 65 | 233 | 0.782 |

**Table 3.3.** Number of (A) total encounters and (B) identified individuals by age or sex and year of sitatunga on the Mayanja River of central Uganda.

(A)

| Year | Males | Females | Lambs | Total |
|---|---|---|---|---|
| 2015 | 200 | 50 | 17 | 267 |
| 2016 | 35 | 31 | 7 | 73 |
| 2017 | 47 | 12 | 6 | 65 |

(B)

| Year | Males | Females | Lambs | Total |
|---|---|---|---|---|
| 2015 | 92 | 32 | 13 | 137 |
| 2016 | 22 | 16 | 4 | 42 |
| 2017 | 23 | 7 | 4 | 34 |

**Table 3.4.** Encounters of unidentifiable or partially identifiable sitatunga by year and (A) age or sex and (B) method of observation. Data from the Mayanja River area of central Uganda

(A)

| Year | Identifiable as male | Identifiable as female | Unknown sex |
|---|---|---|---|
| 2015 | 116 | 60 | 48 |
| 2016 | 44 | 37 | 16 |
| 2017 | 167 | 38 | 28 |

(B)

| Year | Human observer | Trail Camera | Mortality |
|---|---|---|---|
| 2015 | 49 | 173 | 2 |
| 2016 | 18 | 79 | 0 |
| 2017 | 5 | 225 | 3 |

**Table 3.5**. Encounters of (A) identifiable and (B) unidentifiable male sitatunga by age class and year. Data from the Mayanja River area of central Uganda.

(A)

| Year | Adult | Intermediate | Young | Total |
|---|---|---|---|---|
| 2015 | 124 | 52 | 24 | 200 |
| 2016 | 15 | 15 | 5 | 35 |
| 2017 | 39 | 6 | 2 | 47 |

(B)

| Year | Adult | Intermediate | Young | Unknown | Total |
|---|---|---|---|---|---|
| 2015 | 75 | 29 | 6 | 6 | 116 |
| 2016 | 30 | 7 | 3 | 4 | 44 |
| 2017 | 91 | 24 | 7 | 45 | 167 |

**Table 3.6.** Spatial Partial Identity Model (SPIM) point estimates and 95% credibility intervals (CI) for density, scale of the detection function (σ), probability of detection of the animal at a single location on a single occasion if the trap is located at the activity center ($g_0$), parameterizations of the model, effective sample size (*n*) of the model, and acceptance rates for $g_0$ and σ for sitatunga in the Mayanja River area of central Uganda.

| Year | Density (per km$^2$) | Density CI | Mode σ (km) | σ CI (km) | Mode $g_0$ | $g_0$ CI | Iterations | Burn-in | σ Tuning Parameter | Effective *n* | $g_0$ Acceptance Rate | σ Acceptance Rate |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 2015 | 27.2 | 21.7 – 33.5 | 2.04 | 1.71 - 2.70 | 0.0017 | 0.0013 - 0.0020 | 100000 | 0 | 0.175 | 986 | 0.13 | 0.37 |
| 2016a | 10.6 | 6.0 – 16.5 | 2.69 | 1.40 - 8.43 | 0.002 | 0.0010 - 0.0032 | 30000 | 2000 | 0.09 | 132 | 0.28 | 0.83 |
| 2016b | 7.3 | 5 – 12.6 | 3.29 | 2.22 - 30 | 0.0013 | 0.00088 - 0.0025 | 20000 | 2000 | 0.2 | 80 | 0.28 | 0.83 |
| 2017 | 5.9 | 5.1 – 9.5 | 2.32 | 1.63 - 2.74 | 0.0034 | 0.0026 - 0.0054 | 20000 | 1000 | 0.175 | 5.4 | 0.38 | 0.45 |

**Table 3.7.** Maximum likelihood models of density for sitatunga on the Mayanja River area of central Uganda, ranked by Akaike's Information Criterion for small sample sizes (AICc) and weight. Density is the estimated number of animals per km of the river; pmix is the ratio of individuals in each class of the two- or three-class hybrid mixture model; $g_0$ is the probability of detection of a sitatunga at a location on a single occasion if the trap is located at the animal's activity center; σ is the scale parameter for the detection function; hx refers to the group within the hybrid mixture model. I report the point estimate for $g_0$ and the 95% confidence interval for density and σ.

| Model | AICc | ΔAIC | weight | Density | pmix | g0, h1 | σ, h1 | g0, h2 | σ, h2 | g0, h3 | σ, h3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| D ~ year,<br>g0 ~ h2 + year,<br>σ ~ h2 + year | 4763 | 0 | 0.993 | 2015: 17 - 26<br>2016: 9 - 14<br>2017: 4 - 9 | 0.52 : 0.48 | 2015: 0.029<br>2016: 0.023<br>2017:0.019 | 2015: 38 - 59<br>2016: 31 - 48<br>2017: 22 – 42 | 2015: 0.0014<br>2016: 0.00096<br>2017: 0.00079 | 2015: 1129 - 1749<br>2016: 899 – 1411<br>2017: 647 - 1260 | NA | NA |
| D ~ year,<br>g0 ~ h2,<br>σ ~ h2 | 4773 | 10 | 6.69E-3 | 2015: 19 - 29<br>2016: 7 – 11<br>2017: 3 - 6 | 0.51 : 0.49 | 0.00047 | 1089 – 1674 | 0.026 | 39 - 59 | NA | NA |
| g0 ~ h3,<br>σ ~ h3 | 4836 | 73 | 1.4E-16 | 12 to 19 | 0.71 : 0.16 : 0.13 | 0.0041 | 105 – 203 | 0.051 | 31 - 48 | 0.0012 | 1291 - 2417 |
| g0 ~ h2,<br>σ ~ h2 | 4870 | 107 | 5.79E-24 | 9 to 14 | 0.47 : 0.53 | 0.001 | 1094 – 1694 | 0.025 | 39 - 60 | NA | NA |
| D, g0, σ ~ Session | 5081 | 318 | 8.8E-70 | 2015: 13 - 19<br>2016: 7 – 10<br>2017: 3 - 7 | NA | 2015: 0.002<br>2016: 0.002<br>2017: 0.002 | 2015: 826 - 1086<br>2016: 627 - 821<br>2017: 427 - 692 | NA | NA | NA | NA |
| D ~ year,<br>g0 ~ year | 5091 | 328 | 5.93E-72 | 2015: 13 - 19<br>2016: 7 - 10<br>2017: 3 - 6 | NA | 2015: 0.002<br>2016: 0.0015<br>2017: 0.0011 | 773 – 965 | NA | NA | NA | NA |
| D ~ year | 5106 | 343 | 3.28E-75 | 2015: 15 - 2<br>2016: 6 - 9<br>2017: 2 - 4 | NA | 0.0018 | 770 – 982 | NA | NA | NA | NA |
| null | 5205 | 442 | 1.04E-96 | 7.5 - 10 | NA | 0.0018 | 755 – 977 | NA | NA | NA | NA |
| g0 ~ Sex,<br>σ ~ Sex | 5424 | 661 | 2.9E-144 | 7 - 10 | 0.73 : 0.26 | 0.0022 | 635 – 835 | 0.0012 | 950 - 1655 | NA | NA |
| D ~ year,<br>σ ~ h2 | 0 | | | At least one variance calculation failed | | | | | | | |

**Table 3.8.** Total number of seconds trail cameras were deployed and functional, number of seconds an individual sitatunga was recorded in the field of view of a trail camera during the study, and number of seconds an individual sitatunga was in the field of view including probabilistically resolved gap lengths of 20 – 120 seconds between photographic bursts. Data collected in the Mayanja River area of central Uganda.

| Year | Camera deployment (s) | Animal time without gaps (s) | Animal time including resolved gaps (s) |
|---|---|---|---|
| 2015 | 66268800 | 11987 | 17801.7 |
| 2016 | 34387200 | 3247 | 6141.2 |
| 2017 | 134092800 | 5027 | 7927.6 |

**Table 3.9.** Density estimation for time in front of the camera method and 95% confidence intervals calculated from jackknife resampling for sitatunga in the Mayanja River area of central Uganda. EDD is the effective detection distance used in density calculations. Gaps refers to whether or not probabilistically resolved gap lengths between 20 – 120 seconds between photographic events were used in density calculations.

| Year | Model | EDD | Gaps? | Density (/ km$^2$) | 95% CI |
|---|---|---|---|---|---|
| 2015 | T - 1 | 5 | N | 19.7 | 16.7 - 22.8 |
| 2015 | T - 2 | 5 | Y | 29.3 | 26.1 - 32.6 |
| 2015 | T - 3 | 7 | N | 10.1 | 8.52 - 11.6 |
| 2015 | T - 4 | 7 | Y | 12.8 | 13.3 - 16.6 |
| 2016 | T - 1 | 5 | N | 10.3 | 7.96 - 12.7 |
| 2016 | T - 2 | 5 | Y | 19.5 | 16.8 - 22.2 |
| 2016 | T - 3 | 7 | N | 5.26 | 4.06 - 6.46 |
| 2016 | T - 4 | 7 | Y | 9.94 | 8.57 - 11.3 |
| 2017 | T - 1 | 5 | N | 4.09 | 3.51 - 4.67 |
| 2017 | T - 2 | 5 | Y | 6.45 | 5.78 - 7.13 |
| 2017 | T - 3 | 7 | N | 2.09 | 1.79 - 2.38 |
| 2017 | T - 4 | 7 | Y | 3.29 | 2.95 - 3.64 |

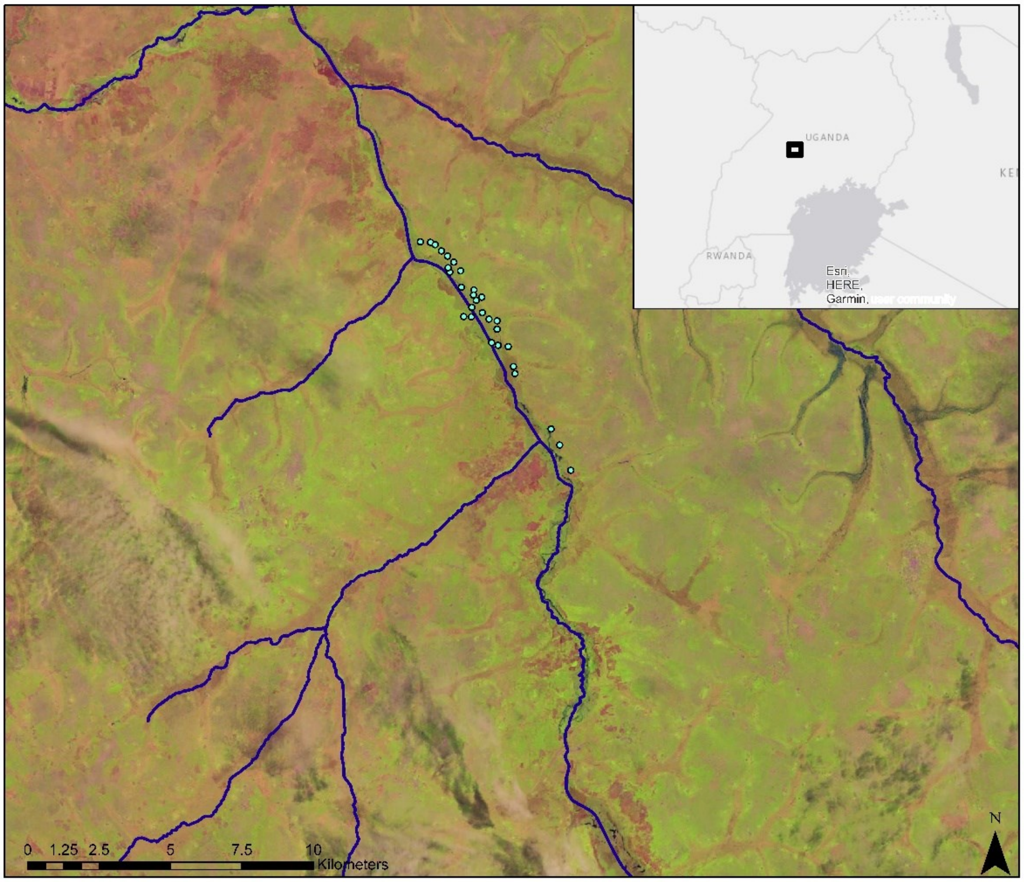


**Figure 3.1.** Mayanja River study area for density estimation of sitatunga via camera traps, central Uganda. Blue dots indicate sampling locations.

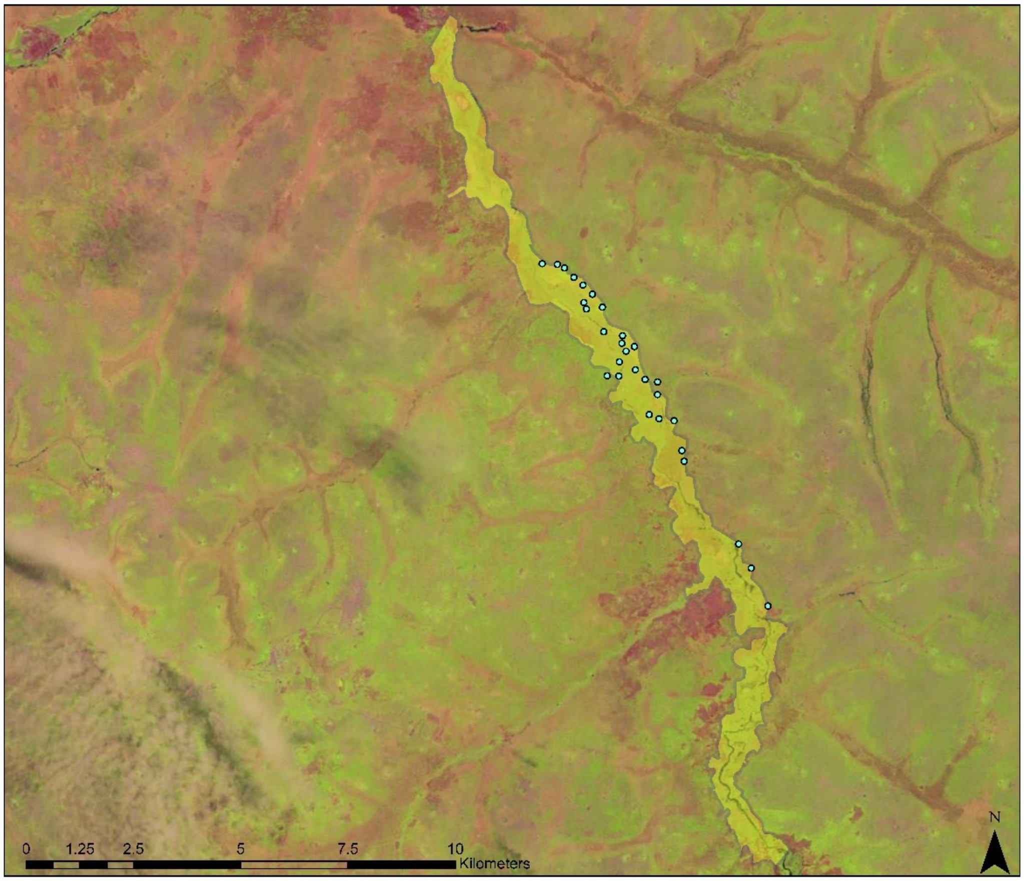


**Figure 3.2.** Wetland habitat mask (yellow polygon) and sampling locations (blue dots) used in Bayesian model of spatially explicit density estimation for sitatunga in the Mayanja River area of Central Uganda.

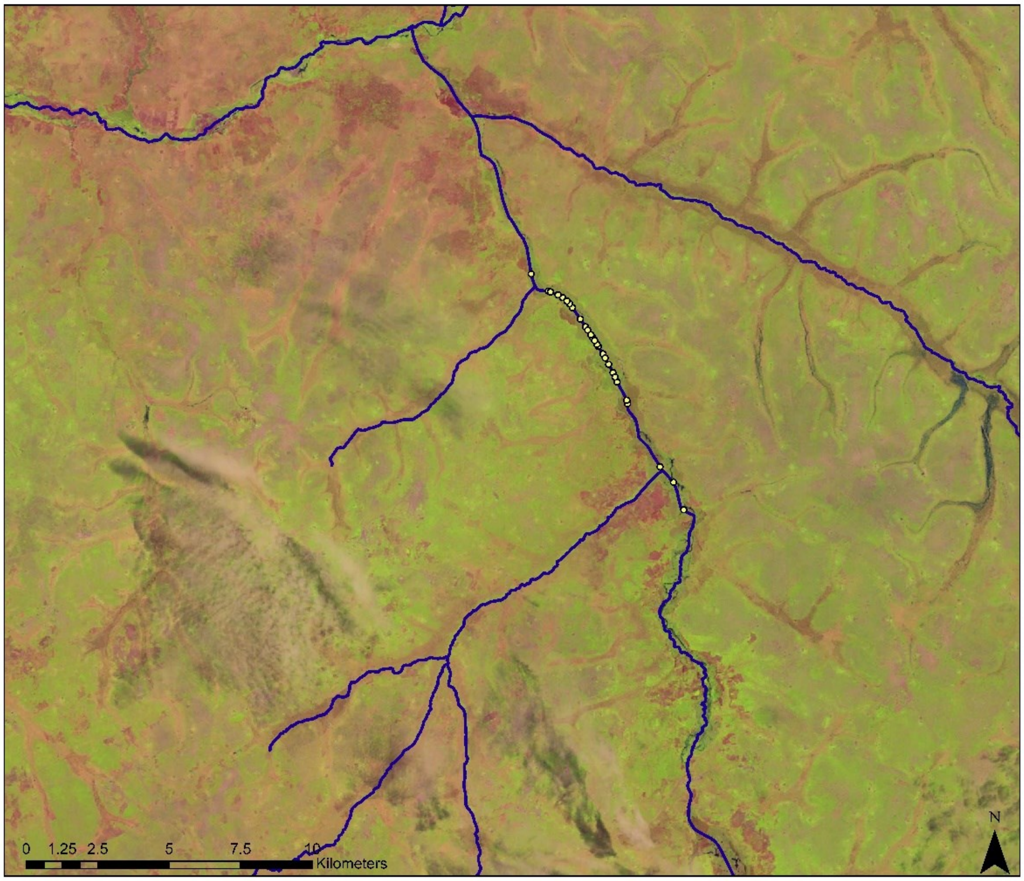


**Figure 3.3.** Network habitat mask and linear trapping array used in maximum likelihood model of spatially explicit density estimation for sitatunga in the Mayanja River area of central Uganda. Yellow dots are the camera traps relocated to the closest river point.

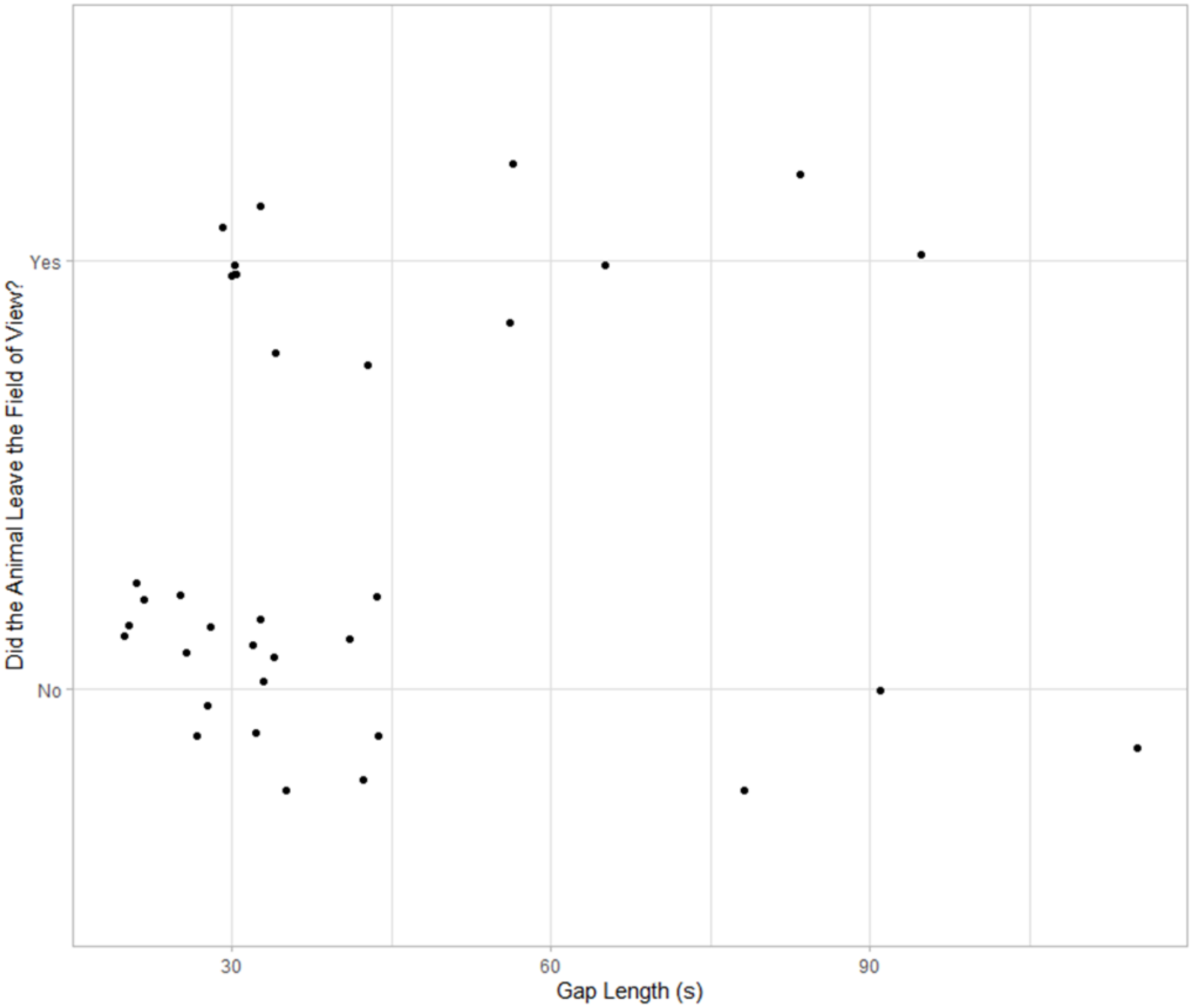


**Figure 3.4.** Record of sitatungas leaving or staying in the field of view of a trail camera during gaps of 20 – 120 seconds between photographic bursts. Data recorded January – April 2018 in the Mayanja River area of central Uganda.

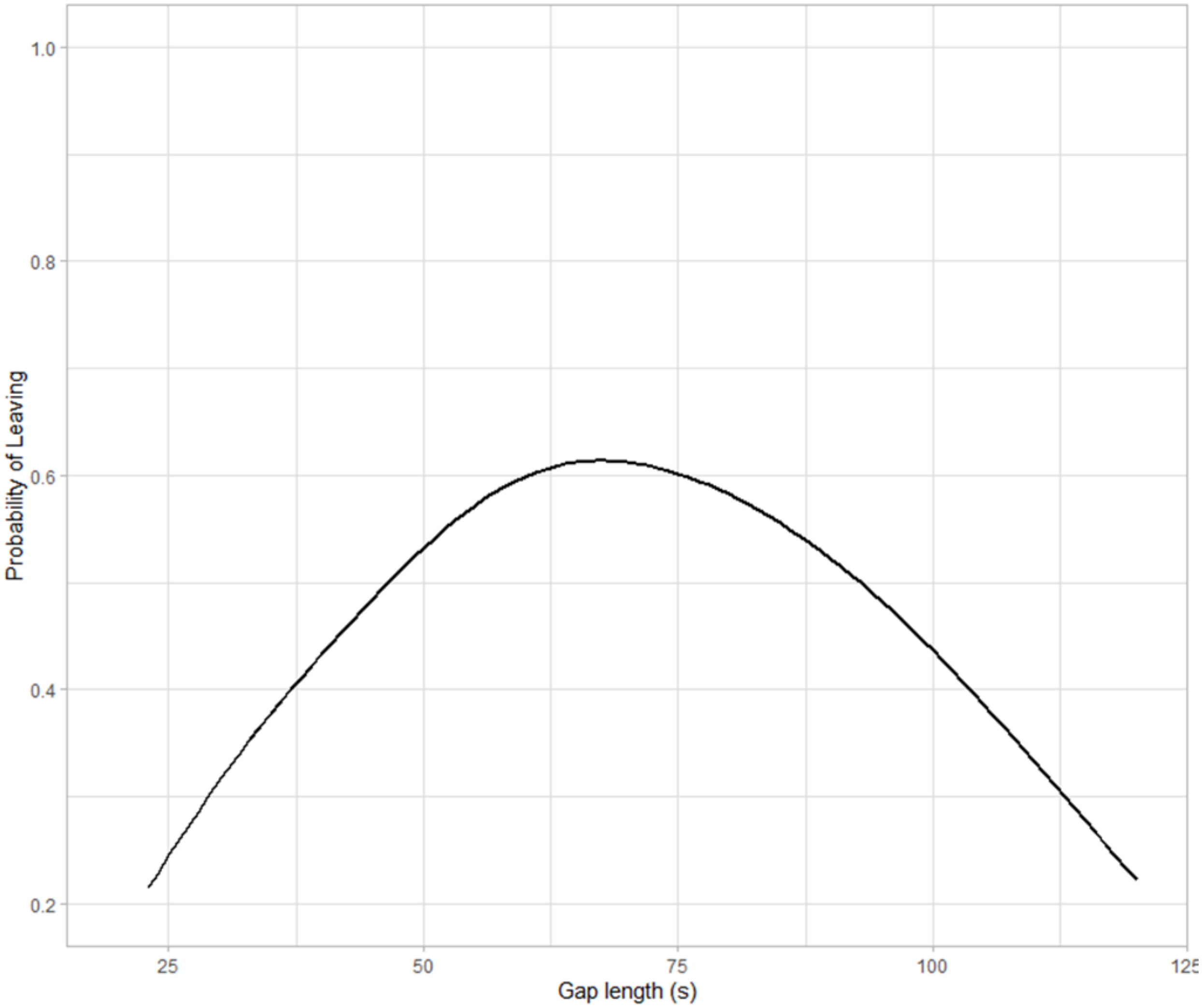


**Figure 3.5.** Fitted probability of sitatunga leaving the field of view of trail cameras as a function of the time between photographic bursts. Data collected January – April 2018 in the Mayanja River area of central Uganda.

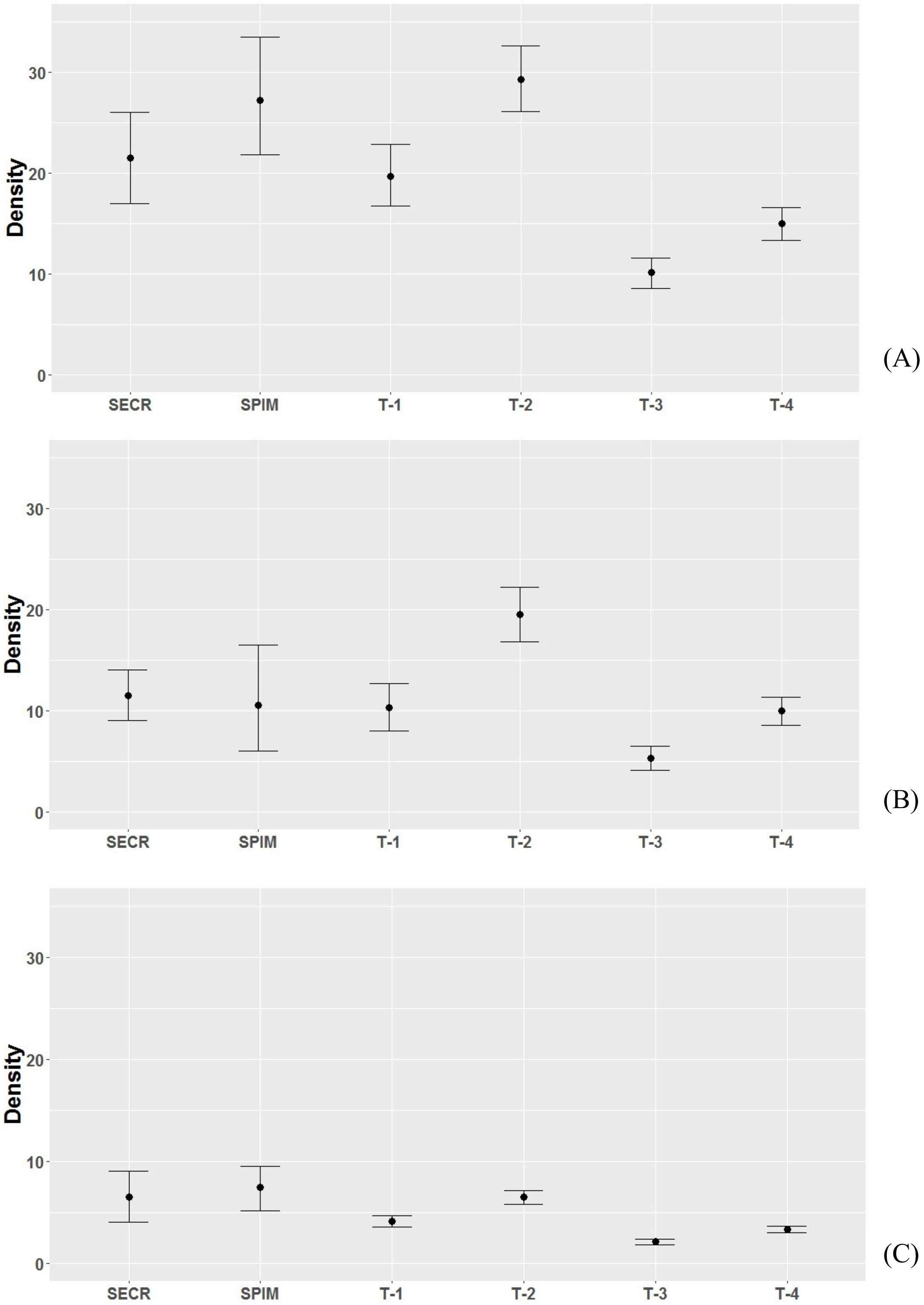


**Figure 3.6**. Comparison of point estimates and 95% confidence intervals calculated by different models for density of sitatunga in the Mayanja River in (A) 2015, (B) 2016, and (C) 2017. Density is animals per km$^2$ except for SECR, which is animals per km of river.

# Chapter 4

## 4 Microsatellite markers and population genetics of free-ranging sitatunga in the Mayanja River area of central Uganda

### 4.1 Introduction

Sitatunga (*Tragelaphus spekii*) is a wetland specialist antelope species with a wide distribution across sub-Saharan Africa (May and Lindholm 2013; Flack 2015). Despite its wide distribution, there are few studies on sitatunga due to the difficulty of working in its dense papyrus wetland habitat (Owen 1970; Manning 1983; Jachmann 2002). As recently as 2008, sitatunga were reported to be endangered in part of their range, but recent studies show that they are more abundant than thought (Ndawula et al. 2011; Chapter 3).

Details of sitatunga dispersal and movement are unclear. As wetland specialists, East African sitatunga primarily use wetland habitats, and are rarely found on dry land (Ndawula et al. 2011; May and Lindholm 2013; Chapter 5).Wetlands are generally patchy in nature, and surrounded by terrestrial habitat (Ceresa et al. 2015). In developing countries, a high proportion of people are dependent on wetland resources (Silvius et al. 2000). The consequences of human use of wetlands include habitat degradation and fragmentation (Sakané et al. 2011), which is exacerbated by climate change (Tockner and Stanford 2002). From 1975 – 2013, Ugandan wetlands decreased in extent by over 45% due to anthropogenic effects, including draining for agriculture (Turyahabwe et al. 2013; Wasswa et al. 2019). Loss of habitats can isolate populations by preventing dispersal and immigration, and isolated populations are at higher risk of decline (Mills 2007). To date, it is unknown if wetland reductions have led to a dispersal barrier for sitatunga. Due to the difficulty in working in sitatunga habitat, we have not observed this facet of sitatunga ecology.

Genetic data provide useful information regarding population connectivity (Lowe and Allendorf 2010; Hoban et al. 2013). Baseline measures of genetic diversity are important for measuring change over time or between subpopulations to detect fragmentation or isolation (Luque et al. 2016). For free-ranging populations, even baseline population genetics such as inbreeding coefficient and single sample estimation of the effective number of breeders can identify populations at risk of decline (Gilpin and Soulé 1986; Morris and Doak 2002). For sitatunga, population genetic data have not been evaluated, and evaluation of single-sample genetic data for sitatunga can provide critical information about extant genetic variability and the connectivity of sitatunga habitat.

In this study, I aim to establish the genetic diversity of a population of sitatunga in central Uganda. My analysis will indicate the connectivity of wetland habitats in the Mayanja River, an area of agricultural and infrastructure development (Uganda Bureau of Statistics 2014; Andama 2019; Bbosa 2019) by evaluating observed heterozygosity ($H_o$), expected heterozygosity ($H_e$), inbreeding coefficient ($F_{is}$), linkage disequilibrium (LD), Hardy-Weinberg equilibrium (HWE), number of subpopulations ($K$), fixation index (in the case of testing for multiple subpopulations, $F_{st}$), admixture ($\alpha$) and estimated size of the breeding population that accounts for the genetic diversity in the present sample ($N_e$). Due to the small area across which I collected samples, I expect all individuals to belong to the same subpopulation ($K = 1$, $F_{st} \approx 0$ (when evaluated), and $\alpha > 1$). I also expect that the Mayanja River area has no barriers to dispersal, thus $H_o \approx H_e$, $F_{is} \approx 0$, no significant LD, and no deviation from HWE.

## 4.2 Methods

The study area consists of 10 km of wetlands encompassing the main channel of the Mayanja River in central Uganda (Figure 4.1). The Mayanja River forms the border between Nakaseke and Kyankwanzi districts. The yearly climate includes two dry seasons, June to August and December to February (Central Intelligence Agency 2014). In Nakaseke district, average annual rainfall is 1282 mm and temperature 22.2° C (Climate-data.org 2019). This land is part of a hunting concession for Uganda Wildlife Safaris, and sitatunga is pursued by hunters mostly from North America and Europe.

I collected samples from sitatunga harvested or found dead in the study area from January 2015 – April 2018. All samples consisted of hide and attached hair. Prior to collection, the hide was dried in salt at ambient temperatures. After collection, I stored samples at ambient temperature in individual paper envelopes inside a sealed plastic bag filled with calcium sulfate desiccant.

Sitatunga DNA samples were purified using QIAGEN DNeasy columns using the tissue protocol (QIAGEN, Hilden, Germany). Wildlife Genetics International (WGI, Nelson, BC, Canada) performed all laboratory work. WGI tested a subsample against 39 microsatellite markers from other ungulate species, including domestic cattle (*Bos taurus*), domestic sheep (*Ovis aries*), and reindeer (*Rangifer tarandus,* Table 4.1). Markers that did not amplify, were invariable, or were difficult to read were excluded from further analysis. Similarly, WGI excluded DNA samples that did not yield high confidence scores for 85% or more of the remaining markers. WGI preformed an error checking protocol to detect genotyping errors. Information about the markers is available at GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

I calculated observed ($H_o$) and expected heterozygosity ($H_e$) using Microsoft Excel. For analysis of $F_{it}$, Hardy-Weinberg equilibrium (HWE) at each locus, and for linkage disequilibrium (LD) between loci, I used Genepop version 4.7.2 (23 June 2019) (Raymond and Rousset 1995; Rousset 2008). For evaluation of HWE, Genepop uses a Markov Chain (MC) algorithm when the loci has four or more alleles. I report $F_{is}$ calculated using the Weir and Cockerham (W&C) method (Weir and Cockerham 1984). Because I made multiple comparisons, I used a Bonferroni correction for analysis of HWE (0.05 / number of loci) and LD (0.05 / number of pairwise comparisons). Null hypothesis for HWE is random union of gametes, and for LD that loci are independent from each other.

To evaluate my prediction that all animals came from a single population ($K = 1$), I used STRUCTURE 2.3.4 (Pritchard et al. 2000; Falush et al. 2003; Falush et al. 2007; Hubisz et al. 2009). I evaluated different numbers of *K,* from 1 – 10, to see if estimated $F_{st}$ varies between models. I configured the simulation with 11 replicates for each K, with 20,000 burn in and 80,000 Markov chain Monte Carlo (MCMC) replications in total. I used the admixture (assuming individuals can have mixed ancestry) model, and independent allele frequency between subpopulations model. I used the simulation outputs to evaluate $F_{st}$ of potential subpopulations and admixture of individual sitatunga in my sample. Specifically, I compared values of $\alpha$, where $\alpha > 1$ implies that most individuals are admixed. I used CLUMPAK to create assignment plots from STRUCTURE output to visually compare admixture between values of *K* (Kopelman et al. 2015).

I estimated effective population size, $N_e$, using the linkage disequilibrium (LD) method (Waples and Do 2010). The LD method generally provides more precise estimates of $N_e$ than other single-sample estimators, and is more effective at small sample sizes

(Waples and Do 2008; Waples and Do 2010). I used NeStimator V2.1 (Do et al. 2014). To decrease bias, I excluded alleles with only one copy in the sample (Waples and Do 2010).

## 4.3 Results

I collected 61 hide samples from adult male sitatunga during the study period. I found 17 of 39 (44%) microsatellite markers amplified and exhibited allelic variation in the sitatunga samples (Table 4.1). Of the 61 samples, 39 yielded high confidence scores for 15 of 17 loci (88%). Thirteen loci appear in all 39 identified individuals. Allelic richness varied from 2 – 10, with a mean of 4.8 ($s = 2.4$).

Expected heterozygosity ($H_e$) per locus varies from 0.30 to 0.80, with a mean $H_e$ of 0.59 ($s = 0.14$, Table 4.2). Observed heterozygosity ($H_o$) per locus varies from 0.26 to 1.0, with a mean $H_o$ of 0.62 ($s = 0.19$, Table 4.1). For loci with more than 4 alleles, I parameterized the MC algorithm with dememorization of 10000, 200 batches, and 5000 iterations per batch to evaluate HWE. Since I performed 17 tests, I used a Bonferroni corrected *P*-value of 0.0029 to evaluate HWE. $F_{is}$ varied from -0.79 to 0.21. I found one loci (BM1225) significantly deviated from HWE; this loci shows an excess of heterozygotes than what would be expected with random mating ($F_{is} = -0.79$, $p < 2.9 \times 10^{-3}$). Mean $F_{is}$ of all loci is - 0.035. Standard error is only reported for loci using the MC algorithm, which was used for loci with more than 4 alleles (Table 4.2). I evaluated LD for each pair of alleles, comprising 136 comparisons. None of the results deviated from the null hypothesis of independent loci (Bonferroni corrected $p > 3.7 \times 10^{-4}$, Table 4.3).

Regardless of number of subpopulations, $F_{st} < 0.06$ (Table 4.4). When $K = 1$, no value of $\alpha$ is returned. However, for $K$ of 2 – 10, $\alpha >> 1$, showing high admixture of individuals. STRUCTURE assignment plots for $K = 2 – 4$ show proportional contributions of DNA for each subpopulation (Figure 4.2).

I calculated two estimates of $N_e$, one with all loci included and one excluding a locus with $H_o = 1$. Results for both analyses include upper confidence limits of infinity (Table 4.5). Including the locus with $H_o = 1$ yielded a high estimate for $N_e$ of 18,383 that was reduced to 1,172 when it was excluded.

## 4.4 Discussion

Results show no evidence of population isolation, as indicated by values for $F_{is}$, $K$, $\alpha$, and $F_{st}$. The inbreeding coefficient including all loci is $F_{is} = -0.5$, and if I exclude BM1222, then $F_{is} = 0$, suggesting no inbreeding in this sample. Because my prediction was that all animals came from a single subpopulation, $K = 1$, I was not able to evaluate $\Delta K$, the second order rate of change of the likelihood, which is often used to estimate an unknown $K$. Similarly, $\alpha$ is not returned for $K = 1$. To support my prediction of $K = 1$, I compared $\alpha$ for larger values of $K$, showing high admixture for all K tested ($\alpha >> 1$). In addition, when I simulated $K > 1$, $F_{st} < 0.06$, suggesting no structure between subpopulations. Finally, STRUCTURE bar plots from CLUMPAK supports my prediction of $K = 1$, with equal proportions of genetic contributions ascribed to each $K$ simulated. Thus I conclude that this population of sitatunga is not reproductively isolated. Results indicate there are no barriers to dispersal or immigration.

Markers developed for other species can be successfully amplified in sitatunga. A recent study of captive bongo (*Tragelaphus eurycerus*) developed microsatellites specific to that species (Combe et al. 2018). Combe et al. (2018) found 9 of the loci from bongo also amplified in sitatunga, which increases the potential microsatellite markers for future sitatunga studies. Because sitatunga and bongo are closely related, it is possible that the successful loci from this study will also amplify in bongo. Recently, Li et al. (2018) mapped the mitochondrial genome for mountain nyala (*Tragelaphus buxtoni*), a close relative of sitatunga. Identification of more multiallelic loci will improve future population genetics studies, provide precise estimates, and facilitate more specific genetic analysis such as parentage (Abdul-Muneer 2014).

Of the loci evaluated, BM1222 showed deviation from Hardy-Weinberg equilibrium. There is an extreme heterozygote excess at this loci, with all individuals having allele 261, and either allele 267 or 269. This type of association cannot be explained by null alleles, thus this loci was included in further analysis. A possible explanation for this pattern is that this loci is associated with the sex chromosomes in sitatunga. Since this sample only included males, it is possible that the Y chromosome includes allele 261, which is why it appears in every individual sampled. The X chromosome, therefore, would have either allele 267 or 269 (D. Paetkau, Wildlife Genetics International, Pers. Comm.). This locus may behave differently in other species due to the peculiarity of the sitatunga sex chromosomes. Sitatunga sex chromosomes are dramatically larger than expected for mammals, and might be due to the translocation of autosomal material in this species. (Wurster et al. 1968). Thus BMC1222 occurs in autosomal DNA in other ungulates, but on the sex chromosomes in sitatunga. Future studies should evaluate female sitatunga at BMC1222 to determine if this explanation holds.

Estimation of $N_e$ is complicated due to the relatively small sample size comprised only of males. In cases of no linkage, the LD method underestimates $N_e$ if the sample size is small (Wang et al. 2016). According to my analysis of LD, it is possible that none of the loci in the sample are linked, but the resulting point estimates for $N_e$ are high. The LD method of $N_e$ estimation improves with a larger sample size – of individuals, loci, and alleles per locus (Waples and Do 2010). Despite data limitations, the $N_e$ estimates of 1172 sitatunga in the breeding population indicates that the sampled sitatunga population in the Mayanja River of Uganda is not reproductively isolated.

Papyrus marshes along the Mayanja River appear to be continuous for at least 70 km, and there are no obvious barriers to dispersal that might impede movement of sitatunga. This result is consistent with the genetic data that indicated no evidence of barriers to dispersal or immigration or that the population was fragmented. Furthermore, the results indicated that the population is well mixed and effective population size is sufficiently large enough to negate concerns about the genetic viability of the population.

**Table 4.1.** Microsatellite loci tested and number of alleles per loci found for sitatunga DNA samples collected from central Uganda 2015-2018.

| Loci | # Alleles |
|---|---|
| BL25 | - |
| BL42 | 9 |
| BM1225 | 3 |
| BM143 | - |
| BM203 | 2 |
| BM2830 | - |
| BM3507 | - |
| BM4028 | - |
| BM4107 | - |
| BM4513 | 6 |
| BM6438 | - |
| BM6506 | 3 |
| BM848 | 5 |
| BM888 | - |
| BMC1009 | 5 |
| BMC1222 | 3 |
| BMS745 | 3 |
| BMS1788 | 5 |
| BOVFSH | 2 |
| CRH | 3 |
| CSSM041 | 6 |
| Eth121 | - |
| Inra011 | 7 |
| Inra107 | 3 |
| OarFCB193 | 10 |
| OheD | - |
| OheQ | - |
| OM51-19 | - |
| OM53-38 | - |
| OM54-23 | - |
| OvirH | - |
| Rt1 | - |
| Rt24 | - |
| Rt27 | - |
| Rt29 | - |
| Rt5 | - |
| Rt6 | 6 |
| Rt7 | - |
| Rt9 | - |

**Table 4.2.** Number of alleles per loci, expected heterozygosity ($H_e$), observed heterozygosity ($H_o$), inbreeding coefficient ($F_{is}$), *p*-value, and standard error (S.E.) for microsatellite loci amplified in 39 sitatunga DNA samples from central Uganda, 2015-2018. *P*-values are testing the null hypothesis of random union of alleles at Bonferroni-corrected $p < 0.0029$.

| Locus | # alleles | $H_e$ | $H_o$ | $F_{is}$ | *p*-value | S.E.* |
|---|---|---|---|---|---|---|
| BOVFSH | 2 | 0.42 | 0.33 | 0.21 | 0.2488 | - |
| BM203 | 2 | 0.42 | 0.54 | -0.28 | 0.1219 | - |
| BMS745 | 3 | 0.49 | 0.54 | -0.08 | 0.769 | - |
| INRA107 | 3 | 0.30 | 0.26 | 0.15 | 0.3965 | - |
| BM1225 | 3 | 0.54 | 0.56 | -0.04 | 0.223 | - |
| BM6506 | 3 | 0.51 | 0.46 | 0.11 | 0.6305 | - |
| BMC1222 | 3 | 0.56 | 1.00 | -0.79 | 0** | - |
| CRH | 3 | 0.65 | 0.57 | 0.14 | 0.6737 | - |
| BMS1788 | 5 | 0.69 | 0.74 | -0.06 | 0.6043 | 0.0028 |
| BM848 | 5 | 0.73 | 0.67 | 0.10 | 0.53 | 0.0029 |
| BMC1009 | 5 | 0.48 | 0.51 | -0.06 | 0.8516 | 0.0026 |
| Rt6 | 6 | 0.56 | 0.59 | 0.01 | 0.4929 | 0.0051 |
| BM4513 | 6 | 0.69 | 0.72 | -0.06 | 0.7721 | 0.003 |
| CSSM041 | 6 | 0.76 | 0.67 | 0.13 | 0.4169 | 0.0038 |
| INRA011 | 7 | 0.80 | 0.86 | -0.06 | 0.8416 | 0.0025 |
| BL42 | 9 | 0.59 | 0.60 | 0.04 | 0.56 | 0.0112 |
| Oar FCB193 | 10 | 0.80 | 0.84 | -0.05 | 0.1181 | 0.0052 |
| AVERAGE | 4.7 | 0.59 | 0.62 | -0.035 | - | - |

* : Standard error calculated when Markov chains are used to calculate p-values (when there are 4 or more alleles at a locus)

** : Deviation from Hardy-Weinberg Equilibrium

**Table 4.3.** Pairwise test of linkage disequilibrium and standard error (S.E.) for microsatellite loci found in $n = 39$ sitatunga DNA samples collected in central Uganda, 2015-2018. Null hypothesis is that loci are independent, at a Bonferroni-corrected $p < 3.7 \times 10^{-4}$.

| Locus#1 | Locus#2 | *p*-Value | S.E. |
|---|---|---|---|
| BMS745 | INRA107 | 0.0480 | 0.0041 |
| BMS745 | INRA011 | 0.6094 | 0.0211 |
| INRA107 | INRA011 | 0.3737 | 0.0189 |
| BMS745 | Rt6 | 0.0184 | 0.0043 |
| INRA107 | Rt6 | 0.7938 | 0.0115 |
| INRA011 | Rt6 | 0.2613 | 0.0266 |
| BMS745 | BM203 | 0.8474 | 0.0043 |
| INRA107 | BM203 | 0.6904 | 0.0059 |
| INRA011 | BM203 | 0.7366 | 0.0120 |
| Rt6 | BM203 | 0.8979 | 0.0055 |
| BMS745 | BM4513 | 0.4039 | 0.0185 |
| INRA107 | BM4513 | 0.8606 | 0.0105 |
| INRA011 | BM4513 | 0.7099 | 0.0312 |
| Rt6 | BM4513 | 0.2128 | 0.0255 |
| BM203 | BM4513 | 0.5599 | 0.0128 |
| BMS745 | BMC1009 | 0.7518 | 0.0112 |
| INRA107 | BMC1009 | 0.6235 | 0.0141 |
| INRA011 | BMC1009 | 0.5550 | 0.0313 |
| Rt6 | BMC1009 | 0.6391 | 0.0238 |
| BM203 | BMC1009 | 0.0890 | 0.0059 |
| BM4513 | BMC1009 | 0.4245 | 0.0312 |
| BMS745 | OarFCB19 | 0.4731 | 0.0227 |
| INRA107 | OarFCB19 | 0.8337 | 0.0128 |
| INRA011 | OarFCB19 | 1.0000 | 0.0000 |
| Rt6 | OarFCB19 | 0.4518 | 0.0334 |
| BM203 | OarFCB19 | 0.1628 | 0.0100 |
| BM4513 | OarFCB19 | 0.5171 | 0.0368 |
| BMC1009 | OarFCB19 | 0.5396 | 0.0317 |
| BMS745 | BM1225 | 0.9928 | 0.0009 |
| INRA107 | BM1225 | 0.9362 | 0.0040 |
| INRA011 | BM1225 | 0.9488 | 0.0072 |
| Rt6 | BM1225 | 0.4355 | 0.0170 |
| BM203 | BM1225 | 0.8254 | 0.0056 |
| BM4513 | BM1225 | 0.3161 | 0.0179 |
| BMC1009 | BM1225 | 0.7059 | 0.0129 |
| OarFCB19 | BM1225 | 0.1779 | 0.0143 |
| BMS745 | BOVFSH | 0.8607 | 0.0043 |
| INRA107 | BOVFSH | 0.1562 | 0.0051 |
| INRA011 | BOVFSH | 0.9993 | 0.0004 |

| Locus#1 | Locus#2 | *p*-Value | S.E. |
|---|---|---|---|
| Rt6 | BOVFSH | 0.4392 | 0.0100 |
| BM203 | BOVFSH | 0.1004 | 0.0038 |
| BM4513 | BOVFSH | 0.8183 | 0.0078 |
| BMC1009 | BOVFSH | 0.2810 | 0.0095 |
| OarFCB19 | BOVFSH | 0.0625 | 0.0057 |
| BM1225 | BOVFSH | 0.6763 | 0.0059 |
| BMS745 | BL42 | 0.9842 | 0.0053 |
| INRA107 | BL42 | 0.2664 | 0.0254 |
| INRA011 | BL42 | 0.1144 | 0.0268 |
| Rt6 | BL42 | 0.9046 | 0.0200 |
| BM203 | BL42 | 0.0870 | 0.0074 |
| BM4513 | BL42 | 0.3324 | 0.0380 |
| BMC1009 | BL42 | 0.1808 | 0.0240 |
| OarFCB19 | BL42 | 0.9897 | 0.0053 |
| BM1225 | BL42 | 0.0650 | 0.0111 |
| BOVFSH | BL42 | 0.3918 | 0.0183 |
| BMS745 | BM848 | 0.3389 | 0.0162 |
| INRA107 | BM848 | 0.0911 | 0.0094 |
| INRA011 | BM848 | 0.1029 | 0.0184 |
| Rt6 | BM848 | 0.3258 | 0.0255 |
| BM203 | BM848 | 0.6395 | 0.0119 |
| BM4513 | BM848 | 0.8229 | 0.0203 |
| BMC1009 | BM848 | 0.8890 | 0.0143 |
| OarFCB19 | BM848 | 0.3931 | 0.0353 |
| BM1225 | BM848 | 0.6581 | 0.0164 |
| BOVFSH | BM848 | 0.2009 | 0.0089 |
| BL42 | BM848 | 0.9683 | 0.0096 |
| BMS745 | BM6506 | 0.0678 | 0.0047 |
| INRA107 | BM6506 | 0.1043 | 0.0059 |
| INRA011 | BM6506 | 0.6323 | 0.0168 |
| Rt6 | BM6506 | 0.3471 | 0.0150 |
| BM203 | BM6506 | 0.9602 | 0.0017 |
| BM4513 | BM6506 | 0.3789 | 0.0169 |
| BMC1009 | BM6506 | 0.7098 | 0.0099 |
| OarFCB19 | BM6506 | 0.6604 | 0.0161 |
| BM1225 | BM6506 | 0.3110 | 0.0092 |
| BOVFSH | BM6506 | 0.5046 | 0.0059 |
| BL42 | BM6506 | 0.8182 | 0.0167 |
| BM848 | BM6506 | 0.0809 | 0.0067 |
| BMS745 | BMC1222 | 0.3320 | 0.0052 |
| INRA107 | BMC1222 | 1.0000 | 0.0000 |
| INRA011 | BMC1222 | 0.2579 | 0.0086 |
| Rt6 | BMC1222 | 0.2867 | 0.0076 |

| Locus#1 | Locus#2 | *p*-Value | S.E. |
|---|---|---|---|
| BM203 | BMC1222 | 1.0000 | 0.0000 |
| BM4513 | BMC1222 | 0.0867 | 0.0042 |
| BMC1009 | BMC1222 | 1.0000 | 0.0000 |
| OarFCB19 | BMC1222 | 0.9215 | 0.0044 |
| BM1225 | BMC1222 | 0.0519 | 0.0025 |
| BOVFSH | BMC1222 | 1.0000 | 0.0000 |
| BL42 | BMC1222 | 0.1212 | 0.0102 |
| BM848 | BMC1222 | 0.4447 | 0.0085 |
| BM6506 | BMC1222 | 0.8577 | 0.0025 |
| BMS745 | BMS1788 | 0.0123 | 0.0031 |
| INRA107 | BMS1788 | 0.7279 | 0.0143 |
| INRA011 | BMS1788 | 0.0270 | 0.0088 |
| Rt6 | BMS1788 | 0.0009 | 0.0005 |
| BM203 | BMS1788 | 0.7159 | 0.0095 |
| BM4513 | BMS1788 | 0.7354 | 0.0274 |
| BMC1009 | BMS1788 | 0.2340 | 0.0261 |
| OarFCB19 | BMS1788 | 0.6558 | 0.0318 |
| BM1225 | BMS1788 | 0.9730 | 0.0037 |
| BOVFSH | BMS1788 | 0.8483 | 0.0080 |
| BL42 | BMS1788 | 0.3603 | 0.0324 |
| BM848 | BMS1788 | 0.4002 | 0.0295 |
| BM6506 | BMS1788 | 0.1377 | 0.0094 |
| BMC1222 | BMS1788 | 0.5519 | 0.0090 |
| BMS745 | CRH | 0.0145 | 0.0028 |
| INRA107 | CRH | 0.1887 | 0.0081 |
| INRA011 | CRH | 0.9066 | 0.0111 |
| Rt6 | CRH | 0.7865 | 0.0129 |
| BM203 | CRH | 0.3224 | 0.0086 |
| BM4513 | CRH | 0.4797 | 0.0190 |
| BMC1009 | CRH | 0.7251 | 0.0152 |
| OarFCB19 | CRH | 0.7430 | 0.0182 |
| BM1225 | CRH | 0.5802 | 0.0099 |
| BOVFSH | CRH | 0.1448 | 0.0051 |
| BL42 | CRH | 0.7008 | 0.0229 |
| BM848 | CRH | 0.0813 | 0.0118 |
| BM6506 | CRH | 0.5230 | 0.0099 |
| BMC1222 | CRH | 0.5111 | 0.0052 |
| BMS1788 | CRH | 0.7711 | 0.0144 |
| BMS745 | CSSM041 | 0.7052 | 0.0174 |
| INRA107 | CSSM041 | 0.1329 | 0.0137 |
| INRA011 | CSSM041 | 0.5184 | 0.0385 |
| Rt6 | CSSM041 | 0.1732 | 0.0208 |
| BM203 | CSSM041 | 0.2841 | 0.0122 |

| Locus#1 | Locus#2 | *p*-Value | S.E. |
|---|---|---|---|
| BM4513 | CSSM041 | 0.4091 | 0.0318 |
| BMC1009 | CSSM041 | 0.0621 | 0.0114 |
| OarFCB19 | CSSM041 | 0.0929 | 0.0221 |
| BM1225 | CSSM041 | 0.8974 | 0.0100 |
| BOVFSH | CSSM041 | 0.9607 | 0.0036 |
| BL42 | CSSM041 | 0.9056 | 0.0219 |
| BM848 | CSSM041 | 0.1580 | 0.0250 |
| BM6506 | CSSM041 | 0.3622 | 0.0162 |
| BMC1222 | CSSM041 | 0.5910 | 0.0098 |
| BMS1788 | CSSM041 | 0.8848 | 0.0175 |
| CRH | CSSM041 | 0.3090 | 0.0187 |

**Table 4.4.** Average estimated probability of the data, variance, admixture (α), and fixation index in the subpopulation ($F_{st}$) values for the number of subpopulations (*K*) simulated in STRUCTURE 2.3.4 for 17 microsatellite loci in 39 sitatunga DNA samples from central Uganda.

| *K* | Ln P(D) | Var[LnP(D)] | α1 | $F_{st\_1}$ | $F_{st\_2}$ | $F_{st\_3}$ | $F_{st\_4}$ | $F_{st\_5}$ | $F_{st\_6}$ | $F_{st\_7}$ | $F_{st\_8}$ | $F_{st\_9}$ | $F_{st\_10}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | -1524.9 | 31.48 | - | 0.002 | - | - | - | - | - | - | - | - | - |
| 2 | -1530.2 | 46.91 | 6.04 | 0.024 | 0.024 | - | - | - | - | - | - | - | - |
| 3 | -1533.3 | 56.17 | 4.76 | 0.038 | 0.058 | 0.033 | - | - | - | - | - | - | - |
| 4 | -1536.6 | 64.28 | 4.07 | 0.043 | 0.042 | 0.039 | 0.052 | - | - | - | - | - | - |
| 5 | -1533.6 | 56.78 | 3.77 | 0.048 | 0.029 | 0.038 | 0.040 | 0.039 | - | - | - | - | - |
| 6 | -1530.3 | 48.02 | 3.87 | 0.032 | 0.029 | 0.029 | 0.033 | 0.028 | 0.035 | - | - | - | - |
| 7 | -1532.9 | 54.08 | 4.83 | 0.044 | 0.043 | 0.048 | 0.036 | 0.032 | 0.044 | 0.038 | - | - | - |
| 8 | -1527.3 | 40.47 | 4.82 | 0.037 | 0.044 | 0.038 | 0.030 | 0.026 | 0.031 | 0.020 | 0.037 | - | - |
| 9 | -1537.6 | 64.92 | 3.36 | 0.031 | 0.034 | 0.032 | 0.036 | 0.040 | 0.033 | 0.042 | 0.042 | 0.051 | - |
| 10 | -1534.1 | 57.25 | 3.26 | 0.037 | 0.033 | 0.038 | 0.034 | 0.036 | 0.042 | 0.042 | 0.035 | 0.033 | 0.054 |

**Table 4.5.** Effective population size ($N_e$) and 95% confidence intervals estimated from microsatellite data of 39 sitatunga DNA samples, excluding alleles appearing in one copy. I performed two tests: all available loci (17), and excluded one loci due to heterozygote excess (16).

| Loci used | Estimated $N_e$ | Lower CI | Upper CI |
|---|---|---|---|
| 17 | 18383 | 161.8 | Infinity |
| 16 | 1172 | 136.9 | Infinity |

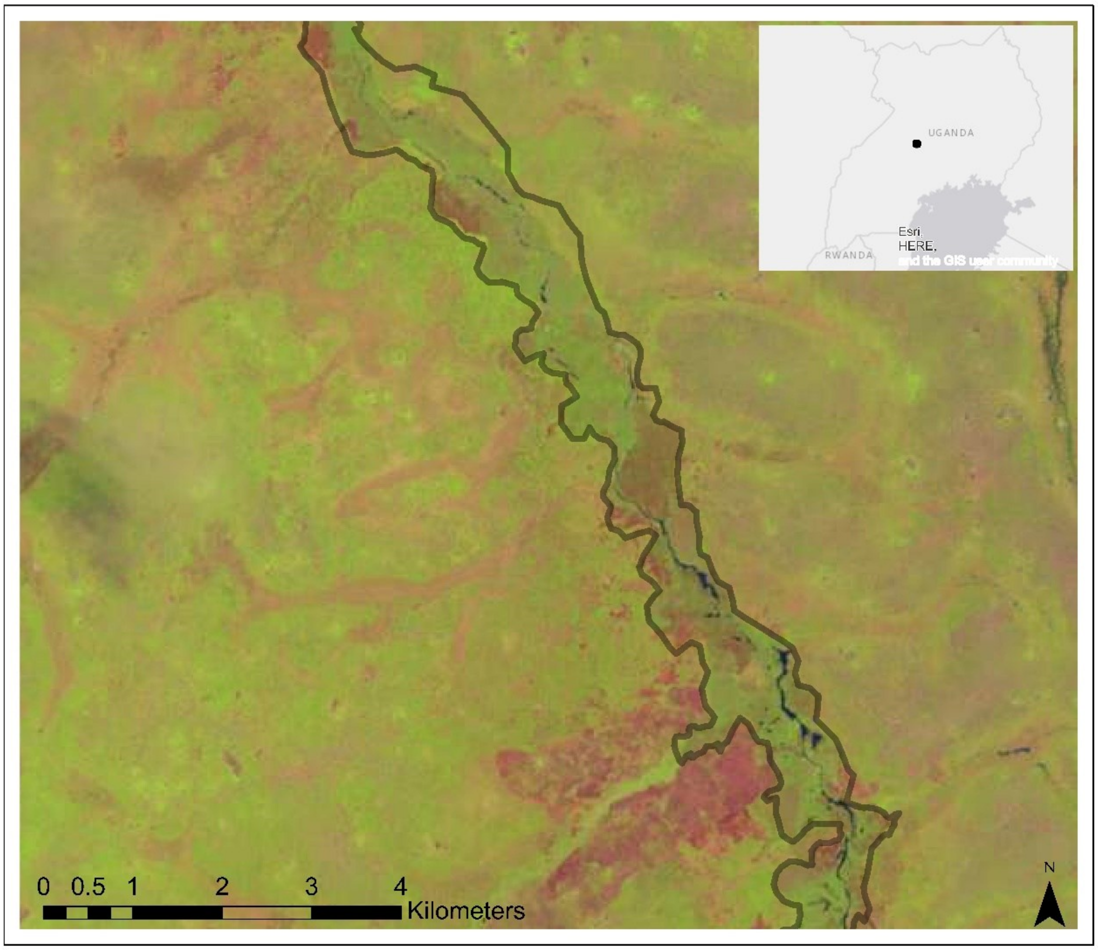


**Figure 4.1** Map of the study area in the Mayanja River area of central Uganda where I obtained sitatunga DNA samples. Grey outline marks the extent of wetland vegetation.

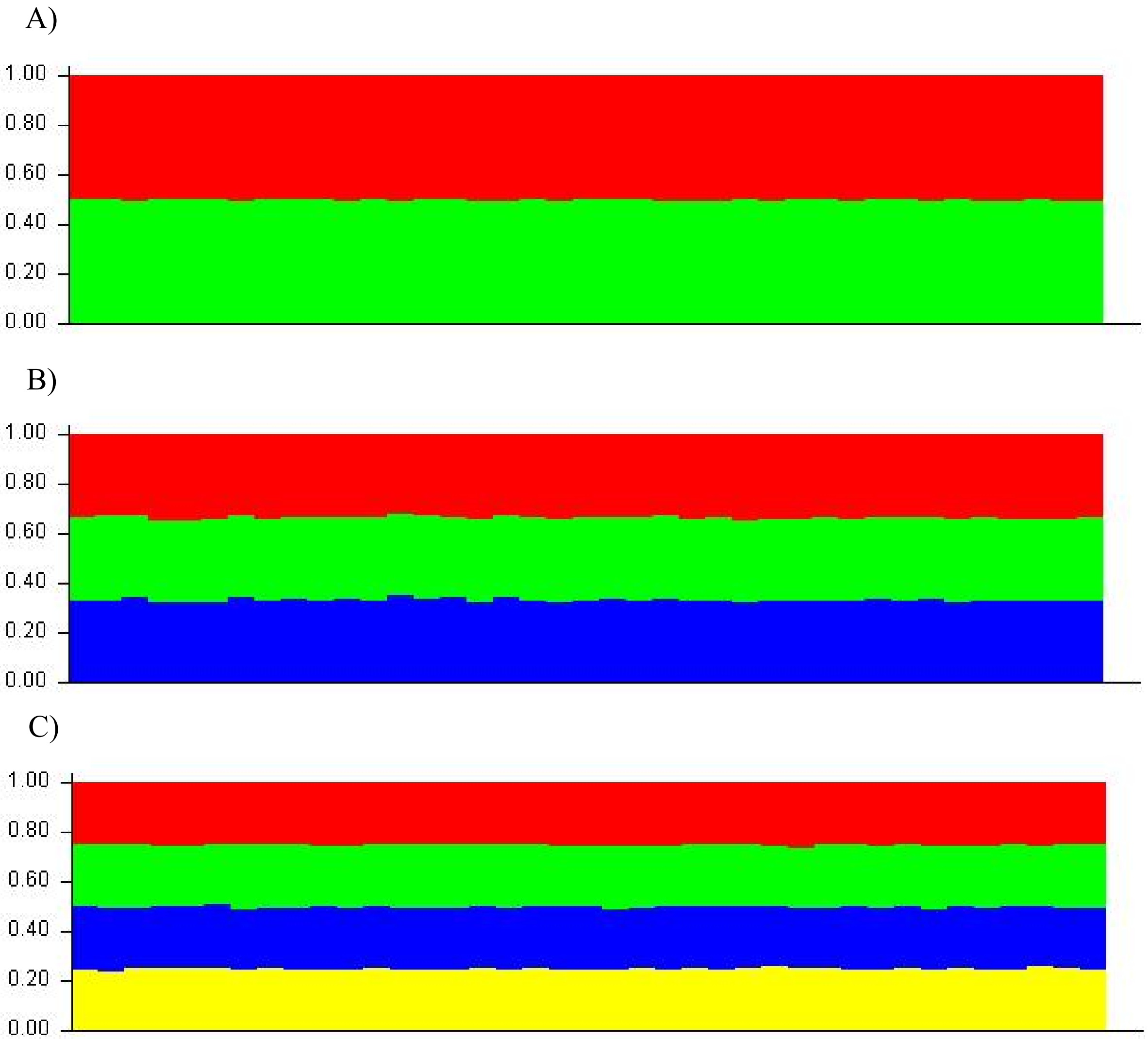


**Figure 4.2.** Bar plots of STRUCTURE results of simulated subpopulation structure for 39 DNA samples of sitatunga from central Uganda identified at 17 microsatellite loci. (A) *K* = 2, (B) *K* = 3, (C) *K* = 4. X-axis is each individual in the data set. Y-axis is the proportion of the individual's genetic profile composed from each *K*. The colors represent the different subpopulations (*K*).

# Chapter 5

## 5 Smoke on the water: Ungulate community dynamics in central Uganda under varying hydrologic conditions

### 5.1 Introduction

Wetlands cover only 6% of the world's land surface, yet they and associated floodplains are among the most altered landscapes worldwide (Tockner and Stanford 2002; Erwin 2009). Wetlands, defined here as ecosystems characterized by inundation at the terrestrial-aquatic interface (Ferrati et al. 2005), are important to well-being, providing benefits such as habitat, carbon sinks, flood control, and peat and fibre production (Groupe d'experts intergouvernemental sur l'évolution du climat 2001). Developing countries have a large proportion of people dependent upon livelihoods involving subsistence agriculture and wetland resources (Silvius et al. 2000). In East Africa, small wetlands are increasingly converted to agricultural production, both for croplands and livestock (Sakané et al. 2011; Namaalwa et al. 2013). In Uganda, where the human population is projected to be over 48 million by 2025 (Uganda Bureau of Statistics 2014), the proportion of wetlands supporting agricultural production and other human uses is expected to increase (Barakagira and de Wit 2017; Mwanjalolo et al. 2018). Previous research has shown that communities living alongside wetlands recognize their value, but that people increase their use of wetland resources and space for cultivation in the absence of regulation and enforcement (Gosling et al. 2017). Even though the value of multifunctional wetlands exceeds the value of wetlands converted to agriculture, the high population of humans living close to wetlands will exacerbate human encroachment (Maclean et al. 2011; Barakagira and de Wit 2017).

In addition to providing ecosystem services to humans, wetlands and riverine floodplains support high biological diversity (Erwin 2009). Ecologists have long been interested in what allows a community of similar species to coexist (Hutchinson 1959). To offset competition, species differ in preferred habitats, food items (e.g. grazers or browsers), or in time of activity (e.g. diel or seasonal scales) (Schoener 1974). In the Serengeti, Sinclair (1985) found that the diverse herbivore community balanced pressures of interspecific competition and predation to facilitate coexistence during seasonal wildebeest migration. The high diversity of large ungulates in Africa extends into wetlands (Junk et al. 2006). In Uganda, this assemblage differs in terms of food items, but habitat use patterns within the floodplain are relatively unknown.

Among the large mammal community in central Uganda, three species associate strongly with water, wetlands, and floodplains. Waterbuck (*Kobus ellipsiprymnus* Ogilby, 1833) are habitat generalists but associate with permanent water (IUCN SSC 2016; Redfern et al. 2003). Hippopotamus (*Hippopotamus amphibious* Linnaeus, 1758), are intermediate in that they rely on water but require grasslands for grazing (Lewison and Pluhacek 2017). Sitatunga (*Tragelaphus spekii* Speke, 1863) are most closely associated with wetlands, having specialized adaptations such as elongated hooves for walking on marsh vegetation (May and Lindholm 2013). However, sitatunga can use dry-land habitats close to swamps and marshes (Ndawula et al. 2011). Other species vary in their use of floodplains and forests along rivers depending on rainfall. A study in Tanzania found that antelope species in a forest-farmland-grassland mosaic used inundated floodplain edges during the wet season (Jenkins et al. 2002), while another study found that large herbivore densities increased in woodlands during the dry season (Dunham 1994). These natural conditions of ungulate communities may not always adapt to anthropogenic perturbations, such as livestock production.

Competition between cattle and native herbivores can occur even if competition between native species does not occur (Voeten and Prins 1999). This is likely due to dietary overlap instead of spatial overlap, as observed in other studies involving native wildlife and livestock (Gordon and Illius 1989; Mishra et al. 2004; Desbiez et al. 2011). Competition for resources is greatest when resources are low, leading to competitive exclusion (Gordon and Illius 1989). While past studies regarding agricultural use of wetlands in Africa have focused on wetland loss to crop production, I am not aware of any that investigated the effects of cattle (*Bos taurus* Linnaeus, 1758) production on wetland wildlife. In semi-arid habitats of East Africa, areas with higher livestock densities had lower mammal species richness, although there is indication that livestock displace wildlife from historic ranges (Ogutu et al. 2014; Kiffner et al. 2019). Similar patterns of species richness and livestock occur in Botswana, but omnivores such as warthog (*Phacochoerus africanus* Gmelin, 1788), were unaffected by human presence (Rich et al. 2016). These results suggest that the responses of wildlife populations to pastoralism are species specific, and should be investigated further. With multiple stressors placed on wetlands in East Africa, understanding the responses of wildlife to these changing conditions is critical for conservation management.

Due to the effects of climate change, hydrologic systems are changing the provisioning of water to wetlands, which only will become more uncertain in the future (Erwin 2009; Engelbrecht et al. 2015). The IPCC predicts new hot climates in the tropics, and extreme weather will increase in frequency and severity (Shukla et al. 2019). Climate change is predicted to increase stress on wetlands, while at the same time the wetlands, and papyrus (*Cyperus papyrus* Linnaeus, 1758) marshes in particular, can buffer against droughts or severe rain events brought about by shifting weather patterns (Erwin 2009; Maclean et al. 2011; Kayendeke et al. 2018; Pacini et al. 2018). Wetland specialist animals, such as sitatunga, face greater risk of extinction due to climate change compared to habitat generalists such as waterbuck (Bennitt et al. 2019). Average annual rainfall in Uganda decreased 12% over the past 34 years, with the greatest decline in agricultural regions, including central Uganda (Ssentongo et al. 2018). In Kenya, aggregate herbivore biomass increased linearly with increasing wet season rainfall in one area, while in another area declines of wildlife occurred due to increased rainfall causing flooding in foraging areas (Ogutu et al. 2012; Ogutu et al. 2017). Due to the reliance of humans and wildlife on wetlands, understanding how populations and ecosystems interact is central for adaptation to climate change and other perturbations.

To assess space use of native and domestic ungulates in various habitats and hydrologic conditions, I used a camera trap array in central Uganda over three years (Amin et al. 2016). I made 5 *a priori* predictions: (1) in forests adjacent to wetlands, there will be an increase in detections of species with strong ecological ties to wetlands or water (hippopotamus, sitatunga, and waterbuck) during high water conditions and a decrease in detections during low water conditions when compared to normal water conditions, (2) wild ungulates that do not associate strongly with wetlands will not vary in detections in the forest according to hydrologic conditions; (3) cattle detections in forests will increase over the course of the study regardless of hydrologic conditions; (4) due to a reduction in available foraging resources outside of wetlands, detections of all ungulate species will increase in accessible wetlands during low water conditions; and (5) in remote wetlands, the wetland specialist species sitatunga will remain high regardless of hydrologic conditions, cattle will not be detected under any condition, and other wild ungulate species will only be detected during low water conditions. Evaluation of these predictions will help unravel mechanisms of species coexistence in and around wetlands under the synergistic effects of livestock production and climate change.

## 5.2 Study Area

The study area lies in central Uganda, in the marshes and floodplain forests of the Mayanja River system, which is part of the Nile watershed (Figure 5.1). In this area, the Mayanja River forms the border between Nakaseke and Kyankwanzi districts. The Equatorial Ugandan climate is generally rainy, with two dry seasons, December to February and June to August, although there is local variation in the length, timing, and duration of the dry seasons (Central Intelligence Agency 2014). In Nakaseke District, the average annual temperature is 22.2 °C, and average annual rainfall is 1282 mm (climate-data.org 2019). Country wide, approximately 11% of the land is cultivated (Central Intelligence Agency 2014).

Ungulate species in the study area included hippopotamus, sitatunga, waterbuck, warthog, bushbuck (*Tragelaphus scriptus* Pallas, 1766), oribi (*Ourebia ourebi* Zimmermann, 1783), bohor reed buck (*Redunca redunca* Pallas, 1767), bushpig (*Potamochoerus larvatus* F. Cuvier, 1822), and common duiker (*Sylvicapra grimmia* Linnaeus, 1758). Forests in the study area were comprised of African fan palm (*Borassus aethiopum* Mart.), acacia (*Acacia sp.*), and other bushland species. Papyrus dominated the wetlands in the study area; giant mimosa (*Mimosa pigra* L.), and various grasses occurred along the wetland/dryland edge, and open water often was colonized by waterlily (*Nymphaea* L.) (C. Warbington, unpublished data). The wetlands within the study area covered approximately 8.1 km$^2$.

During this research, the river level in the study area was markedly higher in 2016 than 2015 (Figure 5.2). High water remained throughout the 2016 field season, April through August. During high-water levels, formerly intermittently inundated soils became saturated, and formerly dry areas adjacent to the wetland were flooded (C. Warbington, Pers. Obs.). In April 2016, culverts under roads crossing the Mayanja river washed away due to high water levels (New Vision, 2016). In 2017, field work began in February, coinciding with the dry season. On the Mayanja River, late 2016 and early 2017 was dryer and hotter than in recent years (Figure 5.3; “Masindi, Uganda Travel Weather Averages (Weatherbase)”, “Masindi, Masindi, Uganda Historical Weather Almanac”; R. Okori and P. Symington, Pers. Comm.). In late January and early February 2017, a substantial portion of wetland burned due to the dry conditions and adjacent shoreline charcoal production. Dry conditions also led to a dieback of normal foraging areas for cattle and a change in water access points due to a retraction of water within the river channel. In 2017, I observed cattle actively entering unburnt shoreline wetlands to eat papyrus and other plants, and to access water; I had not observed this behaviour in previous years. From March 2015 through June 2017, construction of a bridge across the Mayanja River took place upstream from the study area, potentially affecting water flow in the river (Bbosa 2019). The variation in river level allowed me to test hypotheses regarding wildlife and cattle space use during varying wetland conditions.

## 5.3 Methods

For comparisons I defined 2015 as normal-water conditions, 2016 as high water, and 2017 as low-water conditions. For 2015 and 2016, observations were constrained to May through August. In 2016, the water level in the river remained high during this time period. In 2017, field observations occurred February through April, after which the papyrus in burned areas had grown to similar height of unburned areas (C. Warbington, unpublished data).

I separated the floodplain into three zones. (1) Shoreline wetlands were areas of aquatic vegetation visible from a 2-m tall platform situated on dry land, and I accessed trail cameras placed in this zone directly from dry land. (2) River wetlands were not visible from platforms on the shore, and trail cameras in this zone were accessed via canoe across or along a main open-water river channel. (3) Forests were dry-land habitats, defined as areas of non-inundated soils, devoid of aquatic vegetation, comprised mainly of woody stems, and a closed canopy at least 2-m in height. Forest zones were not flooded during the high-water conditions of 2016. I placed Forest trail cameras within 20 m of wetland edge. Undisturbed papyrus grows in high density, thus to increase visibility and chance of capturing unobstructed images I placed Shoreline and River trail cameras in papyrus stands cut to ≤ 20 cm in height by workers using machetes. No bait was used, but I attempted to place all trail cameras in areas with evidence of high use, evidenced by game trails, bedding areas, and wildlife feces. I used some of the same camera locations in each year of the study; due to accessibility during high and low water conditions in the wetlands, locations of some cameras in the Shoreline and River zone varied between years.

I used Reconyx HyperFire trail cameras with semi-covert infrared flash for night time surveillance (Reconyx, Holmen, Wisconsin USA). I programmed the cameras to take pictures at all times when triggered by the motion sensor, with no delay between photographic captures. I programmed the camera to take a picture at noon every day as verification that the camera was still operational even if there was not a triggering event that day. I visited the cameras approximately every four weeks to change memory cards, replace batteries, and clear the camera site from vegetation encroachment.

I defined a unique encounter as a photographic capture of at least one individual of an identifiable species for a unique date and camera combination. I used an interval of 30 minutes to differentiate between encounters. I classified a photographic capture event as “unknown” when not enough of the animal was depicted in the image for identification of species, or when camera malfunction obscured part of the image. The images classified as “unknown” were excluded from analysis. I defined a camera day as a single day that a single camera was deployed and functional. To constrain the test proportions to between zero and one, I defined the numerator as the number of camera days with at least one detection of the species in question, and the denominator is the total number of camera days for a given zone and hydrologic condition.

Within a species-zone combination, I tested for a difference in proportions between years using the function prop.test that calculates a modified chi-squared statistic using program R version 3.5.1 (R Core Team 2018). I compared the calculated *p*-value to a significance level of 0.05 to test hypotheses. I analysed proportions only when there were at least 5 encounters for 2 of the 3 years of the study.

Protocols for animal use were approved by the Animal Care and Use Committee for Biosciences (University of Alberta, Research Ethics Office, protocol AUP00001399).

## 5.4 Results

I deployed a total of 27 cameras in 2015 (normal water conditions), 25 in 2016 (high), and 26 in 2017 (low). During low-water conditions (2017), I experienced a series of camera failures in the Shoreline zone. Malfunctions included one camera that took a picture every second until the batteries failed (approximately 3 days after deployment), camera poles falling into the water, insect invasion, and human interference. The camera failures resulted in an artificially low number of days where cameras were deployed and functional, as well as low detections of any animal, resulting in small sample size and corresponding proportions unsuitable for testing. Thus, the data for Shoreline wetlands during low water were excluded from analysis.

Cameras detected over 20 species of terrestrial vertebrates during the course of the study. Unknown or unidentifiable images constitute < 2.5% of all encounters. In the Forest zone, I met the threshold for detections – 5 or more in at least 2 years of the study – for bushbuck, bushpig, cattle, hippopotamus, sitatunga, warthog, and waterbuck. In the Shoreline and River Zones, I met the threshold for detections for sitatunga only (Table 5.1).

I only detected cattle with camera traps in the Forest (Table 5.1). Within the Forest, the proportion of days with a cattle detection did not differ between normal and high-water years, but the proportion increased during low water (Table 5.2, Figure 5.4).

Cameras detected sitatunga in all three zones over the course of the study. However, there were no sitatunga detections in the Forest during the low-water year (Table 5.1). The proportion of days with a sitatunga detection decreased between normal and high-water conditions in both the Shoreline and the Forest, while staying consistent in the River for all years of the study (Table 5.2, Figure 5.5).

For other species of ungulate in the Forest zone, over the three years of the study I detected increasing proportions of days with a detection of at least one individual for bushbuck, bush pig, hippopotamus, and waterbuck (Table 5.2, Figure 5.4). I did not detect any change in the proportion of days with a detection of warthog over the course of the study, 2015 - 2017 (Figure 5.4).

## 5.5 Discussion

In the Mayanja River area of central Uganda, I expected the ungulate community to alter space use in three habitat types depending on the prevailing hydrologic conditions in the river. Specifically, I predicted more frequent use of wetlands under drought conditions by all species due to resource limitation. I did not detect a strong effect of hydrologic condition, but I did identify partitioning that probably contributes to coexistence for this community (Schoener 1974).

For sitatunga, use of River zone wetlands did not vary according to water level, and use of Shoreline wetlands and Forest decreased during high water levels. Sitatunga possess specialized adaptations for life in wetlands, so it is not surprising that permanent wetlands were their preferred habitats (East 1998). I did not detect cattle in the River wetlands during any part of this study; sitatunga did not compete with cattle because they chose remote wetlands for foraging. Similarly, sitatunga in remote wetlands also avoid the consequences of cattle grazing, including vegetation trampling and water fouling (Games 1983; Pacini et al. 2018). I did record more species using the remote wetlands during the dry year, but a lack of detections in previous years precluded statistical comparison (Table 5.1). These results indicate that sitatunga use of wetlands constitutes spatial segregation from the other ungulates in the community, thus reducing any detrimental effects of competition. This study reiterates the importance of wetlands for sitatunga management.

Cattle are a novel competitor for native ungulates. Due to dietary overlap, we expect cattle to compete with other grazers, hippopotamus and warthogs, as well as intermediate grazers-browsers, waterbucks (Desbiez et al. 2011; IUCN SSC 2016; Lewison and Pluhacek 2017; Oliver 1993). To ensure coexistence, animals with strong dietary overlap might differ in terms of time of activity or space use (Schoener 1974); a companion study used the same set of camera trapping data to explore diel differentiation for this community (Appendix A). Cattle and hippopotamus have low daily temporal overlap, while cattle and warthogs have high overlap. In this study area, herdsmen constantly attend the cattle, driving them to water access points, grazing areas, and bomas for protection overnight. While hippopotamus emerge from the river to graze at night, warthog activity was diurnal, like the cattle (Lewison and Pluhacek 2017, Apendix A). Cattle use of forests was likely due in part for foraging, but also as shelter from heat stress during the day. Surveyed habitats did not include rangeland or grassland where we might expect direct competition for grazing resources. Due to temporal and dietary overlap, spatial segregation between cattle and warthog might be critical to coexistence.

Among other species, waterbuck and bushbuck also show increased use of forests over time and have high temporal overlap (Appendix A). The increase in waterbuck and bushbuck detections in the dry year mirrors the findings from Dunham (1994); however, these species do not have dietary overlap except possibly during periods of resource scarcity (East 1998; IUCN SSC 2016). This could explain the increase in proportion of days with a detection over time for most species in the Forest zone. Warthog detections did not change over the course of the study, likely because forests are not their preferred habitat (Oliver 1993). The increase in bushpig detections in the drought year could be due to relief from the heat, or for underground foraging when other resources are scarce (Oliver 1993). The high daily activity overlap and increased detections in the forests for bushpigs, hippopotamus, and waterbuck are offset by dietary differences (IUCN SSC 2016; Lewison and Pluhacek 2017; Oliver 1993, Appendix A). While overall days with a detection of species increased over time in the Forest zone, the results from the Shoreline zone are not as clear.

Due to equipment failures, I was unable to analyse space use of Shoreline wetlands during low-water levels. Although trail cameras did not record cattle entering the Shoreline zone, I personally observed cattle entering these areas to eat papyrus and access water but only during 2017. Similarly, I cannot conclude that other ungulates did not use Shoreline wetlands during the drought, because detections of native ungulate species increased in the River zone (Table 5.1). During the study, cattle density and charcoal production changed the layout of habitats that herdsman would choose for the cattle (C. Warbington, Pers. Obs.). Change in cattle space use and habitat configuration could affect the space use of ungulates more than the water level in the river (Voeten and Prins 1999; Ogutu et al. 2014). In the forests, sitatunga was the only species that decreased over time. However, since I did not have a dry-land habitat that excluded cattle while allowing sitatunga to access it, I cannot determine if sitatunga were actively avoiding areas with heavy cattle presence, i.e., dry-land habitats. Previous studies indicate that sitatunga will use dry-land habitats in addition to wetlands, thus it remains important for future studies to determine if cattle or human encroachment is affecting sitatunga habitat use (Games 1983; Starin 2000). For social ungulates, including waterbuck and warthog, cattle production affects group size and composition, perhaps to increase vigilance behaviour in altered landscapes (Averbeck et al. 2012). Other herbivore behavioural responses to human presence include changing diet and activity patterns to be more active at night (Desbiez et al. 2011; Gaynor et al. 2018; Ehlers Smith et al. 2019). The projected human population growth in Uganda will increase the amount of anthropogenic disturbance in wetlands and floodplains, thus the impacts of human development on wildlife and habitats must be addressed (Turyahabwe et al. 2013; Uganda Bureau of Statistics 2014; Gideon and Bernard 2018; Mwanjalolo et al. 2018; Wasswa et al. 2019).

## 5.6 Conclusion

Human agricultural development in central Uganda affects the native ungulate community by altering habitat configuration and introducing cattle as a novel competitor. In this study I measured the proportion of days with a detection of at least one individual of each species, an indirect measure of intensity of use of different habitats. Sitatunga are unique in the community, as their use of wetlands remained constant over time while use of dry land decreased. Multiple ungulate species with and without close ties to water increased their use of forest habitats over time regardless of water level, suggesting that other factors affect space use for this community. While there is evidence that niche partitioning is currently sufficient to allow coexistence of native and introduced ungulates, wetland conservation measures are critical to ensure buffering against climate change and for human and ecosystem well-being.

**Table 5.1** Camera-trap detections of mammals under varying hydrologic conditions in three habitat zones of the Mayanja River of central Uganda. Camera days are the number of days that a camera was deployed and functional, summed across all cameras for a given zone / hydrologic condition. Proportion is the proportion of trap days with a detection of at least one individual of the species in question.

| Species | Zone | 2015 Camera Days | 2015 Encounters | 2015 Proportion | 2016 Camera Days | 2016 Encounters | 2016 Proportion | 2017 Camera Days | 2017 Encounters | 2017 Proportion |
|---|---|---|---|---|---|---|---|---|---|---|
| Aardvark | Forest | 318 | 3 | 0.009 | 286 | 2 | 0.007 | 168 | 6 | 0.036 |
| Baboon | Forest | 318 | 7 | 0.022 | 286 | 16 | 0.056 | 168 | 34 | 0.202 |
| Banded Mongoose | Forest | 318 | 0 | 0 | 286 | 1 | 0.003 | 168 | 0 | 0 |
| Bushbuck | Forest | 318 | 46 | 0.145 | 286 | 105 | 0.367 | 168 | 116 | 0.690 |
| Bushpig | Forest | 318 | 24 | 0.075 | 286 | 22 | 0.077 | 168 | 53 | 0.315 |
| Cattle | Forest | 318 | 9 | 0.028 | 286 | 10 | 0.035 | 168 | 20 | 0.119 |
| Colobus Monkey | Forest | 318 | 1 | 0.003 | 286 | 5 | 0.017 | 168 | 7 | 0.042 |
| Hippopotamus | Forest | 318 | 10 | 0.031 | 286 | 26 | 0.091 | 168 | 22 | 0.131 |
| Human | Forest | 318 | 4 | 0.013 | 286 | 5 | 0.017 | 168 | 10 | 0.060 |
| Large Spotted Genet | Forest | 318 | 0 | 0 | 286 | 1 | 0.003 | 168 | 1 | 0.006 |
| Leopard | Forest | 318 | 0 | 0 | 286 | 1 | 0.003 | 168 | 0 | 0 |
| Marsh Mongoose | Forest | 318 | 0 | 0 | 286 | 2 | 0.007 | 168 | 0 | 0 |
| Porcupine | Forest | 318 | 1 | 0.003 | 286 | 5 | 0.017 | 168 | 2 | 0.012 |
| Reedbuck | Forest | 318 | 0 | 0 | 286 | 3 | 0.010 | 168 | 2 | 0.012 |
| Serval | Forest | 318 | 0 | 0 | 286 | 0 | 0 | 168 | 1 | 0.006 |
| Sitatunga | Forest | 318 | 33 | 0.104 | 286 | 4 | 0.014 | 168 | 0 | 0 |
| Unknown | Forest | 318 | 3 | 0.009 | 286 | 1 | 0.003 | 168 | 13 | 0.077 |

| Species | Zone | 2015 Camera Days | 2015 Encounters | 2015 Proportion | 2016 Camera Days | 2016 Encounters | 2016 Proportion | 2017 Camera Days | 2017 Encounters | 2017 Proportion |
|---|---|---|---|---|---|---|---|---|---|---|
| Vervet Monkey | Forest | 318 | 3 | 0.009 | 286 | 16 | 0.056 | 168 | 17 | 0.101 |
| Warthog | Forest | 318 | 17 | 0.053 | 286 | 3 | 0.010 | 168 | 14 | 0.083 |
| Waterbuck | Forest | 318 | 32 | 0.101 | 286 | 40 | 0.140 | 168 | 59 | 0.351 |
| Reedbuck | Shore line | 98 | 0 | 0 | 508 | 3 | 0.006 | † | † | † |
| Sitatunga | Shore line | 98 | 15 | 0.153 | 508 | 25 | 0.049 | † | † | † |
| Marsh Mongoose | River | 1357 | 1 | 0.001 | 587 | 0 | 0 | 1012 | 0 | 0 |
| Genet, Large Spotted | River | 1357 | 2 | 0.001 | 587 | 0 | 0 | 1012 | 0 | 0 |
| Waterbuck | River | 1357 | 0 | 0 | 587 | 6 | 0.010 | 1012 | 0 | 0 |
| Bushbuck | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 1 | 0.001 |
| Bushpig | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 2 | 0.002 |
| Hippopotamus | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 17 | 0.017 |
| Rodent | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 1 | 0.001 |
| Serval | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 2 | 0.002 |
| Unknown | River | 1357 | 0 | 0 | 587 | 0 | 0 | 1012 | 1 | 0.001 |
| Sitatunga | River | 1357 | 157 | 0.116 | 587 | 54 | 0.092 | 1012 | 127 | 0.125 |

†: in the shoreline zone of 2017, multiple camera malfunctions resulted in data loss and inability to calculate statistics

**Table 5.2** Chi-squared test of proportions for the given species during different hydrologic conditions in the stated zone of the Mayanja River, central Uganda. “Comparison” lists the years for which the test was run.

| Species | Zone | Comparison | $\chi^2$ | p-value | Comparison | $\chi^2$ | p-value | Comparison | $\chi^2$ | p-value |
|---|---|---|---|---|---|---|---|---|---|---|
| Bushbuck | Forest | 15, 16 | 38.572 | 5.23E-10† | 16, 17 | 43.006 | 5.46E-11† | 15, 17 | 14493 | 2.2E-16† |
| Bushpig | Forest | 15, 16 | 6.35E-30 | 1 | 16, 17 | 41.959 | 9.32E-11† | 15, 17 | 45.707 | 1.37E-11† |
| Cattle | Forest | 15, 16 | 0.055218 | 0.8142 | 16, 17 | 10.8 | 0.001015† | 15, 17 | 14.556 | 0.000136† |
| Hippopotamus | Forest | 15, 16 | 8.4675 | 0.003616† | 16, 17 | 1.3963 | 0.2373 | 15, 17 | 16.115 | 5.96E-05† |
| Sitatunga | Forest | 15, 16 | 19.577 | 9.66E-06† | 16, 17 | 1.0395 | 0.0379† | 15, 17 | 17.1 | 3.55E-05† |
| Warthog | Forest | 15, 16 | 7.3935 | 0.006546† | 16, 17 | 13.625 | 0.000223† | 15, 17 | 1.1807 | 0.2772 |
| Waterbuck | Forest | 15, 16 | 1.8494 | 0.1739 | 16, 17 | 26.494 | 2.64E-07† | 15, 17 | 43.717 | 3.8E-11† |
| Sitatunga | River | 15, 16 | 2.1406 | 0.1434 | 16, 17 | 3.8266 | 0.05045 | 15, 17 | 0.43864 | 0.5078 |
| Sitatunga | Shoreline | 15, 16 | 12.736 | 0.000359† | -- | -- | -- | -- | -- | -- |

**† -** Significant at $p < 0.05$

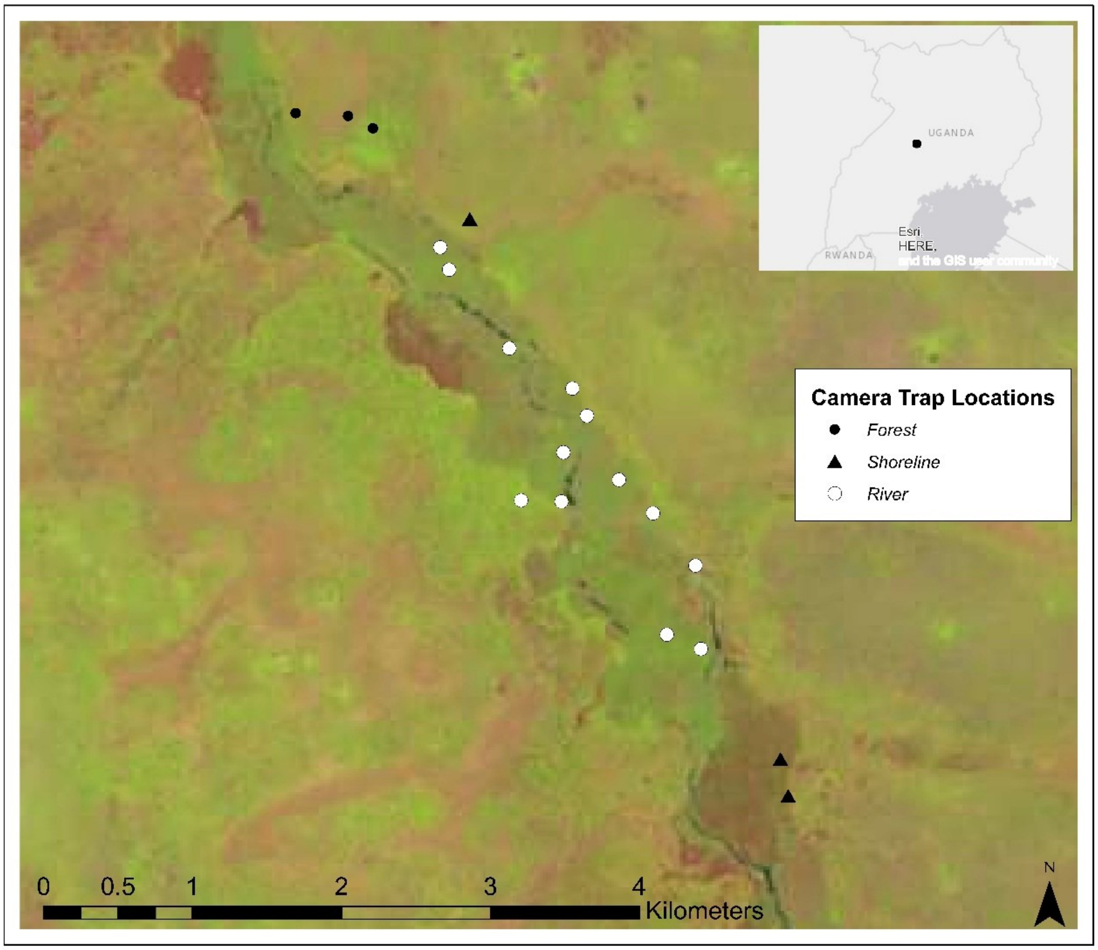


**Figure 5.1** Map of the study area for ungulate space use in three different habitat types on the Mayanja River of central Uganda.

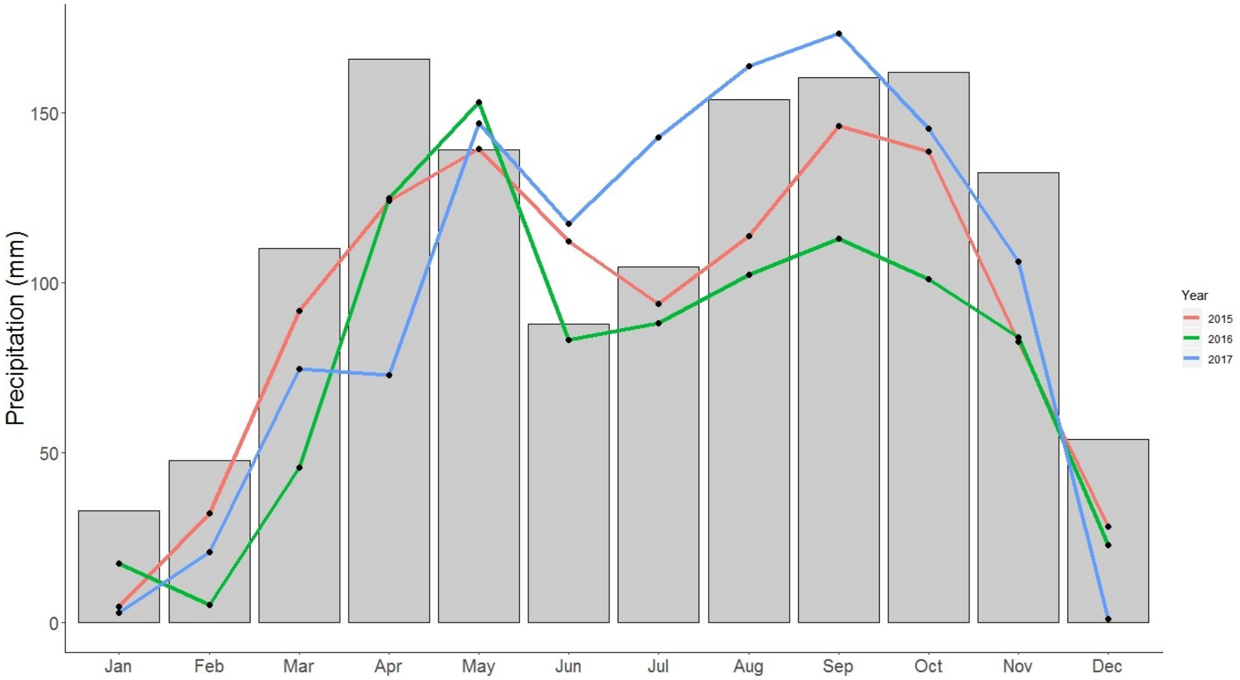
A. 2015

B. 2016

C. 2017

**Figure 5.2** Depiction of the hydrologic conditions encountered on the Mayanja River of Central Uganda during the three seasons of the study. 2015 represents the normal water year, 2016 shows high water conditions, and 2017 low water conditions.

(a)


Precipitation (mm)
0
50
100
150
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Year
2015
2016
2017

(b)

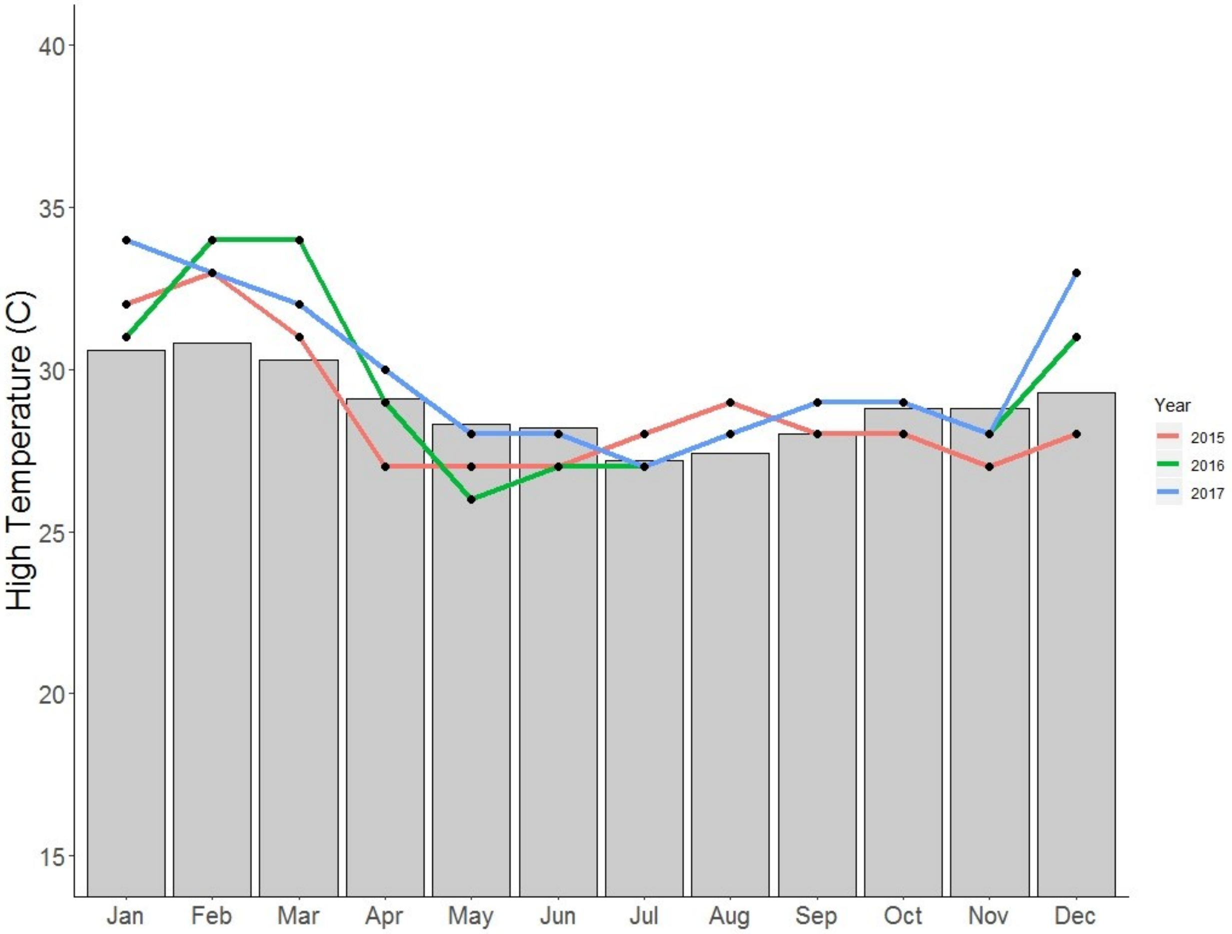
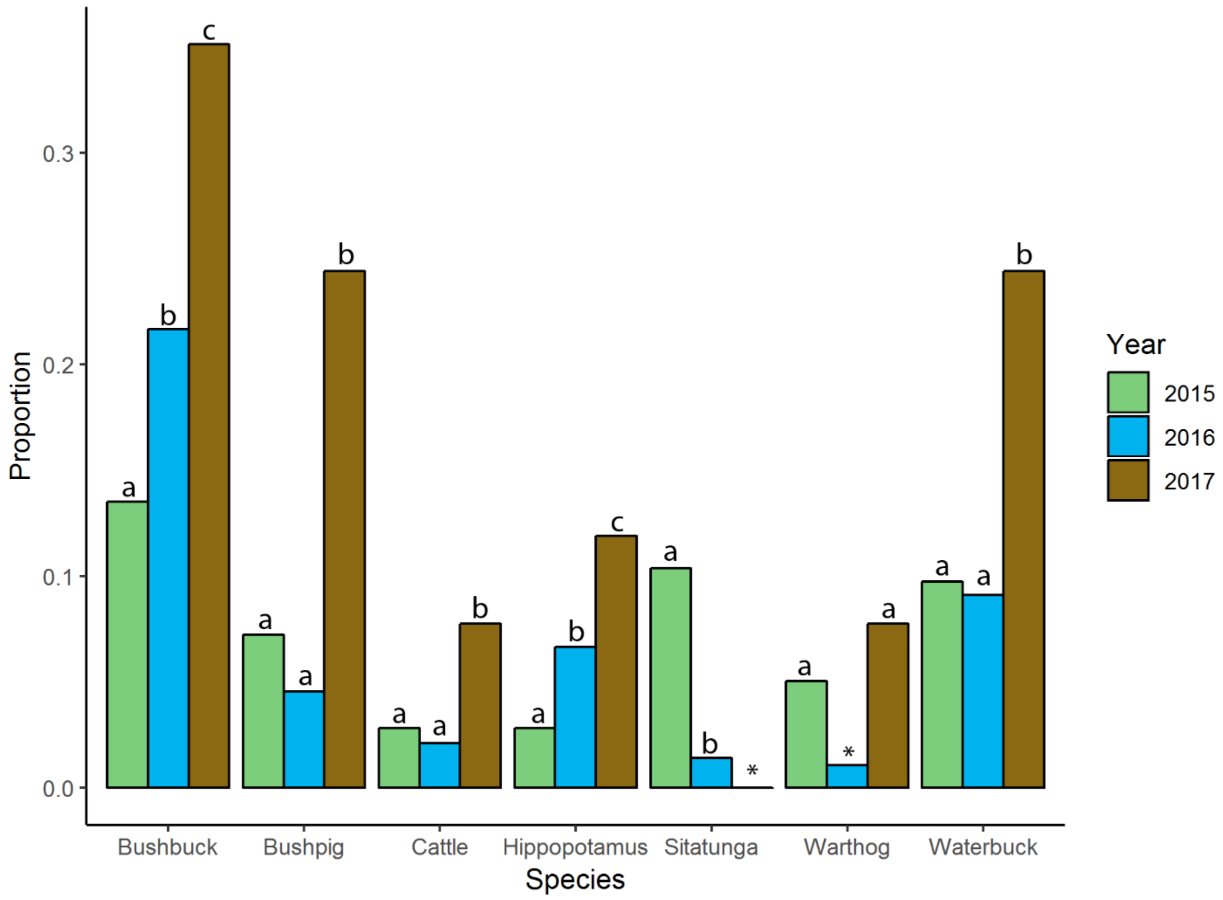
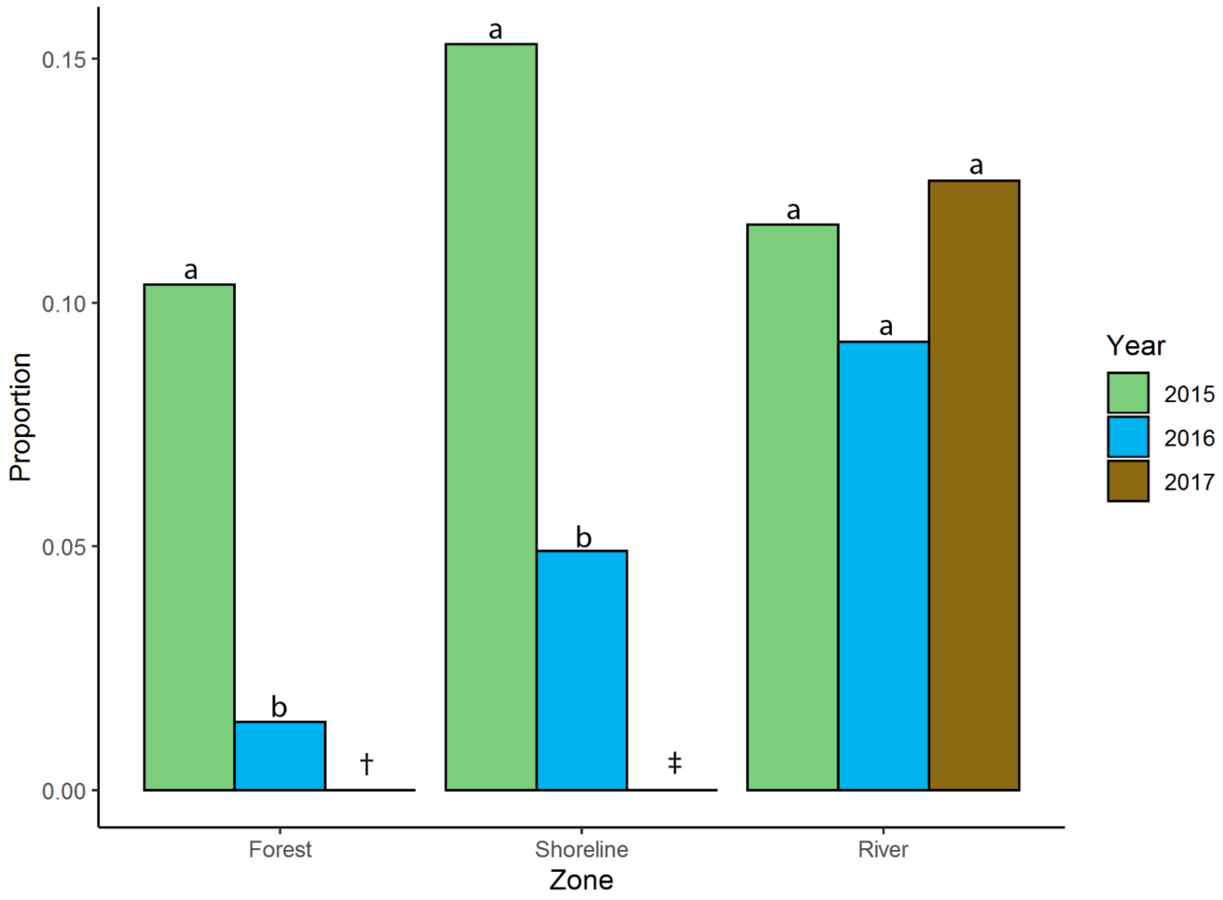


**Figure 5.3** Long-term monthly average rainfall (a) or high temperature (b; grey bars) and actual rainfall or high temperature recorded in Masindi, Uganda from 2015 – 2017.



**: less than five encounters were recorded for the given species/year combination, hence no statistical testing.*

**Figure 5.4** Proportion of days with a detection of at least one animal of the listed species in the Forest zone of the central Mayanja River study area during three hydrologic conditions, 2015 (normal water level), 2016 (flood conditions), and 2017 (drought). Different letters indicate significant differences ($p < 0.05$) in proportions for a given species/zone comparison.



*† - Less than 5 detections. ‡ - camera malfunctions preclude statistical tests.*

**Figure 5.5** Proportion of days with a detection of at least one sitatunga in the three zones for the three hydrologic conditions of the study, 2015 (normal water level), 2016 (flood conditions), and 2017 (drought). Different letters indicate significant differences ($p < 0.05$) in proportions for a given species/zone comparison.

# Chapter 6

## 6 Conclusion

Ecology is undoubtedly a data-intensive science, especially with modern advances in remote sensing, quantitative methods, and computing power (Michener and Jones 2012; Farley et al. 2018). Perhaps it is surprising, then, that only one in 200 harvested species are monitored (Kindsvater et al. 2018). While collecting data to address the uncertainty is a good start, the greater ecological and social context in which the wildlife exists is also a critical consideration. Effective wildlife management involves three interacting themes: humans, habitat, and wildlife populations (Anderson 1999). These three topics as they pertain to conservation in Africa in general and sitatunga in particular are the subject of my research. I explore sitatunga population density and connectivity in Uganda, herbivore community space use in wetlands, and the complexity of wildlife issues affecting conservation in Africa.

Human actions affect habitats, and human attitudes affect conservation decisions – thus managers must understand the attitudes of diverse stakeholders in conservation actions, including both local communities and international attention (Dickman et al. 2011). Chapter 2 illuminates wildlife conservation issues in Africa, including international scrutiny. The good news is that countries in Africa are often ahead of countries in the global North in terms of land under protection and the proportion of GDP allocated to conservation (Lindsey et al. 2017). The bad news is that conservation remains expensive, controversial, and without a one-size-fits-all solution (Blaustein 2007; Mbaiwa 2017; Lindsey et al. 2018; Chardonnet 2019). Luckily, there is a forum dedicated to discussing wildlife management in Africa that brings together diverse stakeholders and experts to discuss and address these issues.

On a local scale, management of harvested species should include a firm understanding of the  population in question and its habitat (Mills 2007). For sitatunga, conflicting results from prior studies coupled with a difficult habitat to work in lead to uncertainty and management by educated opinion (Owen 1970; Beudels-Jamar et al. 1997; Andama 2019).  Chapter 3 focuses on sitatunga populations, and chronicles my effort to estimate sitatunga density using trail cameras.  I explore three methods – maximum likelihood spatially explicit capture-recapture (SECR) with model selection using AIC, Bayesian spatial capture recapture (SCR), and time in front of the camera (TIFC). Each method has its own advantages.  SECR allows for linear habitat and model selection, but requires complete and certain identification of individuals.  SCR allows for uncertain identity, but involves a high understanding of model parameterization and computing power. TIFC does not consider animal movement, and it can include all individuals regardless of identification.  However, TIFC is a new model and some important parts of the model require specification to sitatunga ecology to ensure a precise result. I found reasonably consistent estimates of population density using these three methods despite differences in model structure and data needs, giving me confidence in my estimates of abundance in Uganda. Other findings in Chapter 3 are discussed below.

Human population growth and resource use is placing increasing pressure on habitats such as wetlands, and climate change is exacerbating the situation by changing water provisioning patterns (Silvius et al. 2000; Erwin 2009; Engelbrecht et al. 2015). Sitatunga are wetland specialists; since wetlands in the tropics are under tremendous human pressure, detecting barriers to gene flow is another way to assess habitat connectivity (Luque et al. 2016; Barakagira and de Wit 2017; Mwanjalolo et al. 2018). In Chapter 4, I used genetic analysis to explore the connectivity of sitatunga habitat. I used samples from harvested animals to identify 15 microsatellite markers that amplify for sitatunga. Baseline genetic data from these markers show that the Mayanja River sitatunga population is not reproductively isolated, indicating no barriers to dispersal. This result is further indication that the Mayanja River sitatunga population is stable. In this study I provide microsatellite panel to assess diversity and connectivity of other sitatunga populations, which would identify isolated or at-risk subpopulations, and indicate connectivity and disturbance of wetlands.

Chapter 5 further explores habitat, and also how sitatunga and other ungulates, including domestic cattle, use the wetland and adjacent forests during different hydrologic conditions. Sitatunga are unique in the ungulate assemblage in that they use remote wetland habitat. Whether due to decreased competition or reduced exposure to anthropogenic disturbance, sitatunga use of inaccessible wetlands stays constant regardless of water levels. In the forest, sitatunga decreased use over the three years of this study, while all other ungulates increased use of these habitats by the third year. None of these changes appear to be due to water levels. Among the ungulate community, domestic cattle and warthog have the highest potential for competition, as they overlap in terms of diet and temporal activity; however, cattle detections increased in the forest over time while not changing for warthogs. These results indicate mechanisms of coexistence exist for this assemblage, including the novel competitor (cattle).

In Chapter 3, the SECR best model according to AIC shows one group with over 20 times the movement parameter ($\sigma$) than the other group. Potentially complicating this finding is that during this study, water levels in the Mayanja River varied from flood conditions to drought and fires. Conditions like these affected distribution of Zambezi sitatunga in seasonal habitats (Games 1983; Manning 1983; Games 1984; May and Lindholm 2002). In addition to the two distinct movement groups, the best SECR model also reveals a decreasing trend in population density. However, there is also strong evidence that the trapping array I used was not large enough to capture the full movement of sitatunga in the Mayanja River (Royle et al. 2014b; Sun et al. 2014). Similarly, I monitored the population for three years, which is not enough time to draw conclusions on population trends (White 2019). In light of the findings of habitat connectivity in Chapter 4 and the strong fidelity of sitatunga to core wetland habitat in Chapter 5, I suggest that the sitatunga are reallocating their activity centres during times of excessively high or low water to other areas, either outside of the trapping array or to central wetlands without openings. In this manner, sitatunga are less likely to be detected in the camera traps, and density estimates decrease accordingly. Future studies should include GPS tracking of adult male, juvenile male, and adult female sitatunga to address the highly varied movement between groups. In addition, GPS collars will allow tracking of sitatunga even if they do not use open areas conducive to camera trapping or other visual detection.

Taken together, my research shows that sitatunga are not reproductively isolated, but that they are reliant upon wetlands compared to other habitats. Compared to other ungulates in the community, wetland preference is unique, thus sitatunga have little spatial overlap with other large herbivore species. Further, the indication of high movement and habitat connectivity suggests that this population is not a conservation concern. However, intact and undisturbed wetland must be maintained for successful sitatunga management.

If the sitatunga population in the Mayanja River is going to be hunted, then quality data from the same area as the population of interest will improve management decisions. I hope that the information contained in this dissertation advances not only sitatunga management, but also field and analysis techniques for other cryptic species in difficult habitats. While we still have a lot to learn about many harvested species, my research advances understanding of the human, habitat, and population aspects of East African sitatunga in riverine habitats. Management is not free – thus the developed world should help to pay for conservation if they want their interests appreciated.

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# Appendices

## A Temporal niche differentiation among large herbivores in the Mayanja River, Uganda (By Jocelyn Chui, C. Warbington, and M. S. Boyce)

*Note: Jocelyn Chui prepared a paper as part of the requirements of BIOL 398 at the University of Alberta in Winter Term 2019. Mark S. Boyce and Camille Warbington supervised Chui for this project and provided the data. This version is edited by Chui from the original draft and for submission to academic journals.*

### Abstract

Niche differentiation is an integral part of understanding how a community of similar organisms are able to coexist. In the Mayanja River in Central Uganda, we examined activity patterns of herbivorous mammals are examined to determine if temporal segregation plays a part in the continued coexistence of the species. Species with higher dietary overlap are expected to have less temporal overlap decreasing hostile interactions. Camera trap data were used to study activity patterns from three years (2015, 2016, 2017) for seven herbivores (bushbuck, waterbuck, bush pig, baboon, warthog, cattle, and hippopotamus). Species with greater dietary overlap had lower temporal overlap values while species with lower dietary overlap have higher temporal overlap values suggesting that temporal segregation was occurring. Some species pairs do not follow this pattern which might indicate that other factors such as human activity are playing a part in the study system.

**Keywords:** camera trapping**,** competition, East Africa, herbivore community ecology, human-wildlife conflict, niche differentiation, papyrus wetlands, temporal segregation, Uganda.

## Introduction

Within an ecological community, species with similar ecological requirements have a greater degree of niche overlap. Species that share similar niches are often drawn to the same foraging areas (Schoener, 1971). This attraction to similar foraging areas gives rise to potentially hostile species interactions, which can result in some form of resource partitioning. Without some form of resource partitioning species cannot coexist together for long periods of time before one species drives another species to extinction (Hardin, 1960). To offset negative species interactions, species with similar niches may differentiate spatially, dietary, or temporally (Schoener, 1974).

Spatial segregation is when species with similar traits and resource requirements use different spaces within the larger area (Cecere *et al*., 2018). Through spatial differentiation, differing species can mitigate negative species interactions. But once resources are depleted species are driven to other spaces for resources. With a growing human population in East Africa (Uganda Bureau of Statistics, 2014), land conversion of wetlands into agricultural land increase resulting in smaller habitat and resource patches and greater chances of hostile species encounters (Namaalwa, *et al*., 2013; Sakané *et al*., 2011). With decreases in habitat space, spatial segregation alone is unlikely indicating that sources like dietary differentiation need to be considered. Dietary differentiation in coexisting carnivore systems have been studied (Nagy-Reis *et al.,* 2018) where competitive species interactions are easier to detect.

Whereas, systems that contain herbivores and/or omnivores are often less studied due to difficulties in determining and detecting interactions such as competition (Forsyth and Hickling, 1998; Ferretti *et al*., 2015). Food resources for herbivores such as grasses, leaves, and fruit are often more abundant than prey items, further concealing potential competitive species interactions.

Other than dietary and spatial differentiation, species can segregate temporally. Temporal segregation is when species that are ecologically similar are using the same area at different times of the day (Sladecek *et al*., 2017). By having different activity patterns, similar species are able to avoid coming into contact which lowers the potential for hostile interactions. In the Mayanja River Valley in Central Uganda, various herbivorous mammals coexist, including bushbuck (*Tragelaphus scriptus*), waterbuck (*Kobus ellipsiprymnus*), bush pig (*Potamochoerus larvatus*), baboon (*Papio anubis*), warthog (*Phacochoerus africanus*), cattle (*Bos tarus*), and hippopotamus (*Hippopotamus amphibius*). Within this group, cattle and hippopotamuses are grazers indicating that their main food resource is grasses (Grant *et al*, 1985; Field, 1970). Waterbucks and warthogs are also grazers, but waterbucks also consume leaves and shoots (Kassa *et al*. 2006), while warthogs also consume forbs (Treydte *et al*. 2006). Bushbucks mainly consume leaves and shoots overlapping with waterbucks, while occasionally eating fruits and flowers of dicotyledon trees (Apio and Wronski, 2005). Species that mainly eat fruit include baboons and bush pigs with leaves, flowers and roots as additional parts of their diet (Hill and Dunbar, 2002, Breytenbach and Skinner, 1982). Comparing the primary diets of the herbivores, it is expected that pairs such as baboon and bush pig might have less temporal overlap due to high dietary overlap whereas pairs like warthog and bushbuck would have larger temporal overlap due to dietary dissimilarity.

Sighting times of different species show potential temporal segregation in our study area. In this paper, we analyze the activity patterns and temporal overlap to determine if species with a greater niche overlap as defined by dietary similarity segregate temporally from each other. With changes in climate affecting resource needs of species and increasing human activity in the area, the co-existence of the species in the area might be affected. To mitigate these changes in species interactions, we expect that species with high dietary similarity will show less temporal overlap than species that consume different kinds of food.

## Methods

### *Data Collection*

Mayanja River Valley is an area of wetlands in Central Uganda (Figure 1). The study area lies in the Nakaseke District of central Uganda, in the marshes of the Mayanja River system in the Nile watershed. Climate in Equatorial Uganda is generally rainy (Central Intelligence Agency, 2014) with the Nakaseke District having an average annual temperature of 22.2 °C, and average annual rainfall of 1282 mm (climate-data.org, 2019). Wetlands in the study area covered approximately 8.1 km$^2$.

Camera trapping data used in this analysis is were from approximately 10m from the forest-wetland edge, located on dry soils with a preponderance of woody stems and closed canopy at least 2 m in height. We collected camera-trap data during May to August in two years: 2015, 2016 and from February to July in 2017 using camera traps. Water levels in the three data collection years varied greatly with water levels being stable in the first year (2015), flood conditions in the second year (2016) and drought conditions during the last year (2017). Photos from two trail cameras in 2015, 2017 and five trail cameras in 2016 (Table 1) were used in analysis of large mammal activity patterns. Species sightings data for ungulates like waterbucks, warthogs, and hippopotamuses as well as primates like baboons were collected. Time of sightings were obtained from the time stamp on photos with same species sightings being marked as a new encounter if the clock has passed the thirty-minute mark with no animals detected during the interval. For species that were sighted again before the half hour mark, the photo was not marked as a new individual and the clock was restarted. Data collected in the year 2016 were separated into two groups: area A and area B, corresponding to the placement of trail cameras. These data were analysed separately in addition to having species from both areas pooled in a single analysis. In 2016, carrion was placed within the area with trail cameras by hunters that acted as bait for scavengers. The presence of bait attracted different scavengers/predators which in turn may have affected the activity pattern of the herbivores. For the purpose of reducing statistical error any species with fewer than five sightings were excluded from analyses. With the removal of any species with fewer than five species sightings, kernel density estimates for some 2016 species (for example, warthog) in the separate area analyses of 2016 could not be estimated. Without the kernel density estimate temporal overlap could not be calculated between the pairs. To solve this estimator error, species sighted in both area A and B were pooled into a single matrix for kernel density and overlap estimates.

### *Data Analysis*

Species sightings were plotted onto a rose diagram (Figure 2), and a kernel-density plot. A Rayleigh’s test of uniformity (R-test) for each sighted species was then conducted to determine if there were periods of peak activity or patterns in activity within a 24-hour period. From the results of the R-test, species with non-significant ( $P > 0.05$) result indicate that activity of that species is spread evenly through the day, indicating a cathemeral pattern. Species that had a significant R-test result would have rose diagrams analyzed to determine if species had a diurnal – active during the day, rest during the night – pattern, nocturnal – active at night – pattern, or a crepuscular – active at twilight – pattern (Ikeda *et al*., 2016). We estimated temporal overlap between species using kernel density estimations and a coefficient of overlapping ($\Delta$) that ranges from 0 (no overlap) to 1 (complete overlap). Overlap values were calculated between a species pair such as bushbuck vs. waterbuck or baboon vs. bushbuck for all possible species pairings. Low temporal overlap between all species pairs is represented when all pairs had a coefficient of overlapping < 0.5, while high temporal overlap was when all pairs had a coefficient of overlapping > 0.5. Moderate temporal overlap was represented by all species pairs having coefficient of overlapping spanning the entire possible range (0-1). The estimator $\hat{\Delta}_1$ was used when the smaller sample between two samples was less than 50 (Meredith and Ridout, 2018) while the estimator $\hat{\Delta}_4$ was used when the smaller sample between two samples was greater than 50. Confidence intervals were constructed using estimates from 10, 000 bootstrap samples. Analyses were performed using the packages “circular” (Agostinelli and Lund, 2017) and “overlap” (Ridout and Linkie, 2009) in R (R Core Team, 2018).

## Results

### *Year 2015*

A total of 173 species sightings (Table 1) were compiled during 2015. From the species sightings, only waterbucks appear to be active throughout the 24-hour cycle (R-test, $r = 0.0358$, p-value = 0.9409, $n = 20$), with other species sightings appearing during different intervals during the 24-hour cycle (Figure 3). Warthogs (R-test, $r = 0.8067$, p-value = $4.1522 \times 10^{-7}$, $n = 20$) and cattle (R-test, $r = 0.8443$, p-value = $3.8081 \times 10^{-4}$, $n = 9$) were mainly sighted in the afternoon with cattle also be recorded in the morning. Bushbucks (R-test, $r = 0.5375$,

p-value = $1.6740 \times 10^{-4}$, $n = 54$) and hippopotamus (R-test, $r = 0.6409$, p-value = 0.0126, $n = 10$) were recorded both at dawn/early morning with hippopotamus also being sighted at dusk. Bush pigs (R-test, $r = 0.4244$, p-value = 0.0098, $n = 25$) were active during the morning and the evening while baboons were diurnal (R-test, $r = 0.734$, p-value = 0.0168, $n = 7$).

Overall, between all species pairs there was moderate temporal overlap (Table 2) with cattle and hippopotamus having the smallest overlap ($\hat{\Delta}_1 = 0.3208$) and hippopotamus and bush pigs having the largest overlap ($\hat{\Delta}_1 = 0.9548$).

*Year 2016*

A total of 390 species sightings (Table 1) were compiled for the year 2016. From these sightings, no species showed a cathemeral activity pattern (Figure 4 – Figure 6) but bush pigs (R-test, $r = 0.5413$, p-value = $3.4960 \times 10^{-6}$, $n = 40$) appeared to be strictly nocturnal while baboons (R-test, $r = 0.4326$, p-value = 0.0476, $n = 16$) had a diurnal pattern. Warthogs (R-test, $r = 0.9575$, p-value = $6.0000 \times 10^{-4}$, $n = 6$) and cattle (R-test, $r = 0.8686$, p-value = $2.7373 \times 10^{-6}$, $n = 12$) were recorded only during the afternoon. During the day and at dusk and/or dawn, sightings of bushbucks (R-test, $r = 0.4630$, p-value = $3.4755 \times 10^{-20}$, n =

209), waterbucks (R-test, r = 0.2660, p-value = 0.0076, n = 69) and hippos (R-test, r = 0.5784, p-value = 1.0399 x $10^{-6}$, n = 38) were recorded.

For the pooled analysis (Table 3), baboons and waterbucks had the greatest degree of overlap ($\hat{\Delta}_1$= 0.8810) while hippos and cattle had the smallest degree of overlap ($\hat{\Delta}_1$= 0.2065). Between all species pairs in area A and area B there was moderate temporal overlap (Table 4) with bushbucks and hippos having the smallest overlap ($\hat{\Delta}_1$= 0.4344) in area A and bush pigs and cattle having the smallest overlap in area B ($\hat{\Delta}_1$ = 0.1518). The species pair with the largest temporal overlap in area A was baboons and waterbucks ($\hat{\Delta}_1$= 0.9255), while bushbucks and waterbucks had the largest overlap in area B ($\hat{\Delta}_1$ = 0.8458).

*Year 2017*

A total of 778 species sightings (Table 1) were compiled for the year 2017. From the sightings, only waterbucks (R-test, r = 0.0765, p-value = 0.5502, n = 102) appear to have a cathemeral activity pattern (Figure 7). From the recorded sightings bush pigs (R-test, r = 0.4339, p-value = 8.0630 x $10^{-9}$, n = 99), and hippos (R-test, r = 0.7807, p-value = 2.7809 x $10^{-10}$, n = 37) appear to be nocturnal, while baboons (R-test, r = 0.5412, p-value = 1.3670 x $10^{-6}$, n = 43) have a diurnal activity pattern. Cattle (R-test, r = 0.9305, p-value = 2.8503 x $10^{-15}$, n = 42) and warthogs (R-test, r = 0.8234, p-value = 1.3495 x $10^{-7}$, n = 22) were recorded in the afternoon with warthogs also having sightings in the early morning. Bushbucks (R-test, r = 0.2838, p-value = 7.1645 x $10^{-16}$, n = 433) were sighted throughout the day with main sightings at dusk and dawn.

Between all species pairs there are moderate degrees of temporal overlap (Table 5) with hippos and cattle having the smallest overlap ($\hat{\Delta}_1$= 0.1611) and hippos and bush pigs having the largest temporal overlap ($\hat{\Delta}_1$=0.8493).

## Discussion

The time use of multiple herbivorous and omnivorous species was analysed in a section of the Mayanja River Valley in Central Uganda where there is evidence that species that consume more similar food items demonstrate greater degrees of temporal differentiation. The results of the temporal analyses supported the hypothesis that species with low dietary similarity had higher temporal overlap then species that consumed similar food items.

For the 2016 study year, data were collected from two areas and analyzed both separately and with data pooled. In the separate analyses, temporal overlap between certain pairs was not possible due to a decrease in sample size leading to a failure to generate kernel density estimates. Even with the missing species pairs, we detected similar patterns to 2015 as once again species with a greater dietary overlap such as waterbucks and hippopotamuses had a smaller temporal overlap than species with more dietary differences - waterbucks and bushbucks. After using separate analyses species data from both areas were pooled into a single analysis which showed similar results.

Although there is a general trend appearing in the data, there are also pairs where higher degrees of temporal overlap were expected but did not appear. An example of this was the cattle vs. baboon pair in the 2015 study year which had a low coefficient of overlapping. The presence of values that do not follow the pattern might indicate other factors were affecting the activity patterns. One of the factors that might have affected the temporal use of the species was the flood conditions that occurred during the 2016 year in contrast with normal water levels in 2015. This change in water level might draw in species that require greater sources of water or use water as a form of refuge from predators (Thaker *et al*. 2011) to spend more time in the area than species that might avoid the increased water levels. In 2017, water level conditions took a complete turnaround - instead of flood conditions, the environment saw severe drought conditions. Even with the presence of these environmental conditions, the general trend of our results remained: species with similar dietary preferences species have a smaller temporal overlap, (for example, hippopotamuses and warthogs), and species with different dietary preferences having more temporal overlap, such as bushbucks and baboons. Thus, the temporal patterns that we detected were robust to prevailing water conditions in the river.

Another potential driver of the differing pattern is the presence of parts or whole carcasses. With the presence of carcasses, scavengers and predators were drawn to the area which might in turn drive away study species to avoid the predators. In the overall species sightings, predators such as crocodiles and leopards were recorded but did not meet the threshold of detections to be included in our analysis. Another potential factor affecting activity patterns other than predators or scavengers is human activity. Cattle recorded for this study were not those that are found in the wild but are in fact domesticated animals. As such, the activity pattern of cattle is determined by cow herders – night activity is restricted to pens, and grazing areas and water access is dictated by the herders. This suggests that species that had lower temporal overlap with cattle might not be a result of just similar diet but of human avoidance. The presence of humans might also play a part in the low temporal overlap between species that have different dietary overlap, such as that seen between baboons and cattle.

Another anthropogenic factor affecting the wildlife community is the conversion of habitats into agricultural lands. For species that have narrow niches, habitat conversion could mean that population numbers steadily decrease over the years as the human population grows and more of the wildlife habitats are used for agriculture. As habitat and species conservation become a major issue, a better understanding of species interactions independent of predator-prey influences such as those between coexisting herbivores can be beneficial. By taking into account how species within a system interact and how they use the land, a balance between preserving animal habitats and human land use can be reached.

Overall, the results of the analyses from the three study years suggest that there is temporal segregation between species in the Mayanja River Valley that is robust to hydrologic changes. Temporal segregation in the Mayanja River could be taken as a positive sign because it means that there is a greater assemblage of herbivores in the community leading to greater species richness. Although analyses do indicate patterns of temporal segregation, without following in-depth studies we can only speculate on whether this temporal differentiation was a by-product of community assemblages, hostile species interactions such as competition, predation, or human activity.

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**Table 1**. Total number of species recorded with camera traps for each sample year on the Mayanja River area of central Uganda.

| Species | Baboon | Bush Pig | Bushbuck | Cattle | Hippo | Warthog | Waterbuck | Total |
|---|---|---|---|---|---|---|---|---|
| 2015 | 7 | 25 | 54 | 9 | 10 | 20 | 48 | 173 |
| 2016 | 16 | 40 | 209 | 12 | 38 | 6 | 69 | 390 |
| 2017 | 43 | 99 | 433 | 42 | 37 | 22 | 102 | 778 |

**Table 2.** In lower tiles, coefficient of overlapping values estimated using kernel density estimator $\hat{\Delta}_1$ for all species pairs in the year 2015. Overlap values range from low (0 – 0.5) overlap to high overlap (> 0.5). Confidence intervals estimated from bootstrapping are placed in upper tiles. Bolded values are corrected using logistic scale and back-transformed due to original values falling outside the coefficient of overlapping range (0, 1).

| **Area A** | Baboon | Bush Pig | Bushbuck | Cattle | Hippo | Warthog | Waterbuck |
|---|---|---|---|---|---|---|---|
| Baboon | X | 0.1281 to 0.6837 | **0.5105 to 0.9263** | 0.0844 to 0.6916 | 0.0913 to 0.6778 | 0.0871 to 0.6571 | 0.3151 to 0.8702 |
| Bush Pig | 0.4059 | X | 0.3050 to 0.6570 | 0.1390 to 0.5048 | 0.8740 to 0.9847 | 0.2436 to 0.5841 | 0.5307 to 0.8769 |
| Bushbuck | 0.7836 | 0.4810 | X | 0.0993 to 0.5899 | 0.2377 to 0.6838 | 0.1754 to 0.5069 | 0.5307 to 0.8525 |
| Cattle | 0.3880 | 0.3219 | 0.3446 | X | 0.1109 to 0.5308 | 0.5558 to 0.9421 | 0.1942 to 0.6253 |
| Hippo | 0.3845 | 0.9548 | 0.4607 | 0.3208 | X | 0.2114 to 0.6339 | 0.4766 to 0.9256 |
| Warthog | 0.3722 | 0.4139 | 0.3411 | 0.7489 | 0.4227 | X | 0.3190 to 0.6353 |
| Waterbuck | 0.5927 | 0.7038 | 0.6916 | 0.4098 | 0.7011 | 0.4772 | X |

**Table 3.** In lower tiles, coefficient of overlapping values estimated using kernel density estimator $\hat{\Delta}_1$ for most species' pairs except bushbuck vs. waterbuck pair which used estimator $\hat{\Delta}_4$ in the year 2016 with species pooled between two study areas. Overlap values range from low (0 – 0.5) overlap to high overlap (> 0.5). Confidence intervals estimated from bootstrapping are placed in upper tiles. Bolded values are corrected using logistic scale and back-transformed due to original values falling outside the coefficient of overlapping range (0, 1).

| **Pooled** | Baboon | Bush Pig | Bushbuck | Cattle | Hippo | Warthog | Waterbuck |
|---|---|---|---|---|---|---|---|
| Baboon | X | 0.3820 to 0.7161 | 0.7319 to 0.9734 | 0.2550 to 0.6703 | 0.3658 to 0.7006 | - | **0.7265 to 0.9538** |
| Bush Pig | 0.5490 | X | 0.3945 to 0.5902 | 0.0968 to 0.3465 | **0.9025 to 0.9840** | - | 0.4993 to 0.7406 |
| Bushbuck | 0.8527 | 0.4923 | X | 0.4091 to 0.7562 | 0.3823 to 0.5781 | - | 0.7833 to 0.9515 |
| Cattle | 0.4627 | 0.2216 | 0.5826 | X | 0.0847 to 0.3283 | - | 0.3074 to 0.6427 |
| Hippo | 0.5332 | 0.9598 | 0.4802 | 0.2065 | X | - | 0.4853 to 0.7246 |
| Warthog | - | - | - | - | - | X | - |
| Waterbuck | 0.8810 | 0.6199 | 0.8674 | 0.4751 | 0.6049 | - | X |

**Table 4.** In lower tiles, coefficient of overlapping values estimated using kernel density estimator $\hat{\Delta}_1$ for most species' pairs except bushbuck vs. waterbuck pair which used estimator $\hat{\Delta}_4$ in the year 2016. Overlap values range from low (0 – 0.5) overlap to high overlap (> 0.5). Confidence intervals estimated from bootstrapping are placed in upper tiles. Bolded values are corrected using logistic scale and back-transformed due to original values falling outside the coefficient of overlapping range (0, 1).

| **Area A** | Baboon | Bush Pig | Bushbuck | Cattle | Hippo | Warthog | Waterbuck |
|---|---|---|---|---|---|---|---|
| Baboon | X | 0.3636 to 0.7382 | 0.7199 to 0.9923 | - | 0.3427 to 0.7118 | - | **0.8102 to 0.9731** |
| Bush Pig | 0.5509 | X | 0.3536 to 0.5620 | - | **0.6656 to 0.9468** | - | 0.4142 to 0.7263 |
| Bushbuck | 0.8561 | 0.4578 | X | - | 0.3228 to 0.5461 | - | 0.7437 to 0.9737 |
| Cattle | - | - | - | X | - | - | - |
| Hippo | 0.5272 | 0.8561 | 0.4344 | - | X | - | 0.3889 to 0.7091 |
| Waterbuck | 0.9255 | 0.5703 | 0.8587 | - | 0.5490 | - | X |
| **Area B** | | | | | | | |
| Bush Pig | - | X | 0.4138 to 0.9190 | **0.0375 to 0.4509** | 0.1413 to 0.8354 | - | 0.2585 to 0.7750 |
| Bushbuck | - | 0.6664 | X | 0.2340 to 0.6438 | 0.4300 to 0.8571 | - | 0.7113 to 0.9804 |
| Cattle | - | 0.1518 | 0.4389 | X | 0.1001 to 0.4849 | - | 0.3003 to 0.7198 |
| Hippo | - | 0.4884 | 0.6435 | 0.2925 | X | - | 0.4748 to 0.8495 |
| Warthog | - | - | - | - | - | X | - |
| Waterbuck | - | 0.5168 | 0.8458 | 0.5101 | 0.6622 | - | X |

**Table 5.** In lower tiles, coefficient of overlapping values estimated using kernel density estimator $\hat{\Delta}_1$ for most species' pairs except pairs: Bush Pig vs. Bushbuck, Bush Pig vs. Waterbuck, and Waterbuck vs. Bushbuck which used estimator $\hat{\Delta}_4$ in the year 2017. Overlap values range from low (0 – 0.5) overlap to high overlap (> 0.5). Confidence intervals estimated from bootstrapping are placed in upper tiles. Bolded values are corrected using logistic scale and back-transformed due to original values falling outside the coefficient of overlapping range (0, 1).

| **Area A** | Baboon | Bush Pig | Bushbuck | Cattle | Hippo | Warthog | Waterbuck |
|---|---|---|---|---|---|---|---|
| Baboon | X | 0.3697 to 0.6983 | 0.5519 to 0.9075 | 0.2718 to 0.5722 | 0.2661 to 0.5938 | 0.3101 to 0.6754 | 0.5181 to 0.8952 |
| Bush Pig | 0.5340 | X | 0.5680 to 0.7500 | 0.1058 to 0.2500 | 0.7371 to 0.9615 | 0.1103 to 0.3007 | 0.6385 to 0.8619 |
| Bushbuck | 0.7297 | 0.6590 | X | 0.2793 to 0.4470 | 0.3997 to 0.6179 | 0.2393 to 0.4706 | 0.8536 to 0.9964 |
| Cattle | 0.4220 | 0.1779 | 0.3632 | X | 0.0735 to 0.2261 | 0.3130 to 0.6914 | 0.1904 to 0.3701 |
| Hippo | 0.4299 | 0.8493 | 0.5088 | 0.1498 | X | 0.0651 to 0.2570 | 0.4719 to 0.7284 |
| Warthog | 0.4927 | 0.2055 | 0.3550 | 0.5022 | 0.1611 | X | 0.1829 to 0.4237 |
| Waterbuck | 0.7067 | 0.7502 | 0.9250 | 0.2803 | 0.6002 | 0.3033 | X |

**Figure 1.** Map of Uganda with study area marked by white diamond shape.

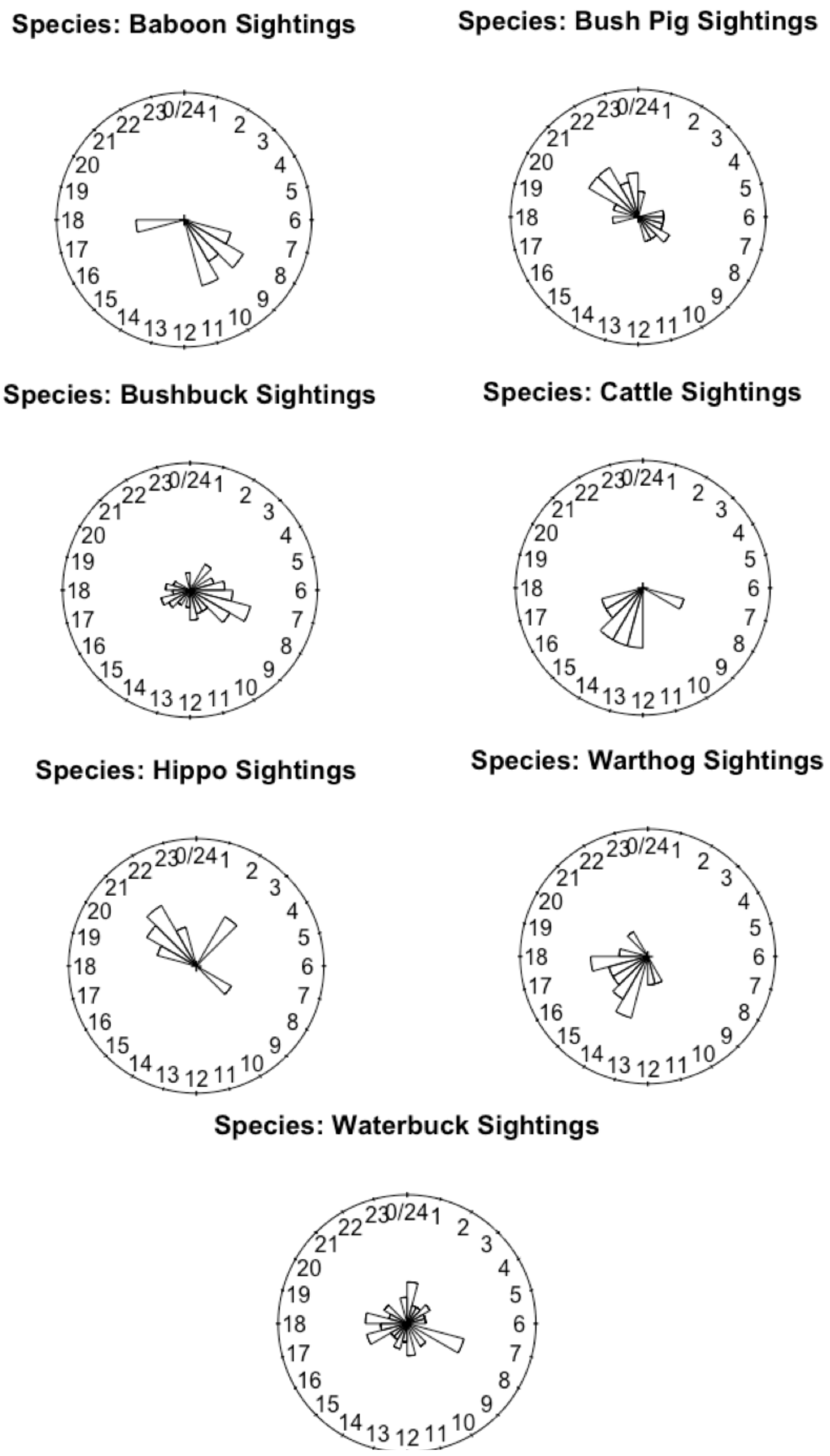
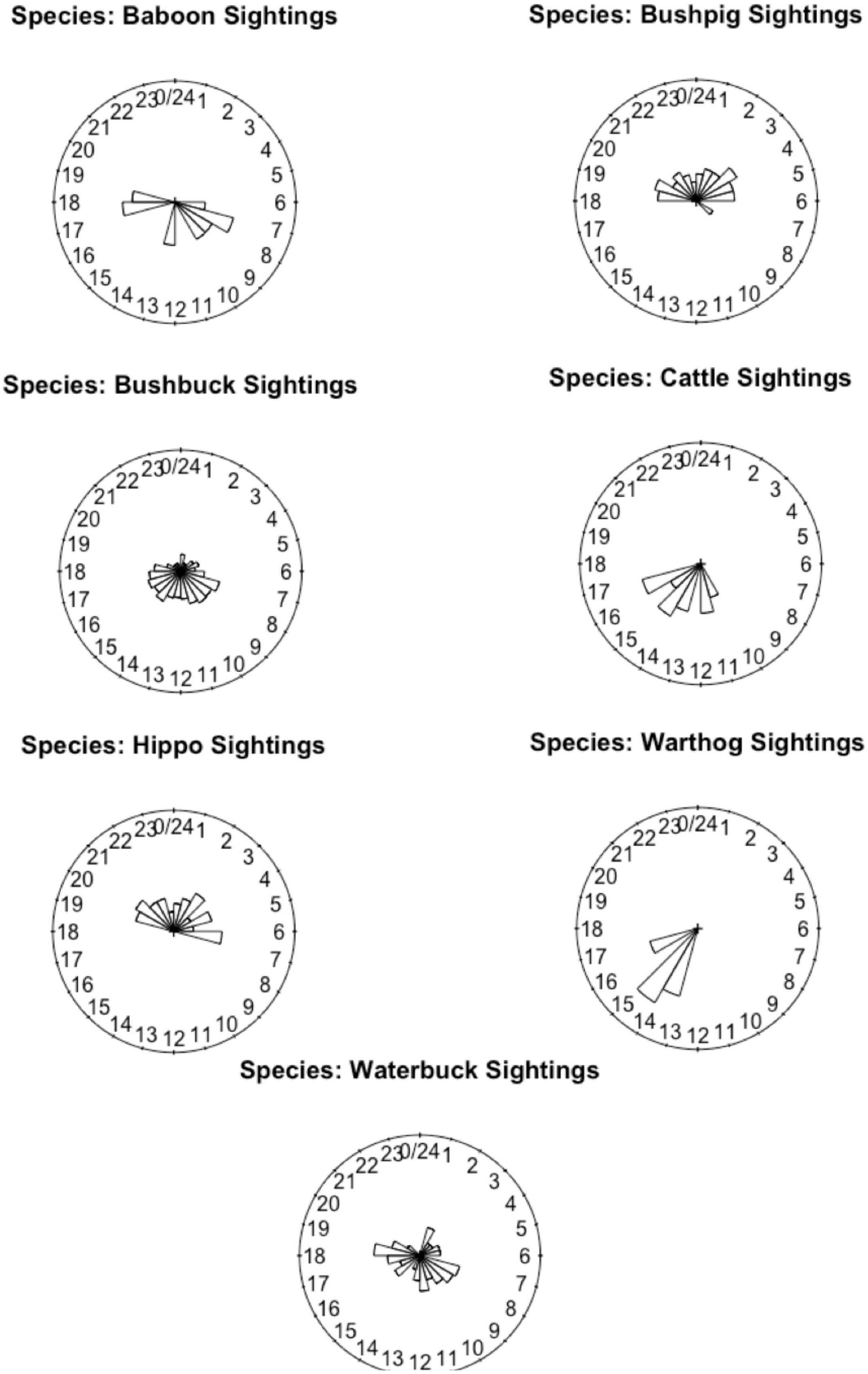


**Figure 2A.** Species sightings recorded with trail cameras for the year 2015 plotted as separate rose diagrams.


Species: Baboon Sightings

Species: Bushpig Sightings

Species: Bushbuck Sightings

Species: Cattle Sightings

Species: Hippo Sightings

Species: Warthog Sightings

Species: Waterbuck Sightings

**Figure 2B.** Species sightings recorded with trail cameras for the year 2016 plotted as separate rose diagrams.

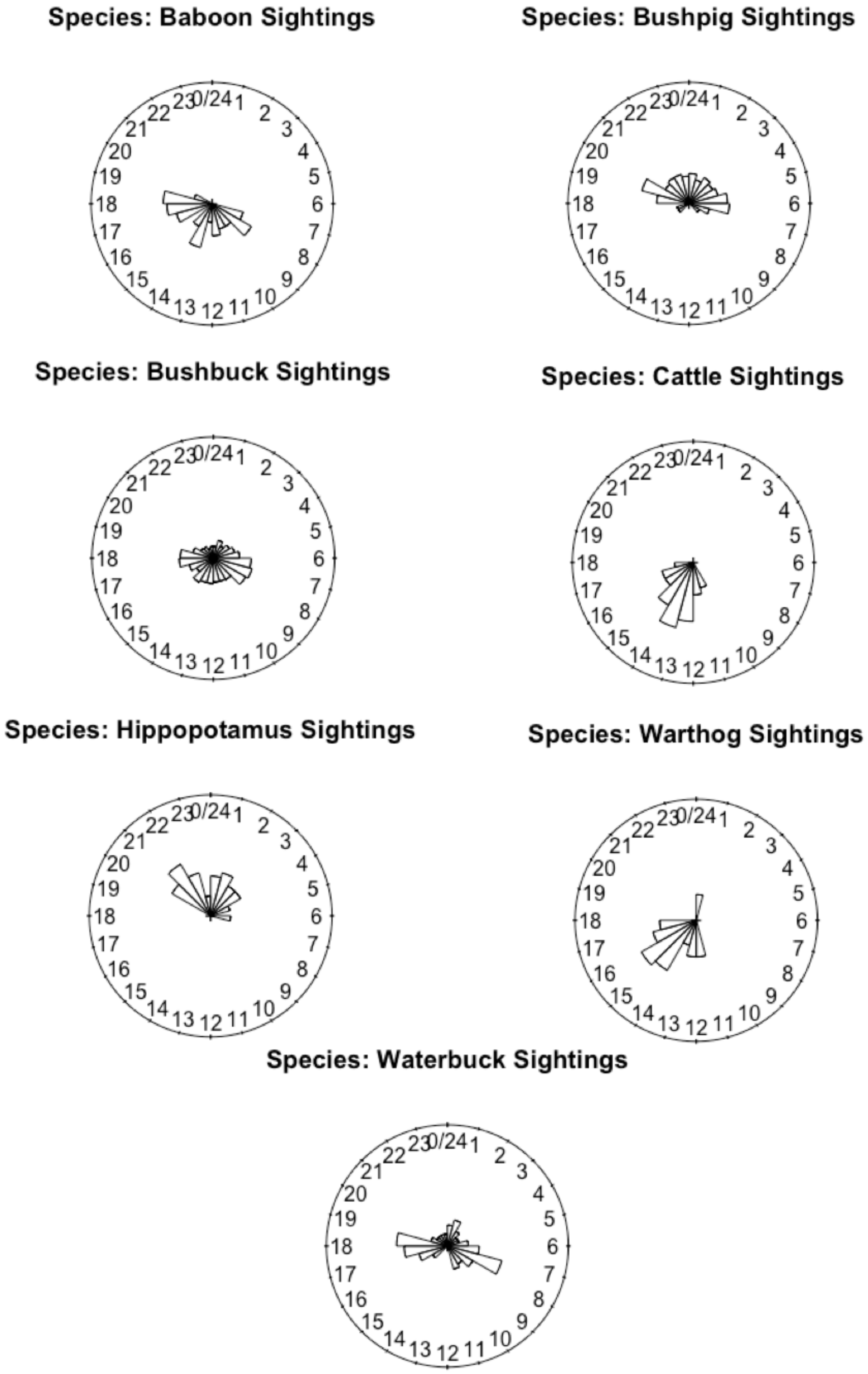


**Figure 2C.** Species sightings recorded with trail cameras for the year 2017 plotted as separate rose diagrams.

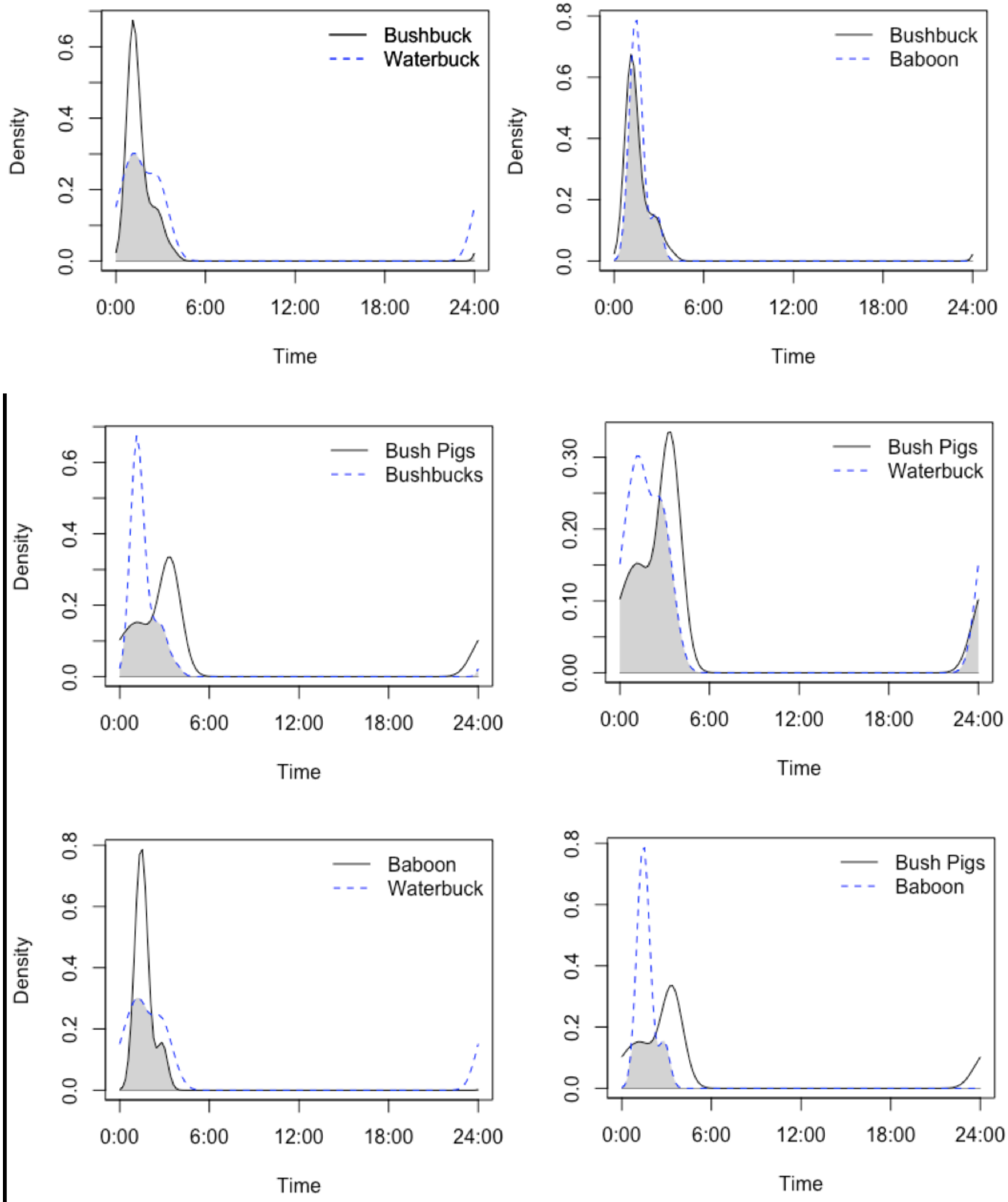


**Figure 3A.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2015. Shaded area represents overlap between two species with lines representing kernel-density estimates.

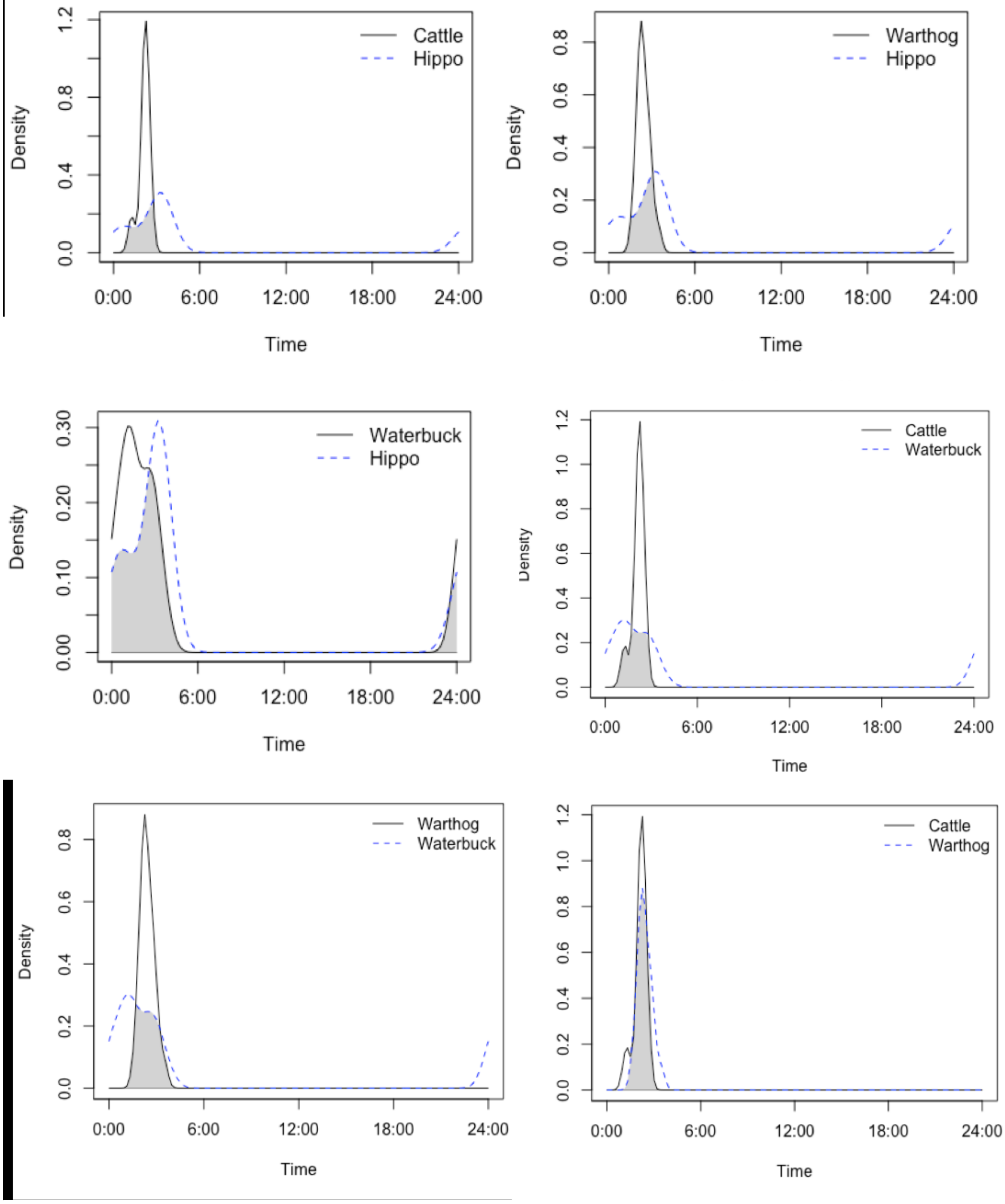


**Figure 3B.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 Area A. Shaded area represents overlap between two species with lines representing kernel-density estimates.

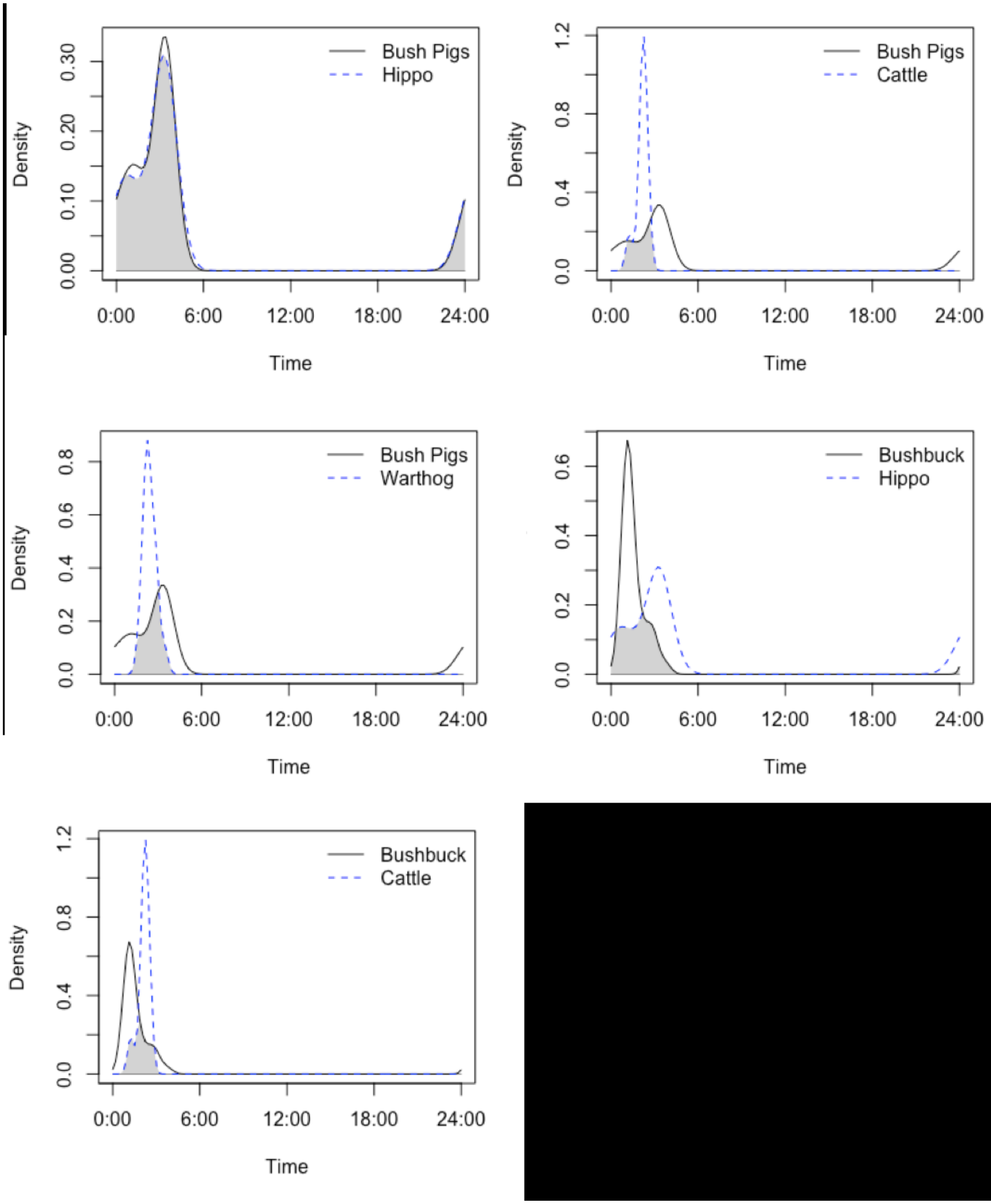


**Figure 3C**. Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2015. Shaded area represents overlap between two species with lines representing kernel-density estimates.

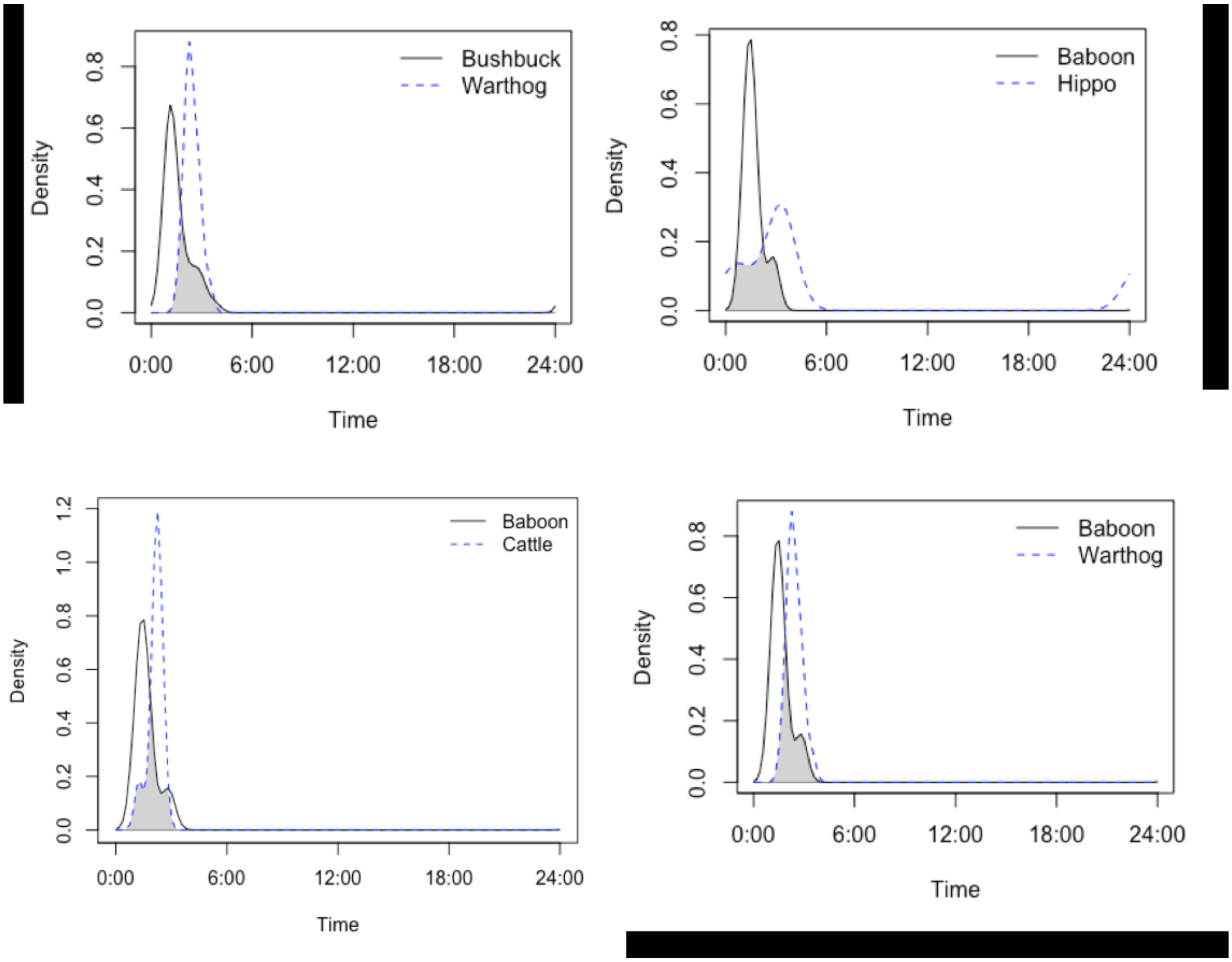


**Figure 3D.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2015. Shaded area represents overlap between two species with lines representing kernel-density estimates.

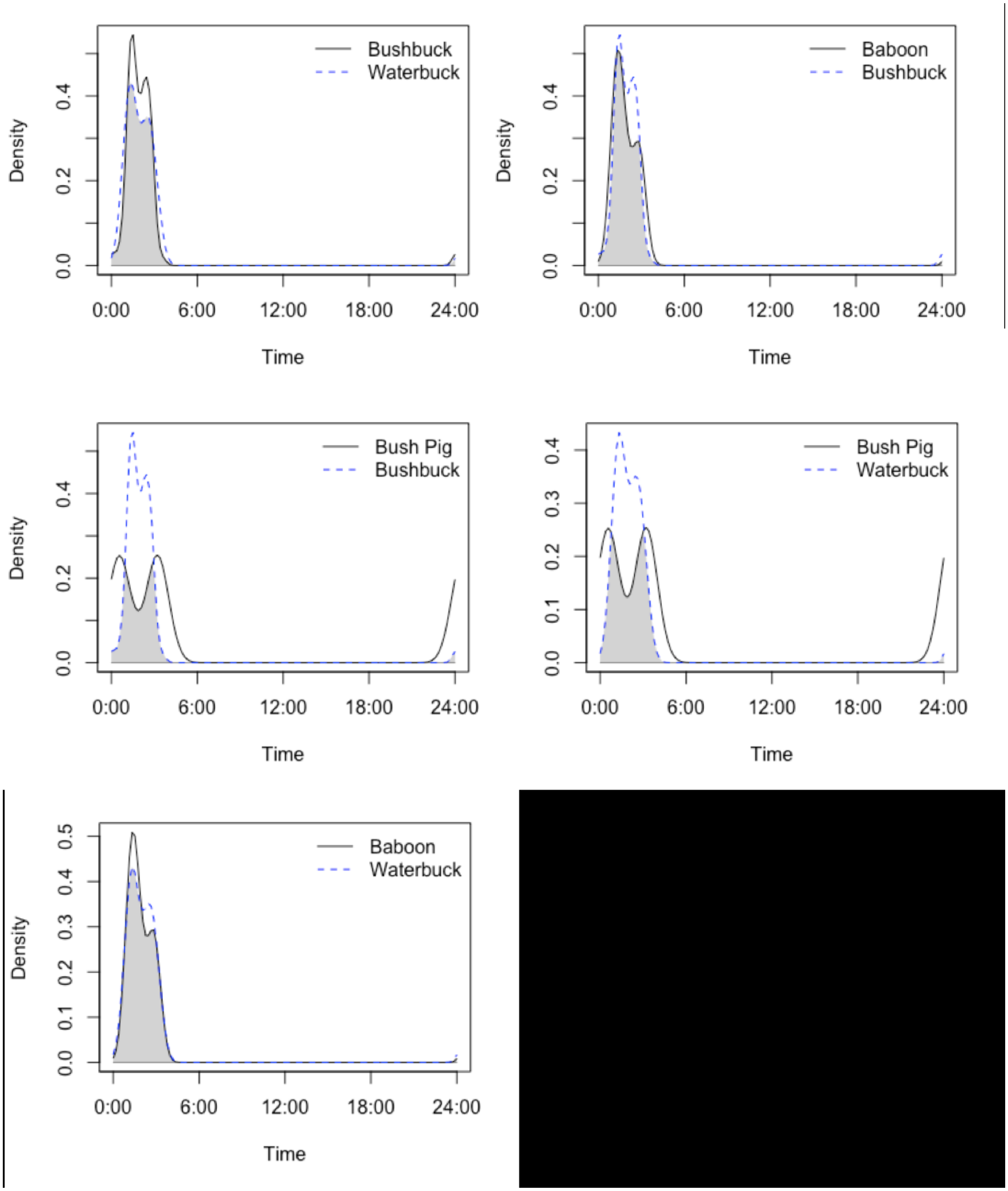


**Figure 4A.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 Area A. Shaded area represents overlap between two species with lines representing kernel-density estimates.

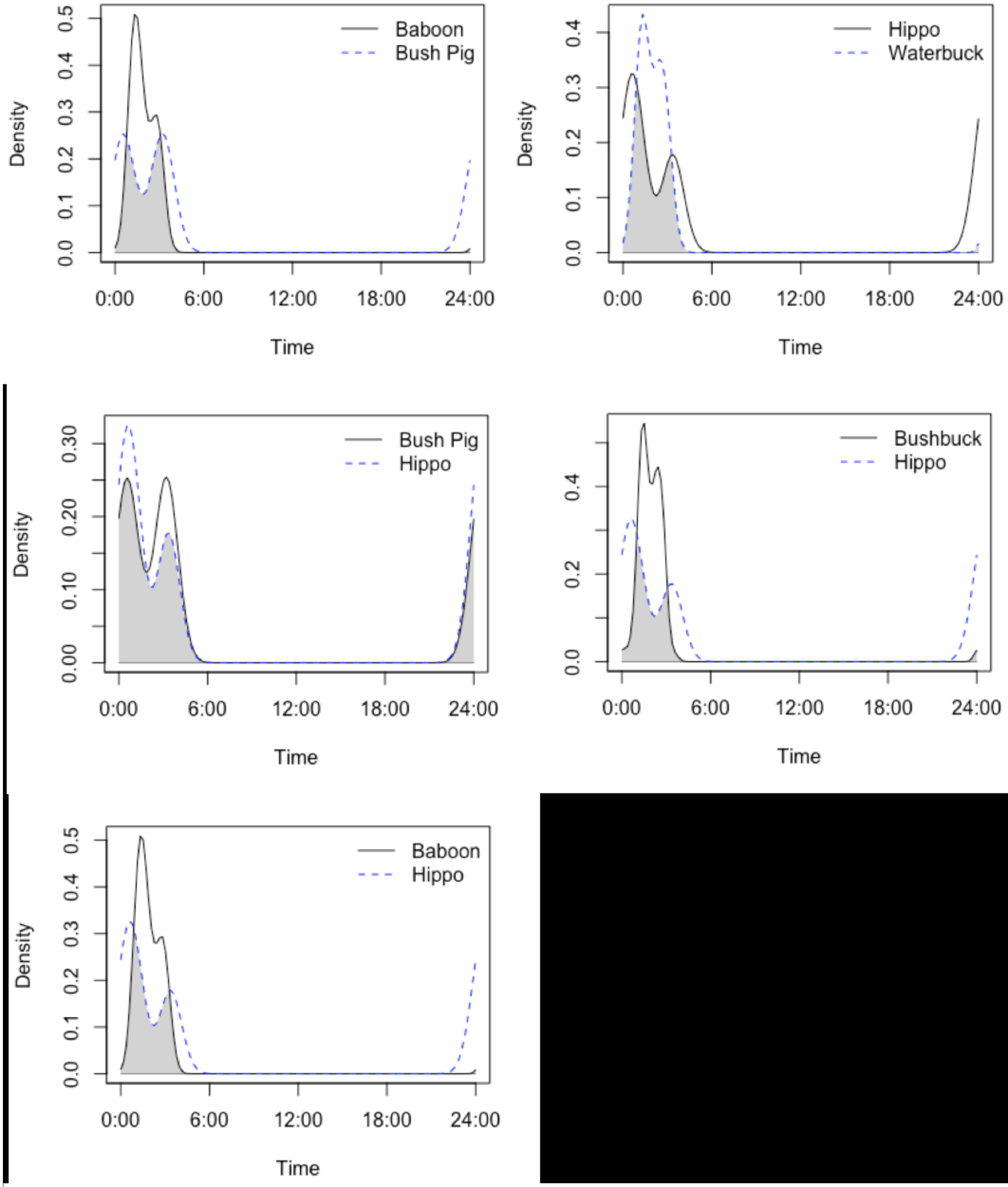


**Figure 4B.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 Area A. Shaded area represents overlap between two species with lines representing kernel-density estimates.

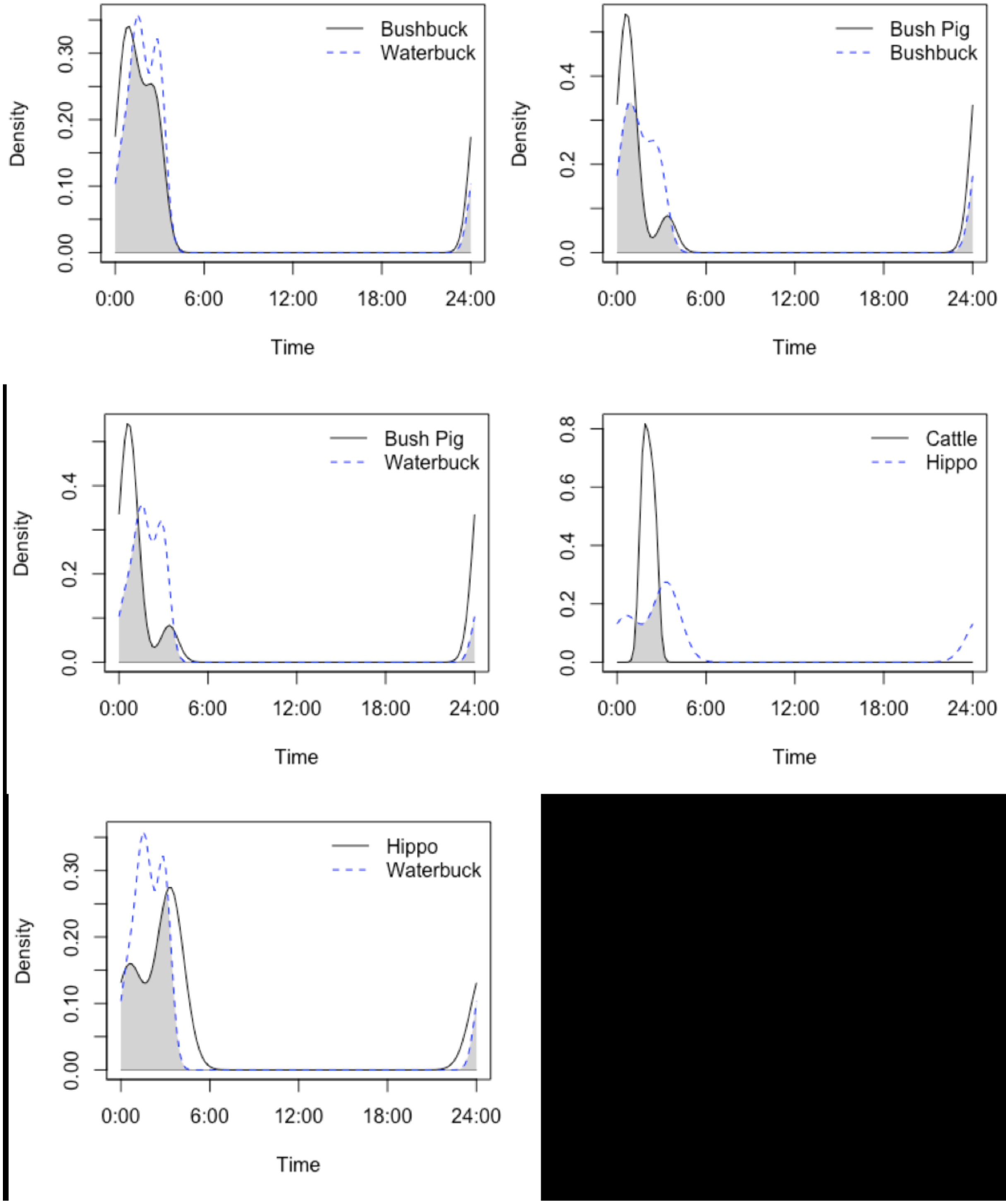


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**Figure 5A.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 Area B. Shaded area represents overlap between two species with lines representing kernel-density estimates.

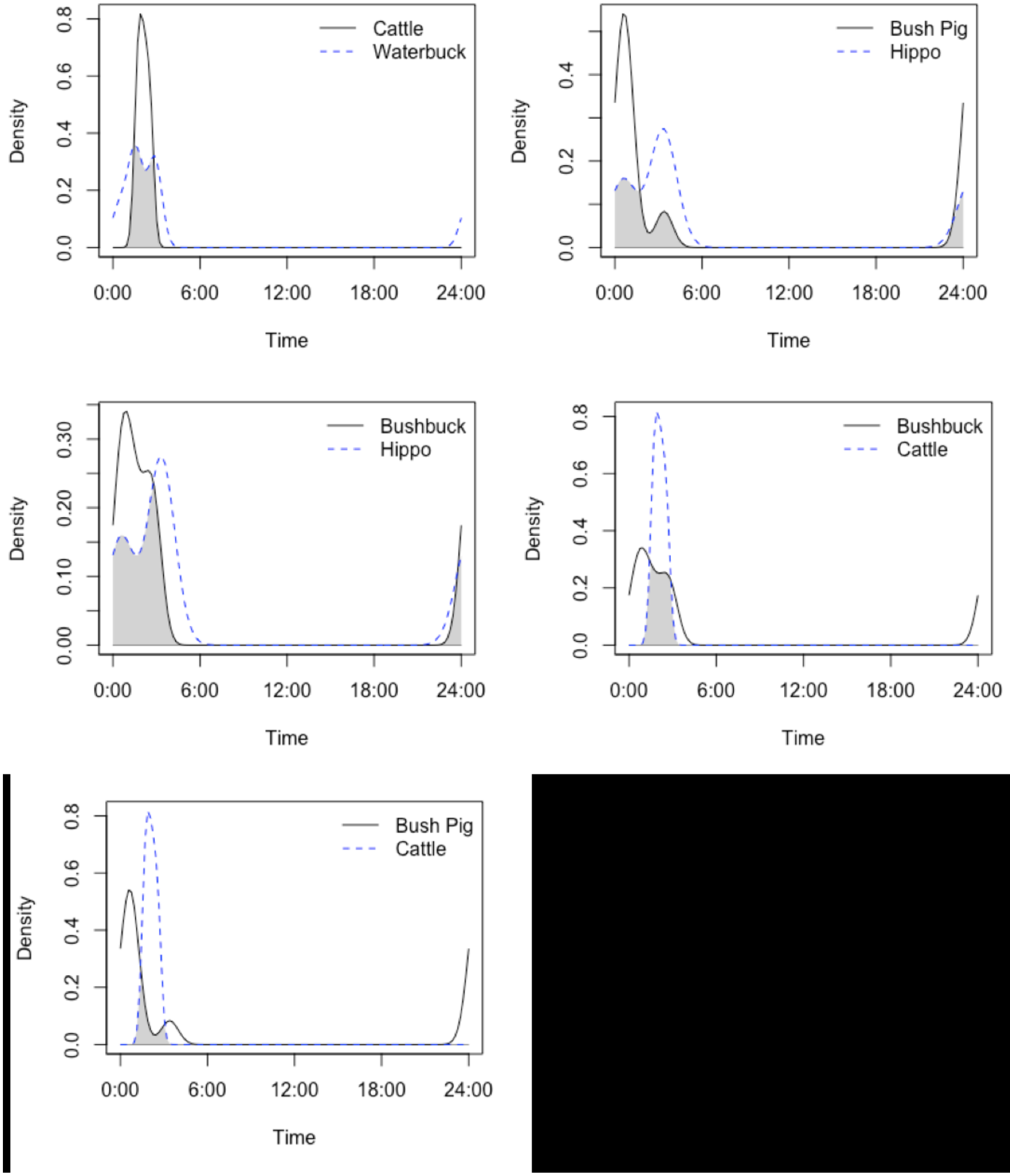

**Figure 5B.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 Area B. Shaded area represents overlap between two species with lines representing kernel-density estimates.

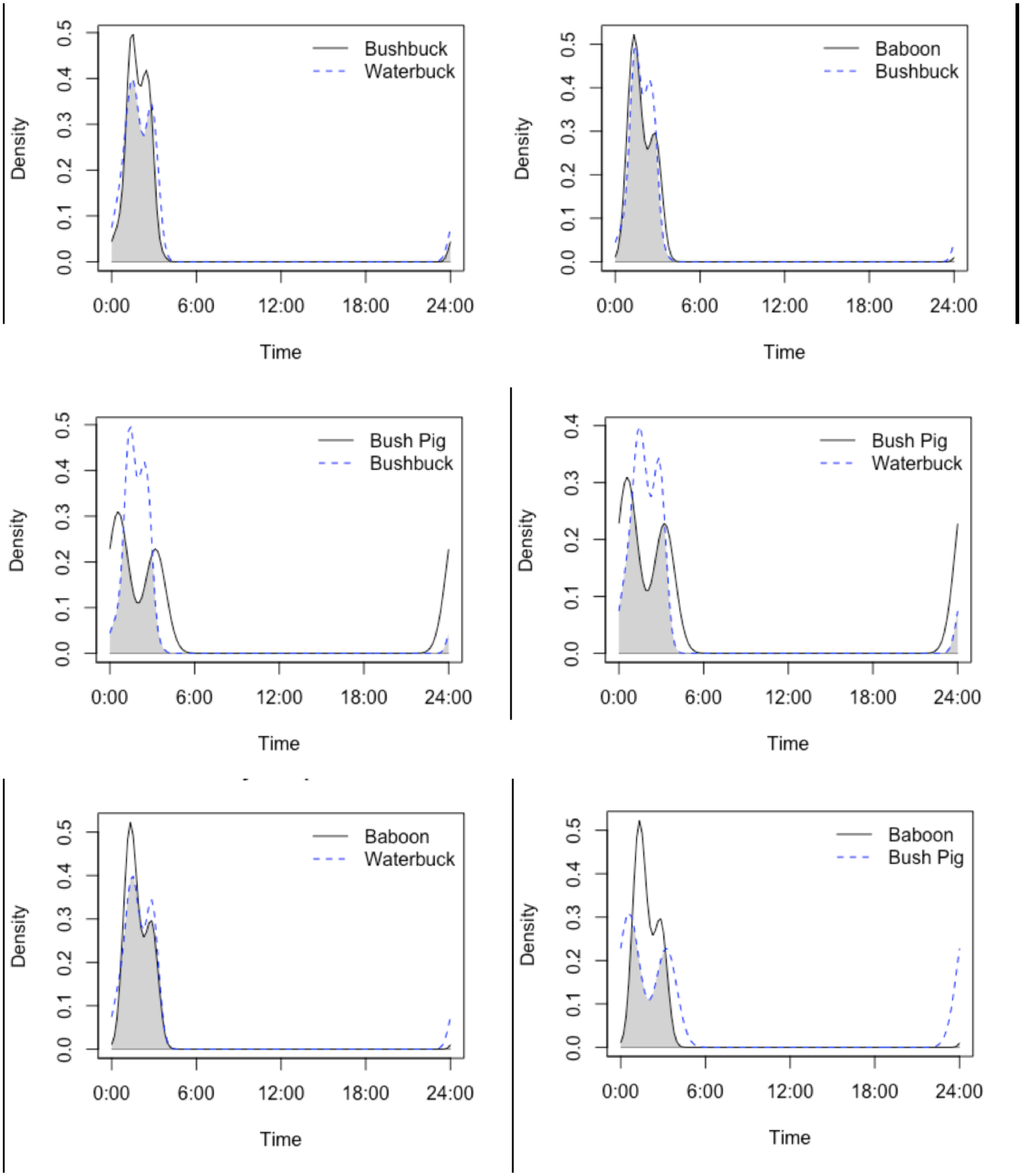

**Figure 6A.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 with species pooled between 2 areas. Shaded area represents overlap between two species with lines representing kernel-density estimates.

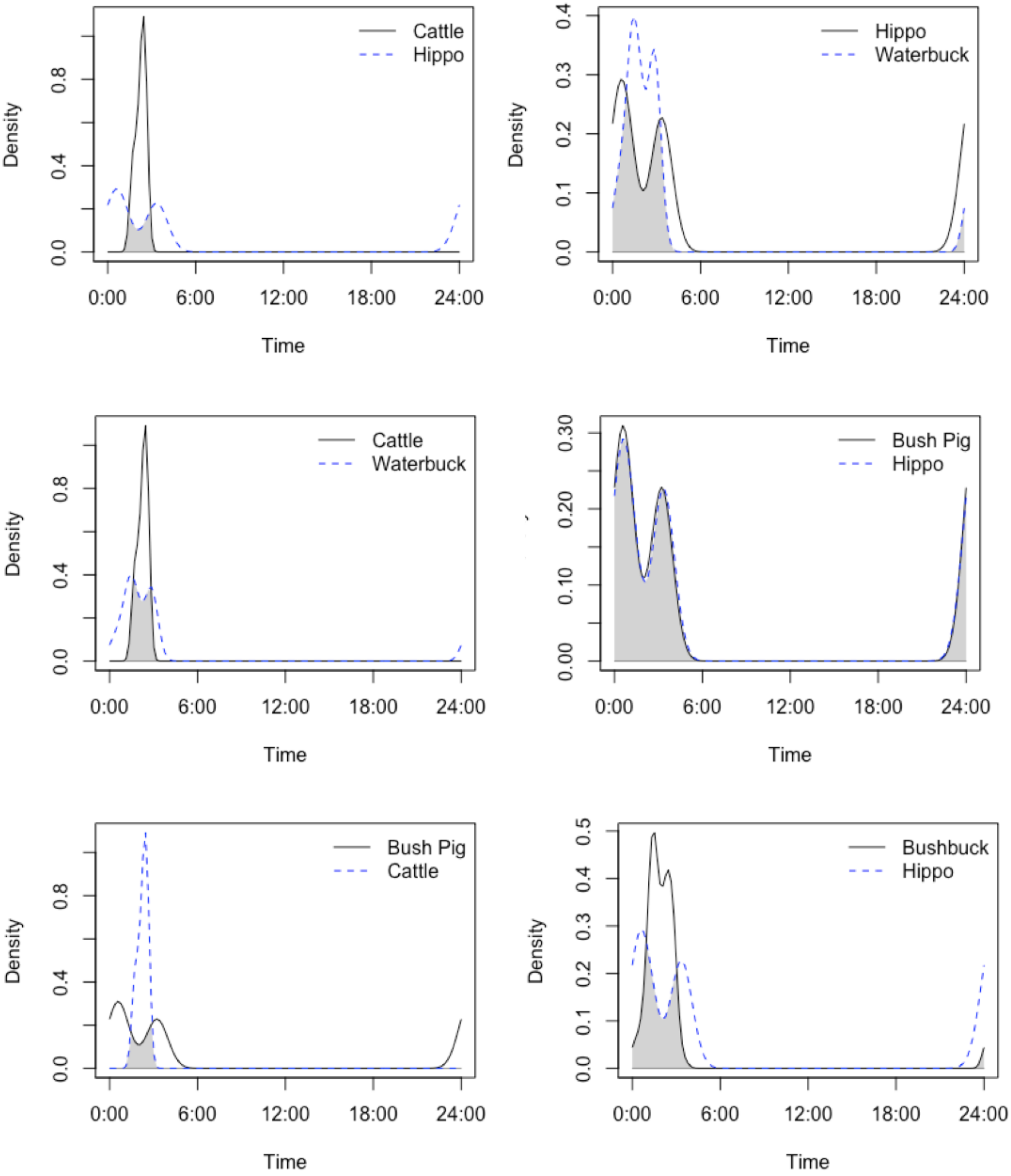

**Figure 6B.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 with species pooled between 2 areas. Shaded area represents overlap between two species with lines representing kernel-density estimates.

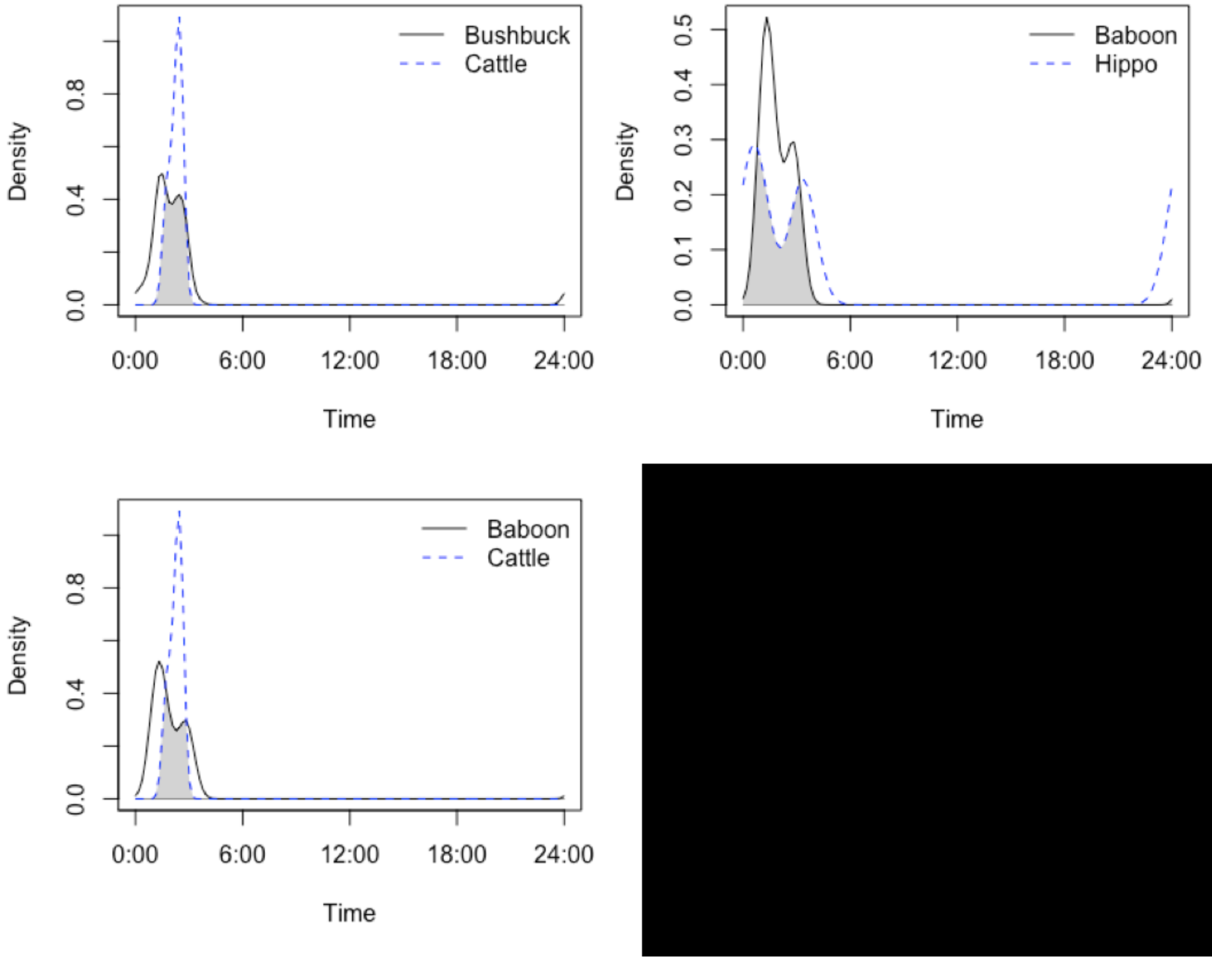

**Figure 6C.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2016 with species pooled between 2 areas. Shaded area represents overlap between two species with lines representing kernel-density estimates.

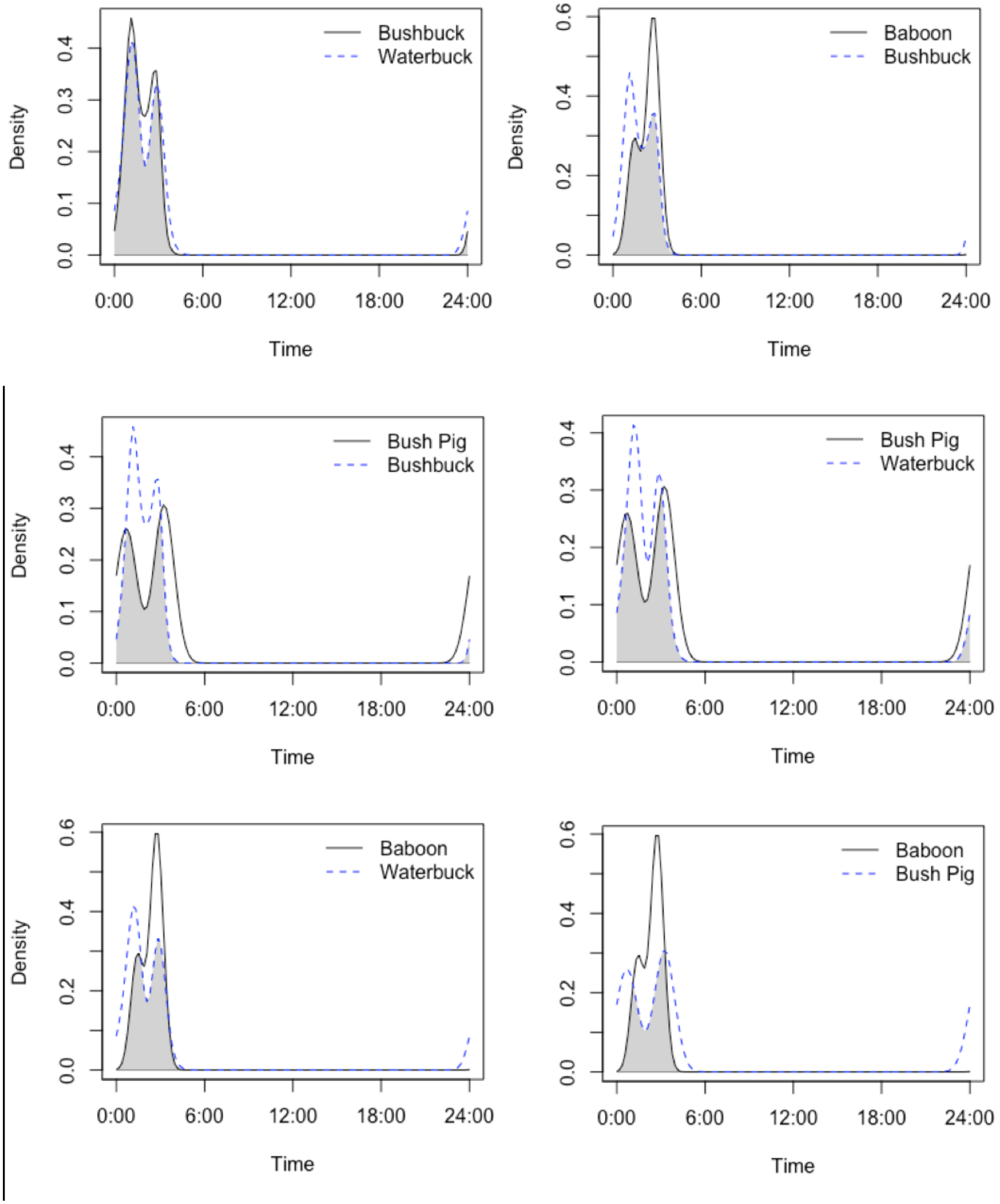

**Figure 7A.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2017. Shaded area represents overlap between two species with lines representing kernel-density estimates.

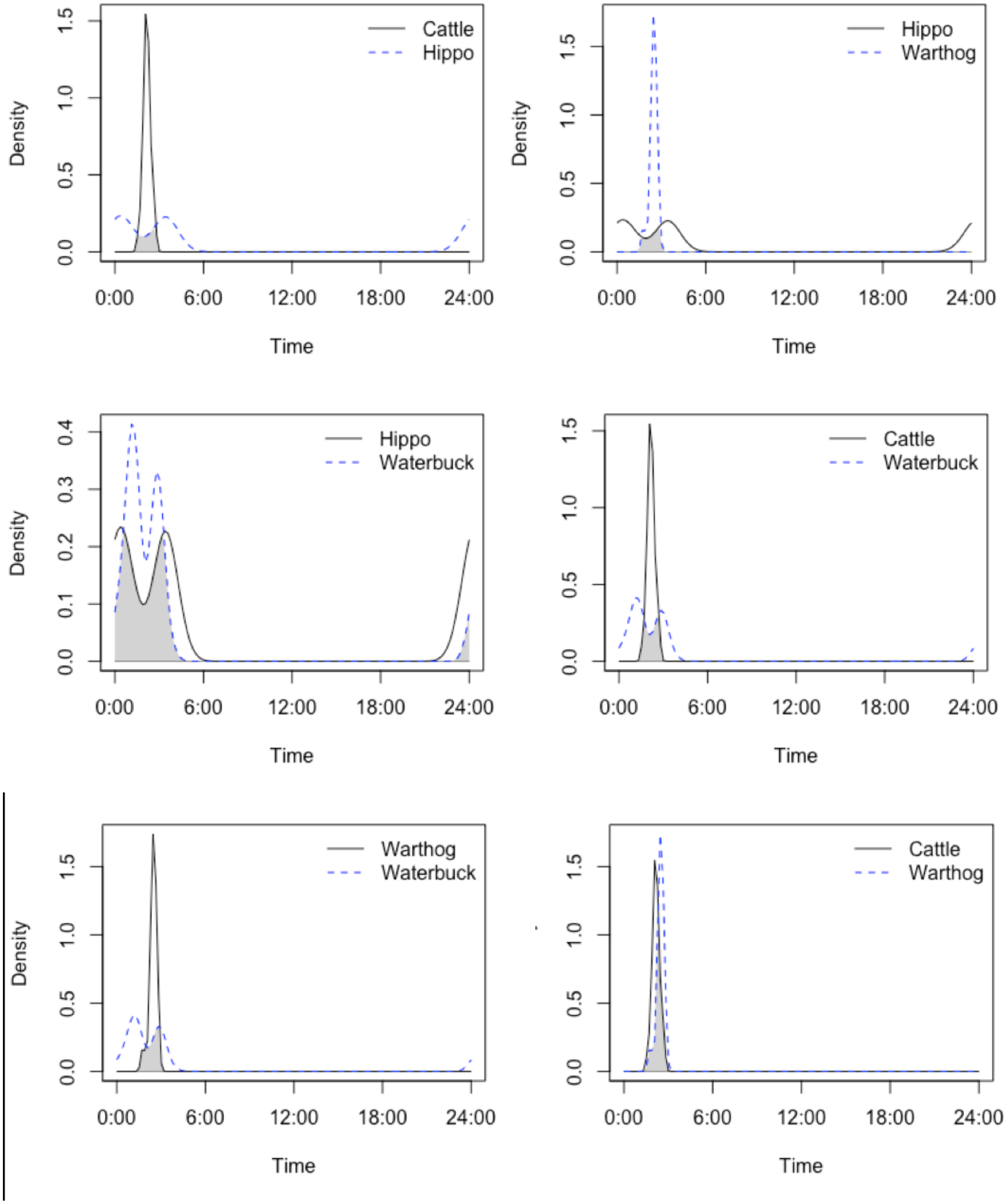

**Figure 7B.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2017. Shaded area represents overlap between two species with lines representing kernel-density estimates.

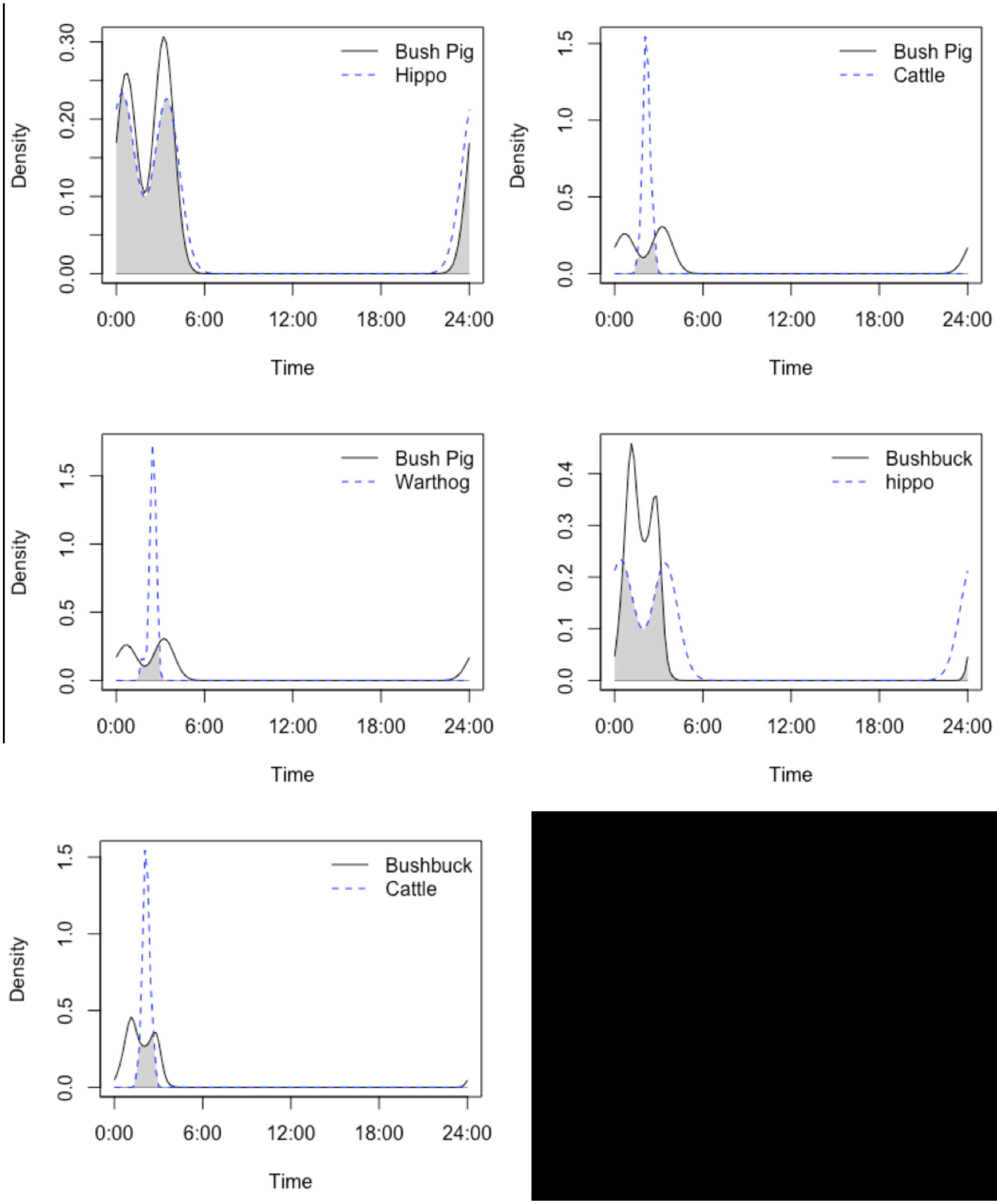

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**Figure 7C.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2017. Shaded area represents overlap between two species with lines representing kernel-density estimates.

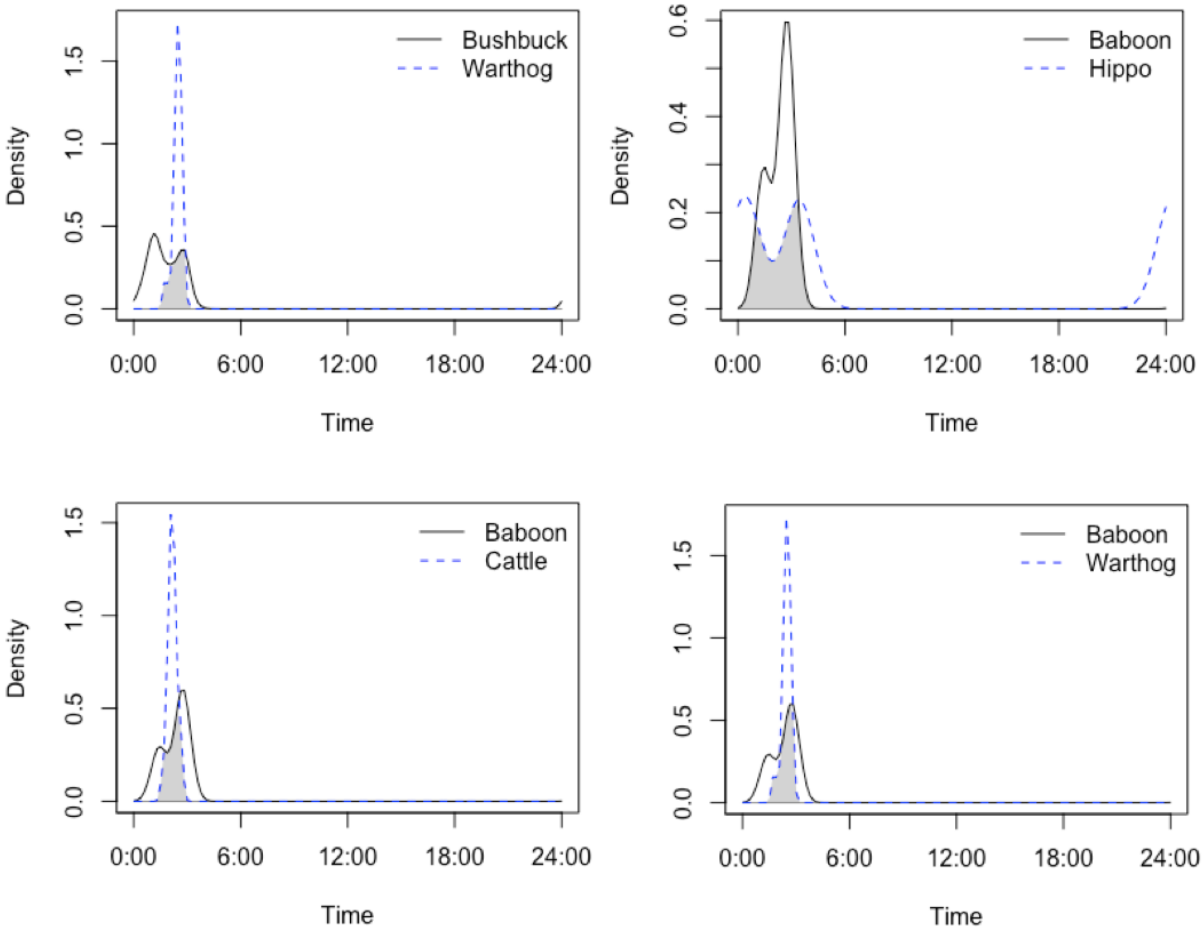

**Figure 7D.** Temporal overlap of herbivorous animals within 10m from forest-wetland edge in Mayanja River Valley, Central Uganda for the year 2017. Shaded area represents overlap between two species with lines representing kernel-density estimates.