Population size, distribution, and small-scale seasonal variations in pod dynamics, habitat selection, and behaviour of hippopotamus (Hippopotamus amphibius) in the Okavango Delta, northern Botswana

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Population size, distribution, and small-scale seasonal variations in pod dynamics, habitat selection, and behaviour of hippopotamus (*Hippopotamus amphibius*) in the Okavango Delta, northern Botswana

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I utilised thirteen years of aerial survey data to examine temporal and spatial patterns of hippo populations in the Delta. Hippos preferentially occurred in large lagoons within seasonal swamps, avoiding the dense aquatic vegetation and deep water of the permanent swamp/main channels. Since the mid-1990s, Botswana's hippo population has grown significantly, likely due to long-term increases in rainfall and inflow. The most recent survey (2018) emphasises Botswana as a stronghold for this species in Africa, however, the exceptionally small flood event of 2019 will likely have led to substantially reduced hippo numbers. This work demonstrates the value in long-term monitoring programs.

I developed a method to monitor (count/age) hippos using a drone, achieving more accurate counts than ground and aerial surveys. Using this method, I examined seasonal changes in hippo pods (size/density/demographic composition/distribution) related to varying surface water availability. In the low flood season, hippos occurred in larger pods in higher densities, aggregating on the minimal water still available. All seasons were characterised by near-constant changes in pods, emphasising their dynamic nature and challenging the notion of stable hippo groupings.

I conducted 24-hour activity budgets within the Delta and Chobe River to increase the currently limited knowledge of hippo behaviour and to investigate how behaviour changed temporally, spatially, and seasonally in variable landscapes. Large differences in behaviour between pods (even those within close proximity) indicate hippos are highly flexible, taking advantage of available resources, but also emphasising the effects of humans on hippo populations.

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Preface

This thesis represents a compilation of my own work with contributions from my supervisors, Dr Keith Leggett and Professor Richard Kingsford, and co-authors, Dr Gilad Bino, Dr Mitchell Lyons, and Dr Michael Chase. The thesis contains seven chapters: a general introduction which contextualises my research in relation to our current knowledge of hippos, five data chapters of original research, and a general discussion in which I summarise and discuss the findings of the thesis. Data chapters are either published or intend to be published (see below for publication details and author contributions), which has resulted in repetition of some information, particularly in the introductions. I have attempted to minimise this by referencing previous chapters where appropriate and through the inclusion of a general methods section. References have been consolidated into a single bibliography at the end of the thesis, as has supplementary information. Please note, I use collective terms in data chapters to acknowledge the assistance of co-authors.

Chapter 2 - Automated inundation mapping over large areas using Landsat data and Google Earth Engine

Author list: Inman, V.L. & Lyons, M.B.

Contributions: VLI led the conceptualization, data collection, analysis, and writing; MBL contributed to analysis and writing.

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Chapter 3 - Temporal and spatial patterns of hippo populations in the Okavango Delta, Botswana

Author list: Inman, V.L., Bino, G., Kingsford, R.T., Chase, M.J. & Leggett, K.E.A.

Contributions: VLI and RTK led the conceptualization; VLI and GB designed the study and conducted analyses; MJC provided data; VLI collected data and led the writing of the manuscript with contributions from all authors.

Chapter 4 - Drone-based counting and ageing of hippos

Author list: Inman, V.L., Kingsford, R.T., Chase, M.J. & Leggett, K.E.A.

Contributions: VLI and KEAL conceptualised the study; VLI designed the study, collected, and analysed the data, and led the writing of the manuscript with contributions from all authors.

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Chapter 5 - Seasonal changes in hippo pod size, density, demographic composition, and distribution

Author list: Inman, V.L. & Leggett, K.E.A.

Contributions: VLI and KEAL conceptualised the study; VLI designed the study, collected, and analysed the data, and led the writing with contributions from KEAL.

Chapter 6 - Hippo behaviour, diurnal and nocturnal activity budgets, social grouping, and habitat use

Author list: Inman, V.L. & Leggett, K.E.A.

Contributions: VLI and KEAL conceptualised the study, VLI designed the study, collected, and analysed the data, and led the writing with contributions from KEAL.

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Abstract

There is limited biological and ecological data on hippos, most of which originates from riverine/lacustrine populations, with none on the Okavango Delta population in its unique wetland habitat. This thesis aimed to investigate the Delta's hippo population (size/distribution) and examine small-scale seasonal variations in hippo pod dynamics, habitat selection, and behaviour. The research provides baseline ecological and behavioural data on hippos in wetland habitats and gives insight into their adaptability to changes in water availability. This is particularly important as the Delta's waters are threatened by climate change and human pressure, which will reduce habitat for hippos.

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Chapter 1: General introduction

1.1 Overview of hippo biology, behaviour, and ecology

The common (or Nile or river) hippopotamus (*Hippopotamus amphibius*) (hereafter called hippo) is an unmistakable species with a large, almost hairless, barrel-shaped body, huge head and relatively short legs (Eltringham, 1999; Klingel, 2013). Hippos are nocturnal semi-aquatic megaherbivores, thought to spend the majority of daytime hours resting in water (Klingel, 1991b; Eltringham, 1999). They are adapted to this amphibious lifestyle with nostrils and eyes in a raised location on top of their snout and head, allowing them to see, hear, and breathe with the majority of their body submerged in water (Clough, 1967; Eltringham, 1999). Hippos can hold their breath for up to six minutes, moving through the water by walking or pushing themselves off the bottom (Eltringham, 1999; Klingel, 2013). When resting in deep water they either lie/stand on the bottom fully submerged, reflexively moving to the surface to take breaths (Lyamin et al., 2013 in Dell et al., 2016), or stand on their back legs so their head is above water (Klingel, 2013). In shallow water, with their heads and backs exposed, they often appear to be floating but are actually lying/standing on the river bed (Eltringham, 1999; Klingel, 2013).

Perhaps the most well-known aspect of hippo anatomy is their large canines often exposed by their enormous gape, which are only used for fighting and intimidation (Eltringham, 1993b, 1999; Klingel, 2013). Their teeth are not used for obtaining food, instead they use their strong lips to pluck terrestrial grasses, swinging their head back and forth as they move and feed, with their molars taking the role of masticating (Pienaar et al., 1966; Scotcher et al., 1978; Eltringham, 1993b, 1999; Klingel, 2013). Grazing is thought to predominately occur on land at night as an individual activity, except young hippos will remain with their mothers (Klingel, 1991b, 2013; Eltringham, 1993b, 1999). The distance that hippos travel to their nightly feeding locations varies depending on the season and productivity of the area, ranging from directly adjacent to their daytime refuge to up to 10 km away (Field & Laws, 1970; Lock, 1972; Harrison et al., 2008; Wengström, 2009; Prinsloo, 2016; Stears et al., 2019).

Hippos are gregarious animals in the water during the day, generally occurring in large groups referred to as pods or schools (Figure 1.1). Pods can be either nursery groups,

where there is a dominant bull (male hippo) but the majority of individuals are females with young, or bachelor groups made up mainly of bulls, though members of either sex can be in each group (Laws & Clough, 1966; Kayanja, 1989; Klingel, 1991b; Eltringham, 1999). Hippos that are solitary are almost always bulls, though may be females about to give birth (Ansell, 1965a; Laws & Clough, 1966; Olivier & Laurie, 1974b; Marshall & Sayer, 1976; Karstad, 1984; Kayanja, 1989; Klingel, 1991b). The dominant bull exhibits strong territoriality in the water, being dominant over all conspecifics and having exclusive mating rights within that territory, though will tolerate other bulls as long as they act subordinately (Clough, 1967; Karstad & Hudson, 1986; Kayanja, 1989; Klingel, 1991b; Eltringham, 1999). When competing over territories male hippos use their canines to fight, sometimes fatally (Klingel, 1991b; Eltringham, 1999). In a river ecosystem around 10% of adult bulls control a territory, with boundaries extending along the shoreline and varying in size depending on hippo density (Klingel, 1991b). Hippos do not appear to have territories on land (Clough, 1967; Laws, 1968b; Klingel, 1991b). After feeding nocturnally, hippos tend to return to the same aquatic area from the previous day, which leads to generally consistent groups (Klingel, 1991b). However, there are no true stable associations within pods (except mother and young), with each hippo having a home range that may overlap, but does not necessarily match, that of a dominant bull (Klingel, 1991b). Home ranges are determined by river dynamics and resource availability and, if sufficient resources are available, hippos may remain in an area for several years (Karstad & Hudson, 1986; Eltringham, 1999; Klingel, 2013; Stears et al., 2019).

Figure 1.1. A pod of hippos resting in shallow water in Chobe National Park, Botswana.

Due to their large size and use of both aquatic and terrestrial habitats, hippos exert a substantial impact on their environment (McCarthy et al., 1998b; Eltringham, 1999). Hippos act as ecosystem engineers through three different (though related) activities: the creation of hippo lawns, the transfer of nutrients, and the creation of hippo paths. A hippo lawn is a grassland that has been heavily grazed by hippos, with the remaining short grass being better quality (having higher density, leaf to stem ratio, digestibility, and levels of protein) than in non-grazed areas (Eltringham, 1999; Verweij et al., 2006; McCauley et al., 2018). In addition, hippo lawns dispersed within areas of un-grazed grasslands leads to a mosaic landscape (Verweij et al., 2006; Kanga et al., 2013). Both of these impacts are beneficial to other herbivores (Eltringham, 1999; Verweij et al., 2006; Kanga et al., 2013). Hippos transfer nutrients they have consumed on land to their aquatic resting sites through their excretions (McCauley et al., 2015; Subalusky et al., 2015; Stears et al., 2018; Dawson, 2019). Studies have determined these to be significant nutrient sources for rivers, used by fish and invertebrates, with the presence of hippos potentially impacting fisheries productivity (McCauley et al., 2015; Subalusky et al., 2015). However, where natural river flow has been altered due to human activities, these excretions can lead to eutrophication (Stears et al., 2018). Hippos moving between terrestrial and aquatic environments also leads to the creation of paths through the riparian vegetation and on land. As hippos tend to follow the same paths daily, over time they form trenches and as more hippos use it they form gullies (Eltringham, 1999; Klingel, 2013). In wetland ecosystems, hippo paths in floodplains promote water flow, provide habitat for crocodile, fish, and amphibians, and assist in maintaining connectivity between habitats (Lock, 1972; McCarthy et al., 1992, 1998b; Naiman & Rogers, 1997; Jachmann, 2001; Deocampo, 2002; Mosepele et al., 2009; Klingel, 2013).

1.2 Hippo distribution and conservation

In 2006 the conservation status of hippos was raised from lower risk/least concern to Vulnerable (Lewison & Pluháček, 2017), with hippos experiencing substantial declines in both numbers and geographical range (Eltringham, 1999; Lewison & Pluháček, 2017). There are believed to be five subspecies of the common hippo, but these are not fully researched, are almost never distinguished in studies, cannot be distinguished in the field, and ranges appear to be indistinct (Eltringham, 1993b, 1999; Klingel, 2013). Historically, hippos were found throughout most rivers, lakes and swamps of sub-Saharan Africa, but

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more recently their distribution has become restricted and localised (Figure 1.2), often to protected areas where human pressure is minimal, particularly in the southern extent of its range (Clarke, 1953; Clough, 1967; Eltringham, 1993b, 1999; Klingel, 2013; Lewison & Pluháček, 2017). There are marked differences in hippo population sizes throughout their range, with the majority of hippos occurring in eastern and southern Africa (Lewison & Pluháček, 2017) (Figure 1.2). The current Africa-wide estimate of hippos is 115,000–130,000 (Lewison & Pluháček, 2017), though difficulties in accurately surveying hippos (Zisadza et al., 2010; Kanga et al., 2011; Mackie et al., 2012; Stommel et al., 2016) and the repetition of outdated/incorrect estimates (Mackie et al., 2012), leads to low confidence in the accuracy of this estimate. Further, improvements in counting techniques over time can lead to the appearance of population increases when compared to historic baseline estimates (Scotcher, 1978).
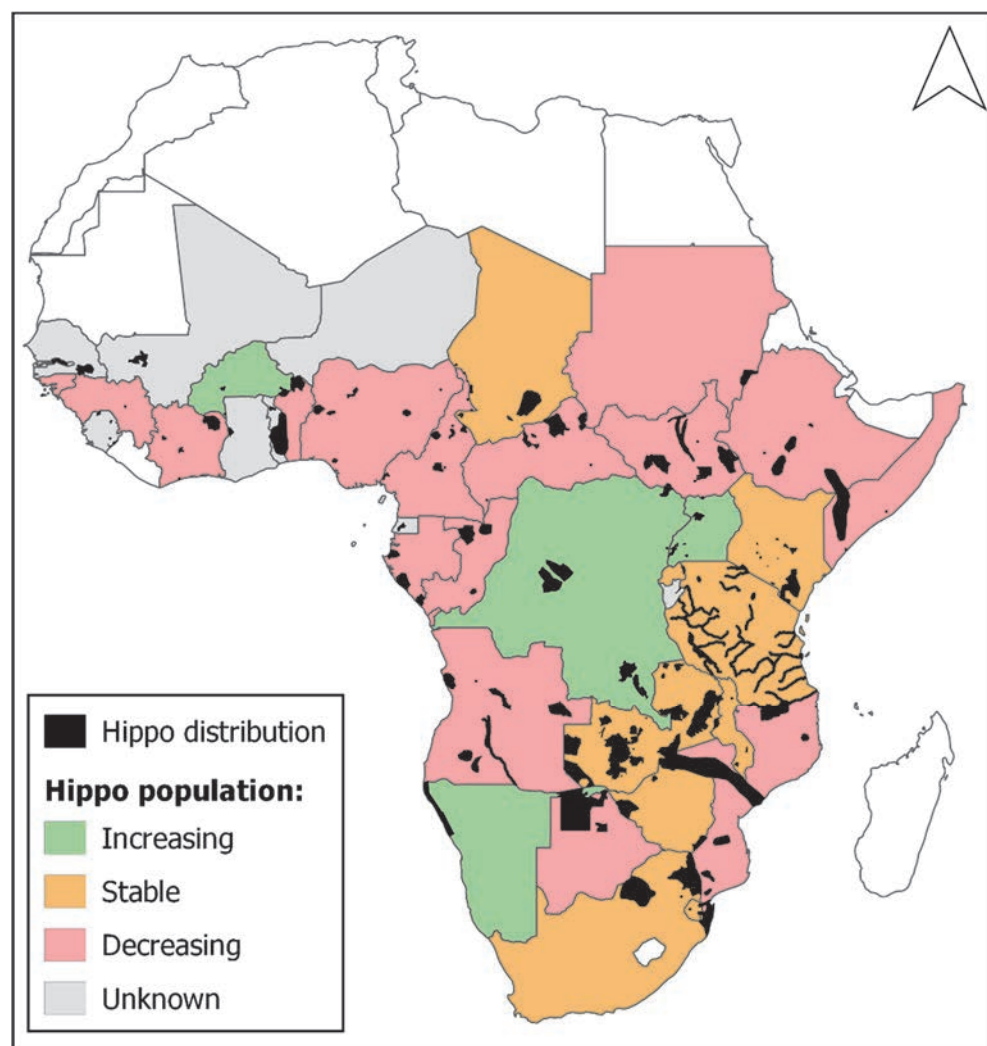
Figure 1.2. Hippo distribution within Africa and status of populations within countries. Data taken from IUCN (2017).

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Hippos are threatened by habitat loss for agriculture, grazing competition with livestock, climate change, hunting and poaching for meat and ivory (hippo ivory trade increased following the international elephant ivory ban), disease, retaliatory killing from human-wildlife conflict, and reduced dispersal due to increases in protected area boundaries (e.g. fences) (Marshall & Sayer, 1976; Karstad, 1984; Eltringham, 1993b; Weiler et al., 1994; Mkanda & Kumchedwa, 1997; Lewison, 2007; Wilbroad & Milanzi, 2010; Perry, 2015; Lewison & Pluháček, 2017). Hippos are particularly vulnerable in areas subject to civil unrest (e.g. Democratic Republic of Congo and Mozambique) and where populations are isolated and small (e.g. West Africa) (Kayanja, 1989; Eltringham, 1999; Shoumatoff, 2000 and Hillman Smith et al., 2003 in Lewison, 2007; Perry, 2015; Lewison & Pluháček, 2017; Stalmans et al., 2019). Population projection models have been used to assess how interactions between threats can endanger hippo populations; Lewison (2007) predicted that the combination of wetland destruction and moderate hunting pressure would yield declines to 50% of the original population size within 100 years. These results emphasize the importance of a holistic assessment of threats, as even relatively low levels of human disturbance could result in significant population declines when coupled with environmental changes.

Hippos' susceptibility to threatening processes is exacerbated by their reliance on freshwater ecosystems, ecosystems that are highly utilised by people and are at risk of development (Revenga et al., 2005; Nel et al., 2009). Further, climate change is projected to alter rainfall, temperature, and evaporation patterns, meaning the availability, quality, and distribution of aquatic ecosystems within the hippo range will change (Mitchell, 2013; IPCC, 2014; Bamutaze et al., 2019). Hippo distribution models highlight the vulnerability of this species to changes in water; models incorporating streamflow abstraction resulted in widespread, marked decreases in hippo habitat, with relatively small diversions of streamflow resulting in significant habitat reductions (Nuñez, 2017). Hippos have relatively small home ranges compared to other megaherbivores, reflecting their reliance on diurnal aquatic refuges (Stears et al., 2019). This means they are particularly vulnerable as they have limited opportunities for dispersal due to their specialised habitat requirements, so environmental changes can be disastrous for a population if there are no nearby refuges (Ansell, 1965a; Eltringham, 1999; Stears et al., 2019).

1.3 Previous hippo research

Despite its status as a charismatic species, compared to many other threatened African megafauna, hippos are understudied (Figure 1.3). Of the 38 countries that contain hippos, the majority of studies have focussed on populations in only a few countries, particularly in Queen Elizabeth National Park in Uganda (e.g. Luck & Wright, 1964; Laws & Clough, 1966; Field, 1970; Thornton, 1971; Lock, 1972; Klingel, 1991b) and the Luangwa River in Zambia (e.g. Attwell, 1963; Ansell, 1965; Sayer & Rakha, 1974; Marshall & Sayer, 1976; Tembo, 1987; Chansa et al., 2011b; Chomba, 2013). In other countries, hippos have been subject to little or no investigation.
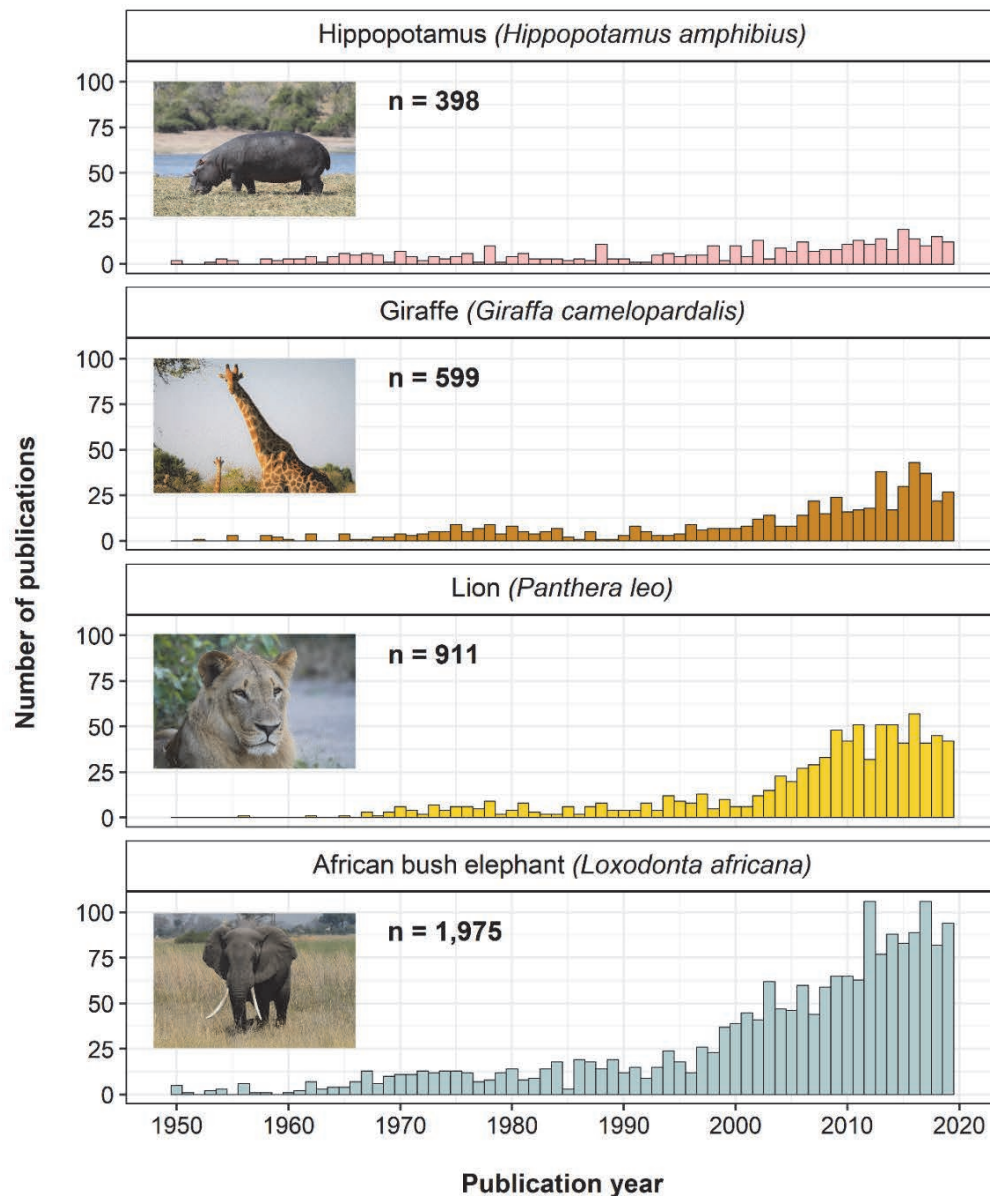
Figure 1.3. Number of scientific publications on hippo, giraffe, lion, and African elephant since 1950. Details of literature search are described in Supplementary Text S1.1.

In the 1960s and 1970s in Uganda, South Africa, and Zambia, hippos were considered overpopulated and to be damaging the environment. Subsequently, they were culled in large numbers and the carcasses collected and studied (e.g. Laws & Clough, 1966; Laws, 1968a; Sayer & Rakha, 1974; Skinner et al., 1975). Much of the current knowledge of hippo ecology and biology originates from these studies (Graham et al., 2002). However, there are likely to be inherent biases in these data due to this collection method. For example, younger and smaller animals are more difficult to shoot and recover and hunters tended to focus on large pods that were likely to include more females than males, meaning these age classes/sexes are likely to be under/overrepresented in samples, respectively (Laws & Clough, 1966; Clough, 1967; Marshall & Sayer, 1976). Further, these data were from just a few populations, and ones which were thought to be under considerable stress from overpopulation. Re-collecting these data from a different population, using less-biased methods, would provide a valuable addition to our understanding of hippo biology, particularly demography.

Given information has originated from studying just a few populations and predominately those in riverine and lacustrine habitats, the significance of the information to other populations is unknown (Graham et al., 2002). Populations occurring in vastly different ecosystems are subject to different pressures, which may result in variations in their behaviour and ecology (Stears et al., 2019). Researching a broad range of populations ensures intra-species variability is captured, which may be important when planning conservation and management. Further, collecting data on hippos in different areas is also essential to obtain baseline information (e.g. population size) from which variations in the populations can be assessed (Eltringham, 1993a). Monitoring the status/trends of hippo populations, even those that are stable, can ensure actions are implemented to protect populations before their conservation status changes (Laws, 1968b; Eltringham, 1993a; Lewison, 2002).

The lack of research on hippos is at least partially due to the difficulty in studying them; they can be aggressive, have a nocturnal, amphibious lifestyle, and often occur in inaccessible areas, meaning extensive observations and experimentation are often not viable and collection of accurate data are difficult (Karstad, 1984; Krueger, 1997; Lewison, 2002). Research should therefore not only aim to fill knowledge gaps, but also

to find ways to reduce these obstacles. For example, an inability to accurately count hippos has been noted as a significant barrier to research/monitoring (Laws, 1968b; Eltringham, 1993b), even by organisations that conduct hippo surveys (Department of Wildlife and National Parks, 2003, 2005, 2012), and therefore improvements on current techniques used to count hippos would be invaluable.

Accurate knowledge of hippo populations, and their biology and ecology, is required for effective management and conservation, and is particularly important in times of unprecedented ecological change (Eltringham, 1993a, 1999; Graham et al., 2002; Lewison, 2002; Nuñez, 2017; Stears et al., 2019). Understanding their habitat use will help conservation and land managers account for hippo space needs and can be used to mitigate issues such as human-hippo conflict, often triggered by human encroachment into hippo habitat (Lewison, 2002; Nuñez, 2017; Stears et al., 2019). Specific areas of hippo research that have been flagged as requiring further effort include hippo population sizes and trends, distribution, life history, spatial ecology, home ranges, habitat use, and behaviour (activity/time budgets), with an emphasis on how these are affected by seasonal and climatic variations (Laws, 1968b; Eltringham, 1993a; Krueger, 1997; Lewison, 2002; Perry, 2015; Lewison & Pluháček, 2017; Nuñez, 2017).

1.4 Hippos in Botswana

Given the aridity of Botswana, hippos are restricted to the north of the country, occurring in the Okavango Delta (hereafter called the Delta) and Chobe, Linyanti, and Kwando River systems (Eltringham, 1993b; Lewison & Pluháček, 2017; Chase et al., 2018). The IUCN Red List has identified the hippo population in Botswana as having a restricted distribution and low density, providing a population estimate of "1,600 in the wet season and 500 in the dry" (Lewison & Pluháček, 2017), an estimate that originates from at least 1993 (Eltringham, 1993b). They report Botswana's hippo population as declining, but having total legal protection and a fair level of enforcement of this protection, and indicate no concern regarding its conservation status (Lewison & Pluháček, 2017). However, estimates from recent surveys (Chase et al., 2018) differ substantially from those provided by the IUCN, estimating Botswana's hippo population at around 13,000 and increasing. This puts Botswana with the third largest hippo population in Africa, with 95% of the population occurring within the Delta and surrounding areas.

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Hippos have long been recognised as an integral part of the Delta; their paths in the floodplains are prolific and assist in expanding the swamp, with some paths developing into significant channels (McCarthy et al., 1992, 1998b; Eltringham, 1999; Mosepele et al., 2009). The presence of hippos and their movement through the landscape is sometimes the only factor preventing aquatic vegetation from growing over and closing channels (McCarthy et al., 1998b). Their important role emphasises the necessity of conserving them and ensuring their continued presence in the ecosystem (McCarthy et al., 1998b; Eltringham, 1999).

> *"The hippopotamus is an important component of the Okavango ecosystem whose influence is far greater than that of any other mammalian species. There can be no doubt that without hippos, the characteristics of the system would be different. The conservation of hippos is therefore essential and moreover, detailed study of the hippos in the Okavango is overdue"*
> - *T.S. McCarthy, 1998*

1.5 Project aims and objectives

In this thesis I aim to investigate the Okavango Delta's hippo population (size/distribution) and examine small-scale seasonal variations in the pod dynamics, habitat selection, and behaviour of hippos in the region. This thesis has seven chapters; this general introduction chapter, five data chapters (Chapters 2–6) and a general discussion chapter (Chapter 7):

- Chapter 2: I detail my implementation of a remote sensing method to develop accurate, high-resolution maps showing flooding over a large area (the Delta) for both discrete time periods and long-term patterns, necessary for Chapter 3.

- Chapter 3: I use the flood mapping method developed in Chapter 2, in conjunction with surface water and vegetation maps and inflow and rainfall records, to examine drivers of spatial and temporal variations in hippo abundance in the Delta using thirteen years of aerial survey data. I determine the broad-scale preferred habitats of hippos and examine the temporal trends in the Delta population.

- Chapter 4: Traditional survey methods (aerial, ground, boat) undercount hippos, therefore, I develop a method to monitor (count/age) hippos using a drone, comparing the results to ground and aerial survey counts. I adapt the ageing

method to increase the numbers of hippos able to be assessed, also investigating the utility of the drone to differentiate hippo sexes and assess their body condition.

- Chapter 5: I use the drone method I developed in Chapter 4 to examine seasonal changes in hippo pods (size/density/demographic composition/distribution), and how these varied in relation to surface water availability.

- Chapter 6: I conduct 24-hour activity budgets of hippos in the Delta and another study area (Chobe River) to increase the currently limited knowledge of hippo behaviour, and to investigate how behaviour changed temporally, spatially, and seasonally in variable landscapes.

- Chapter 7: I synthesise the results of the thesis and highlight future research directions.

Despite their importance to the ecosystem, this thesis is the first dedicated study on hippos in Botswana. Therefore, my research provides baseline ecological and behavioural data on hippos in the Delta, and more generally to wetland habitats. The dynamic nature of the Delta (discussed below) means hippos in this region must respond to large variations in their daily living space both inter and intra-annually. Therefore, investigating this population gives us insight into the ability of hippos to react to changes in water availability, more so than examining a population that occurs in a more static ecosystem.

1.6 Study area

All studies were conducted in the Okavango Delta, located within the Ngamiland District in northern Botswana (Figure 1.4). The Delta is divided into management areas (concessions) which are subject to various land uses, including tourism and wildlife management (game reserve, wildlife management areas) and community use (farm, pastoral and residential) (Figure 1.4). Sports hunting, which was supported in many wildlife management areas, was banned in 2014 (though reinstated in late 2019), with non-consumptive tourism (e.g. photography) being the current largest contributor (Winterbach et al., 2015). Chapters 2 and 3 examine the Delta as a whole, and Chapters 4, 5, and 6 were conducted on a smaller-scale in the Abu Concession (Figure 1.4), with the study area boundaries specified in the relevant chapters. The Abu Concession is a wildlife management area (referred to as NG26) used for non-consumptive tourism (hunting ceased in 2008) with three luxury lodges within the concession.

In addition, behavioural data (Chapter 6) were also collected along the Chobe River in the Chobe District in the northeast corner of Botswana (Figure 1.4). The Chobe riverfront extends along the northern section of the Chobe National Park and the Kasane/Chobe Forest Reserves and continues past the township of Kasane. The riverfront portion of Chobe National Park is subject to intensive, high-use tourism, considered by some to be overused (van der Sluis et al., 2017). Kasane is a rapidly developing township, with urban areas, small-scale industries and local farming/horticulture (van der Sluis et al., 2017).
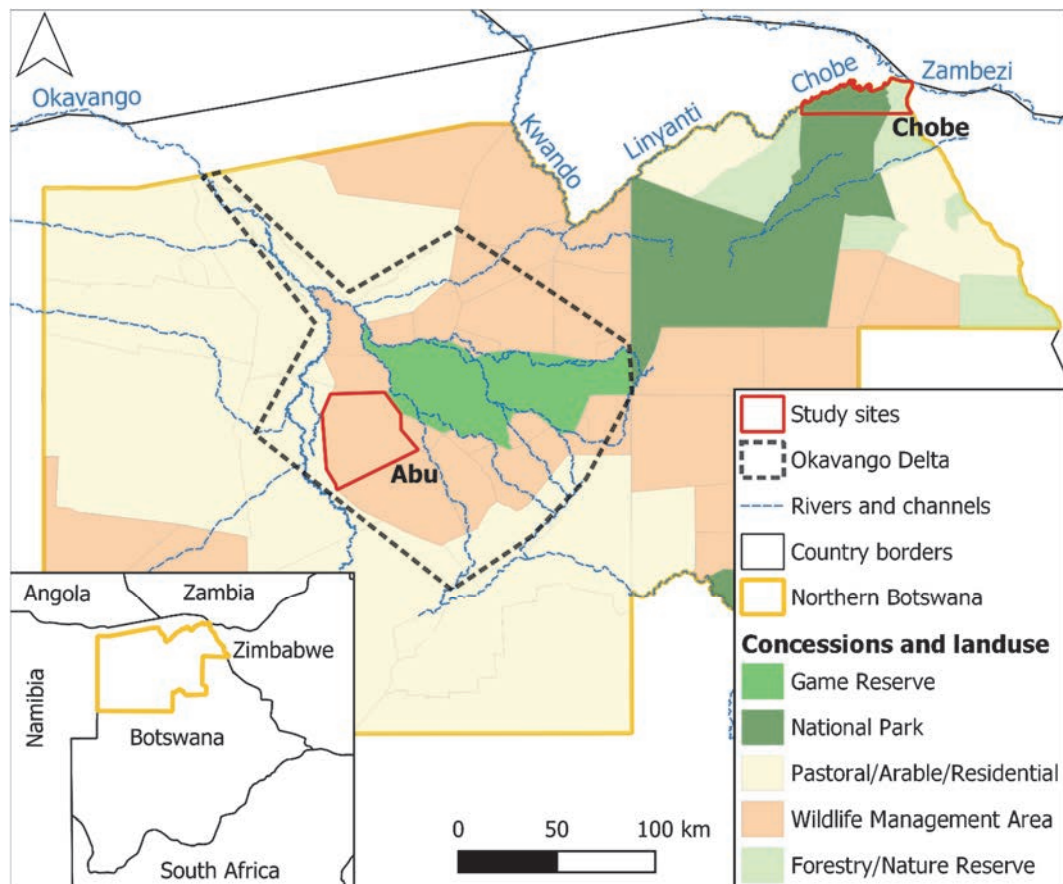
Figure 1.4. Map of northern Botswana showing the Okavango Delta, and Abu Concession and Chobe riverfront study sites.

1.6.1 Climate and flooding

The Delta, referred to as the 'Jewel of the Kalahari' (Ross, 1987), has a semi-arid climate with wet summers (October–April) (Figure 1.5) (McCarthy & Ellery, 1993; Okavango Research Institute, 2019). The Delta consists of a panhandle region, a meandering river system surrounded by permanent swamps, and a large, low gradient (1:3300) alluvial fan (McCarthy et al., 1998a; Ellery et al., 2003; Gumbricht et al., 2004b). The fan is flanked by permanent swamps and more distally by seasonal swamps, whose inundation depends

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on the extent of the flooding in any given season/year (McCarthy et al., 1998a; Gumbricht et al., 2004b). The Delta is a flood pulsed system subject to an annual flood event (Wolski et al., 2008). The flood waters originate from the high rainfall areas in Angola, flow into the Quito and Cubango Rivers which combine to form the Okavango River, passing through Namibia and entering Botswana at the panhandle, with peak inflow into the Delta occurring in April/May (Gumbricht et al., 2004b; Milzow et al., 2009b). The flood waters move slowly down the fan through a combination of channel, overland, and subsurface flow (Milzow et al., 2009b), with peak flood extent occurring in July–September (Figure 1.5) (McCarthy et al., 2000; Gumbricht et al., 2004b; Tooth & McCarthy, 2007). A central feature of the Delta is the asynchronicity between the local rains (those occurring over the Delta) and the flood event, with maximum flood extent occurring several months after the wet season ends (Figure 1.5), allowing water to be available for much of the year (Wolski et al., 2005). There may also be some small-scale flooding due to local rainfall (McCarthy, 2006).
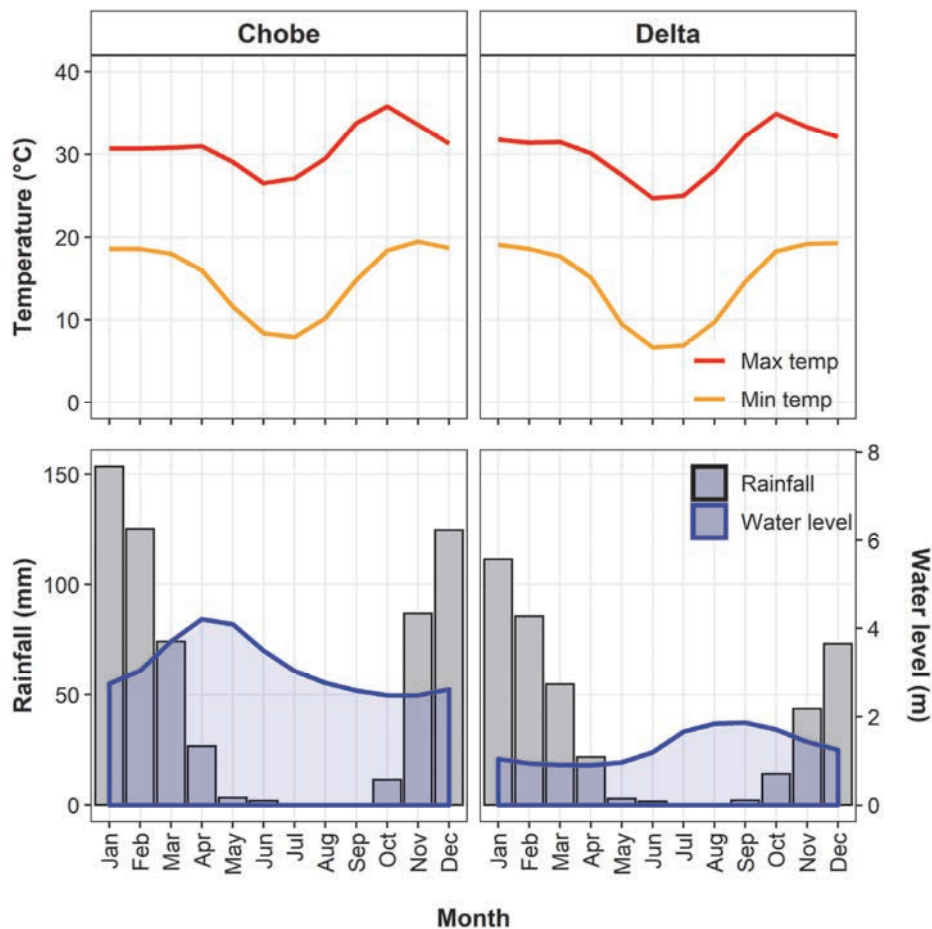
Figure 1.5. Average monthly climatic and water levels for Chobe and the Okavango Delta. Note: Maun is at the distal end of the Delta and so water levels in Abu peak earlier than in this figure.

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As well as seasonal variations in flooding, there is also significant variability in the extent of the annual flood between years, with large flood-events being to twice as large as low flood years (Thito et al., 2016). This intra and inter-annual variation results in a mosaic of vegetation within the Delta, including permanent rivers and swamps, seasonally flooded grasslands, dry grasslands, riverine woodlands, and dry woodlands (Ramberg et al., 2006; Department of Environmental Affairs, 2008; Milzow et al., 2009b). This mixture of habitat types results in a complex and dynamic ecosystem, which supports a rich diversity of flora and fauna. The Delta is listed as a Wetland of International Importance under the Ramsar Convention (Ramsar, 2014) and is a World Heritage Site (UNESCO, 2014). In addition to its biological importance, the Delta is vital to the livelihoods of the local people and is essential to Botswana's tourism industry (Wolski & Murray-Hudson, 2006b; Milzow et al., 2009a).

The Chobe River forms part of the Zambezi-Chobe-Kwando-Linyanti system (van der Sluis et al., 2017) and like the Delta is subject to an annual flood event, fed predominantly from the Zambezi River (Pricope, 2013; van der Sluis et al., 2017). Water enters the floodplains of the Chobe River in late March, with maximum inundation extent occurring in April and May (Figure 1.5) (Pricope, 2013). Depending on the year, the Chobe River may then receive additional water through the Kwando River system in June/July (Pricope, 2013). As in the Delta, local rainfall plays a limited role in inundation in the system, though may lead to localised flooding during strong wet seasons (van der Sluis et al., 2017).

1.6.2 Data collection seasons (Chapters 4–6)

Field data collection for Chapters 4–6 spanned from August 2017 to November 2018 with specific study dates stated in the relevant chapters. As discussed above, flooding of the Delta and Chobe River systems does not correspond with local rainfall in the wet season, instead peaking just after (Chobe River) to several months after (the Delta) the rains stop. The dry season therefore covers both a high flood period initially and then as the dry season progresses and the flood extent reduces, a period of medium to low flood (Figure 1.5). Given hippos are likely to be influenced both by season (wet season and dry season) as well as flood height (high flood to low flood), I have tried to capture both variables. Therefore, I distinguish three seasons: the wet season when the flood is low (hereafter

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referred to as "wet season (low flood)"), the dry season when flooding has peaked ("dry season (high flood)"), and the dry season when flooding has begun to recede ("dry season (med-low flood)"). My study consisted of two dry season (med-low flood) periods (mid-late 2017 and mid-late 2018); though I combined data from these two periods into a single dry season (med-low flood) given my goal in the relevant chapters was to quantify seasonal, rather than inter-annual, effects.

The onset of the wet season varies yearly and therefore I categorised it as beginning with the first rains over 10 mm and ending with the last rains of the season. For the Abu Concession, I classified the 2017 dry season (med-low flood) period as beginning in October and finishing on the 4 December 2017 (first rains > 10 mm). The wet season (low flood) continued until 30 March 2018 (last rains). The start of the dry season (high flood) begun July 2018 and continued until September 2018, after which flooding begun to recede and I categorised it as the dry season (med-low flood) period. In Abu, the 2018/2019 wet season begun on 21 October 2018, ceasing data collection for the dry season (med-low flood). For Chobe, I classified the 2017 dry season (med-low flood) as beginning in August and finishing on the 20 October 2017 (first rains > 10 mm) after which the wet season (low flood) commenced and extended until 5 April 2018 (last rains). The dry season (high flood) begun and continued until end of July 2018, after which the flood begun to recede, and I categorised the following months as the dry season (med-low flood). For Chobe, rainfall (2001–2018) and temperature (1982–2012) data were taken from Kasane Airport (17.82°S, 25.15°E) and water levels (1970–2020) from Mowana Lodge (17.78°S, 25.16°E). For the Delta, rainfall (1979–2016) and temperature (1982–2012) data were taken from Maun Airport (19.98°S, 23.43°E) and water levels (1970–2019) from Thamalakane-Maun Bridge (20.00°S, 23.43°E) (Government of Botswana, 2019).

1.7 General methods (Chapters 4–6) - sexing and ageing hippos

Due to their lack of individually identifiable features, their propensity to be at least partially submerged, and the subtle nature of hippo sexual dimorphism, it is difficult to consistently and accurately differentiate hippo age and sex categories and to identify individual hippos (Olivier & Laurie, 1974b; Karstad, 1984; Ngog Nje, 1988; Barklow, 1997; Eltringham, 1999; Beckwitt et al., 2002; Timbuka, 2012; Perry, 2015; Prinsloo,

2016). Nonetheless, in Chapters 4–6, where possible, I sexed hippos and assigned them into age categories but made no attempts to identify individuals. Methods used to assess age and sex are discussed below and more details are provided in chapters where relevant.

The sex of individual adult hippos was determined by the following characteristics. Male hippos are larger, having substantially larger necks and heads than females, with larger canines (visible when yawning), which results in a bulge behind their nostrils when their mouth is closed (Attwell, 1963; Clough, 1967; Karstad, 1984; Eltringham, 1999; Klingel, 2013). On land, differentiating the two sexes is easier (Olivier & Laurie, 1974b) due to the ability to better observe their size, as well as the presence of external genitals on males and a pair of inguinal nipples on females (Klingel, 2013). Certain behaviours were also used as indicators of hippo sex. Dung paddling, where a hippo defecates whilst moving its tail back and forth spreading dung, is a male trait and therefore was used as a determinate of sex (Olivier & Laurie, 1974b; Karstad & Hudson, 1986; Klingel, 1991b; Eltringham, 1993a) though there are rare reports of females paddling (Karstad & Hudson, 1986; Blowers et al., 2012). Dung paddling was almost always associated with a clear view of the male genitals. Nursing is a female only behaviour that was used to identify adult females. Some consider that juveniles occur only in association with adult females (Eltringham, 1993a; Chomba, 2013), however others report they also associate with adult males (Ansell, 1965a; Olivier & Laurie, 1974b). Therefore, being close to a juvenile was not used as a determinate of sex but having a juvenile resting on them was (to indicate an adult female). No attempt was made to sex subadult or juvenile hippos given sexual dimorphism at this age is more cryptic (Karstad, 1984).

Hippos are long lived, with a maximum longevity of approximately 40 years in the wild (Clough, 1967; Marshall & Sayer, 1976; Eltringham, 1999). In studies of culled hippos, jaw length, tooth eruption and wear patterns, eye lens size, body weight, body length, and chest girth have been used to assign hippos to twenty age classes. Actual ages (in years) were then assigned to these classes based on the estimated ages of the oldest hippos and by comparison with a limited number of animals of known age (Longhurst, 1958 in Laws, 1968a; Laws & Clough, 1966; Pienaar et al., 1966; Clough, 1967; Laws, 1968a; Sayer & Rakha, 1974). Most of the ageing methods used in anatomical studies (e.g. tooth eruption) are impossible to implement in field studies. However, body size can be estimated in the

field, and given there is a known body length – age relationship (Ansell, 1965b; Pienaar et al., 1966; Laws, 1968a; Skinner et al., 1975; Martin, 2005), I used this to assign approximate ages to hippos.

Research on culled hippos indicated age of sexual maturity averaged nine years (range 7–15 years) for females and 7.5 years (range 6–13) for males, though there were reports of a three year old sexually mature female and the age of maturity in males reduced if a different assessment method was used (Laws & Clough, 1966; Sayer & Rakha, 1974). Studies on predominately captive hippos reported them reaching maturity younger, from three to five years of age (Mouquet, 1919; Vosseler, 1923; and Sailer, 1950 in Clough, 1967; Kerbert, 1922; Bourliere & Verschuren, 1960; Goss, 1960; Pienaar et al., 1966; Dittrich, 1976; Graham et al., 2002; Blowers, 2008). These may not reflect ages of sexual maturity in the wild as captive hippos are subject to different conditions (Clough, 1967; Graham et al., 2002). Alternatively, they may be more accurate representatives of age of sexual maturity due to exact age being known, whereas the culled studies extrapolated ages from other information (Dittrich, 1976). Age of sexual maturity is also thought to be flexible, as is pregnancy rate and calving interval, being related to density or grazing availability, so that when conditions are favourable reproduction is promoted and therefore can be used as an indicator of the availability/quality of grass (Laws & Clough, 1966; Clough, 1967; Laws, 1968b; Sayer & Rakha, 1974; Marshall & Sayer, 1976). In this thesis, I have considered hippos greater than four years old to be adults (given the lower-end estimates of age of sexual maturity), hippos two to four years old as subadults and hippos less than two years old as juveniles (hippos produce a calf about once every 1.5 to two years; Laws & Clough, 1966; Clough, 1967; Graham et al., 2002).

Chapter 2: Automated inundation mapping over large areas using Landsat data and Google Earth Engine

2.1 Introduction

The Okavango Delta (the Delta) in northern Botswana is a wetland of international and domestic significance (Wolski & Murray-Hudson, 2006b; Milzow et al., 2009a; Ramsar, 2014), yet pressures on its water resources from water abstraction (taking/extracting water for agriculture/industry and human consumption), damming for power generation, and climate change are growing (Gumbricht et al., 2004a; Milzow et al., 2009a, 2009b). This large wetland consists of a panhandle region, a channel system surrounded by permanent swamps, and a large, low gradient alluvial fan (McCarthy et al., 1998a; Gumbricht et al., 2004b; Milzow et al., 2009b). The Delta is subject to an annual flood event asynchronous with the local wet season; rainfall in the highlands of Angola flows into the Okavango River, entering the Botswana panhandle and slowly moves down the fan, reaching maximum inundation extent in July–September (McCarthy et al., 2003; Gumbricht et al., 2004b; Wolski & Murray-Hudson, 2006b; Milzow et al., 2009b; Thito et al., 2016; Wolski et al., 2017). There are intra and inter-annual variations in the frequency, duration, and extent (i.e. total area) of flooding. These, along with inter-annual variations in the spatial distribution of inundation, produce a complex mosaic of vegetation, supporting a vast number of ecological niches and a rich diversity of flora and fauna (Ramberg et al., 2006; Department of Environmental Affairs, 2008; Milzow et al., 2009a).

The hydrology of the Delta, including temporal and spatial changes in its inundation history, have been investigated through inundation maps (Milzow et al., 2009a). These maps can be used to study the past and present state of the Delta, to predict its future transformations, and to understand how it is affected by natural processes, climate change, and human use (Fluet-Chouinard et al., 2015). They may also be incorporated into management strategies and biodiversity studies. Inundation maps can be created using satellite imagery, which are available from a range of spatial and temporal resolution products. While differentiating open water (e.g. channels, lagoons) from dryland vegetation (e.g. shrublands, grasslands) is relatively simple, there is substantial overlap in the spectral values of inundated areas covered in aquatic vegetation (e.g. floodplain) and some dryland vegetation classes, making the separation of these classes difficult and

traditional water classification methods unviable (McCarthy et al., 2003; Ringrose et al., 2003; Wolski & Murray-Hudson, 2006b; Murray-Hudson et al., 2015; Thito et al., 2016; Wolski et al., 2017). For example, the normalized and modified normalized difference water index (NDWI and MNDWI), which were specifically developed to map waterbodies, had the least ability to classify inundation compared with six other methods (Wolski et al., 2017). Therefore a range of classification methods (unsupervised, supervised, band thresholding, band ratios, indices, and combinations of these methods) have been implemented (McCarthy et al., 2003; Gumbricht et al., 2004b; Wolski & Murray-Hudson, 2006b; Milzow et al., 2009b; Murray-Hudson et al., 2015; Thito et al., 2016; Wolski et al., 2017). Recently, band thresholding has been successful (Wolski & Murray-Hudson, 2006b; Murray-Hudson et al., 2015; Thito et al., 2016), with thresholding of the short wave infrared (SWIR) band producing high accuracy results on Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (Wolski et al., 2017). The SWIR band is highly sensitive to moisture content (Islam et al., 2010) and can differentiate densely vegetated inundated areas from non-inundated vegetation (Wolski et al., 2017). As well as its accuracy, the advantage of this method is its relative simplicity, meaning it is easily automated, which reduces the time (and thus cost) of implementation compared with more complex methods.

The majority of Delta inundation studies have used imagery with broad spatial resolution (MODIS (250 m, 500 m, and 1 km) (Murray-Hudson et al., 2015; Thito et al., 2016; Wolski et al., 2017) and National Oceanic and Atmospheric Administration Advanced Very-High-Resolution Radiometer (NOAA AVHRR) (1 km) (McCarthy et al., 2003; Gumbricht et al., 2004b)), taking advantage of the high temporal resolution of these sensors, which allows daily and sub-monthly analysis of inundation (Wolski et al., 2017). However, dependent on the intended use of the inundation maps, such broad spatial resolution may result in unacceptable simplification of the complex mosaic of the Delta (Thito et al., 2016). Further, high spatial resolution information can increase confidence in associated decision-making (Seto et al., 2002; Kalluri et al., 2003; Bechtel et al., 2004; Allen et al., 2005; Fu & Weng, 2016; Ouellette & Getinet, 2016; Simons-Legaard et al., 2016; Heiskanen et al., 2017; Hermon, 2019). Broad spatial resolution can be downscaled to achieved finer spatial resolution, if access to high temporal resolution data is a pertinent factor (Chen et al., 2013; Ticehurst et al., 2015; Thito et al., 2016; Fayne et al., 2017). In

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addition, broad spatial resolution increases the likelihood of mixed pixels (e.g. pixels containing both inundated and dry areas) which can confuse classification attempts (Milzow et al., 2009b; Danaher & Flood, 2014; Wolski et al., 2017), although methods exist to reduce this issue (Verhoeye & De Wulf, 2002; Li et al., 2015; Ticehurst et al., 2015).

Computational power, data procurement, management, and storage, and processing times have also traditionally been a motivation for using broad spatial resolution images, particularly when creating time series over large areas (Milzow et al., 2009b; Murray-Hudson et al., 2015; Thito et al., 2016; Wolski et al., 2017). Recent advances in computing power and cloud-processing infrastructure (e.g. Google Earth Engine (Gorelick et al., 2017)) have enabled much wider access to satellite image time series, along with the capacity to process and analyse these data.

In this paper we utilised the family of Landsat satellite sensors to create the longest time series of inundation maps for the peak flood season for the Delta at high spatial resolution (30 m pixels) to date. We adapted a previously developed method based on thresholding of the SWIR band (Wolski et al., 2017), and implemented an automated version in Google Earth Engine (Gorelick et al., 2017), a cloud-based geospatial analysis platform. We created a time series of peak inundation for the last 30 years, up to and including the flood event of 2019, thought to be the lowest flood season on record (Thalefang, 2019b). Further, we provide validation results that confirm the accuracy of the SWIR thresholding method. The inundation maps and Google Earth Engine code are provided (Supplementary Data S2.1) for use and adjustment by stakeholders, land managers, and researchers.

2.2 Methods

2.2.1 Annual (July–September) Landsat composites

Unless otherwise stated, all processing was conducted using Google Earth Engine. Every tier 1 atmospherically corrected surface reflectance Landsat (Landsat 5 TM, Landsat 7 ETM+, Landsat 8 OLI) scene covering the Okavango Delta (Figure 2.1) for the peak inundation period (1 July to 30 September) from 1990 to 2019 was used (step one in Figure 2.2). Scenes occurred within six Landsat path/row footprints (174/073, 174/074,

175/073, 175/074, 176/072, 176/073). These sensors capture scenes with 30 m spatial resolution, containing eight (Landsat 5 and 7) and eleven (Landsat 8) bands, including the SWIR band (band 7) used in this study. For each scene, pixels classified as cloud or cloud shadow on the Landsat cloud mask band were masked (step two in Figure 2.2). These and other missing pixels (e.g. from the Landsat 7 Scan Line Corrector failure) were then filled using the median value for the pixel from a year before and after the scenes' date, using a gap-filling algorithm (Scaramuzza et al., 2004) (step three in Figure 2.2). The SWIR band was selected for each scene (step four in Figure 2.2) and then, for each year, a composite was created from the median value of all the scenes for that year (step five in Figure 2.2). Annual composites with large areas missing (e.g. there were no scenes available for a path/row) were filtered out (step six in Figure 2.2). This occurred five times (1993, 2000, 2009, 2010, and 2012).
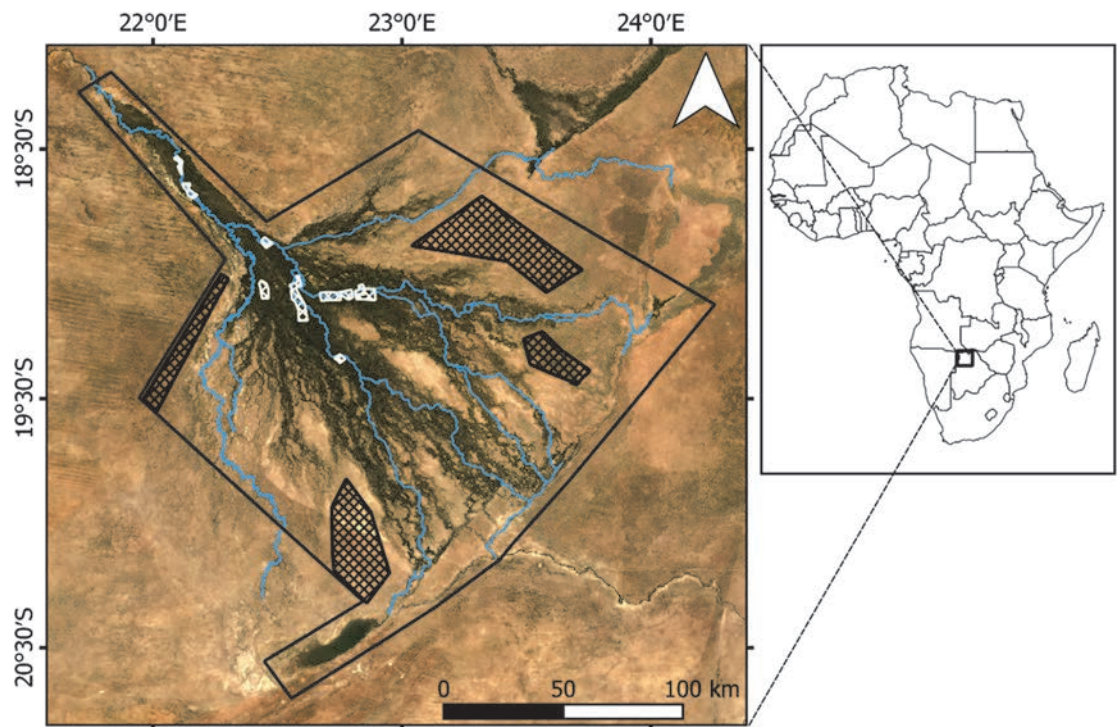
Figure 2.1. Okavango Delta study area (black outline) in northern Botswana. White and black hatched areas are the permanent water (permanent swamps and channels) and dry areas, respectively, used in calculating the threshold value and blue lines are the major channels of the Delta.

2.2.2 Annual (July–September) inundation maps

The composites were transformed into inundation maps using a SWIR thresholding technique. To apply this method, we assessed and digitised areas that had permanent

water (e.g. permanent swamp or main channels) or were permanently dry, based on Wolski et al.'s (2017) designated areas but altered slightly to suit our use of higher spatial resolution imagery (Figure 2.1, step seven in Figure 2.2). The median SWIR value for the inundated ($SWIR_{wet}$) and dry ($SWIR_{dry}$) areas was calculated for each individual composite, and a composite-specific $SWIR_{threshold}$ value was calculated using Equation 1 (taken from Wolski et al. (2017)) (step eight in Figure 2.2).

$$SWIR_{threshold} = SWIR_{wet} + 0.3 * (SWIR_{dry} - SWIR_{wet}) \quad (1)$$

The relative frequency of SWIR values for the wet and dry areas is shown in Supplementary Figure S2.1, with the $SWIR_{wet}$, $SWIR_{dry}$, and $SWIR_{threshold}$ values marked. Pixels with a SWIR value below the threshold were classified as inundated and vice-versa for dry pixels (step nine in Figure 2.2). Calculating the threshold value separately for each image accounts for the dynamic (seasonal and annual) nature of inundation in the Delta (Wolski et al., 2017). The multiplier of 0.3 represents the value needed to calculate the correct threshold to classify a pixel with an inundation fraction of 50% as inundated, as recommended by Wolski et al. (2017). Owing to the different imagery used in this study, we confirmed the value of 0.3 was appropriate by also assessing inundation maps developed using values of 0.25 and 0.35 (see Supplementary Table S2.1). Further details about this classification method and its development are provided in Wolski et al. (2017).
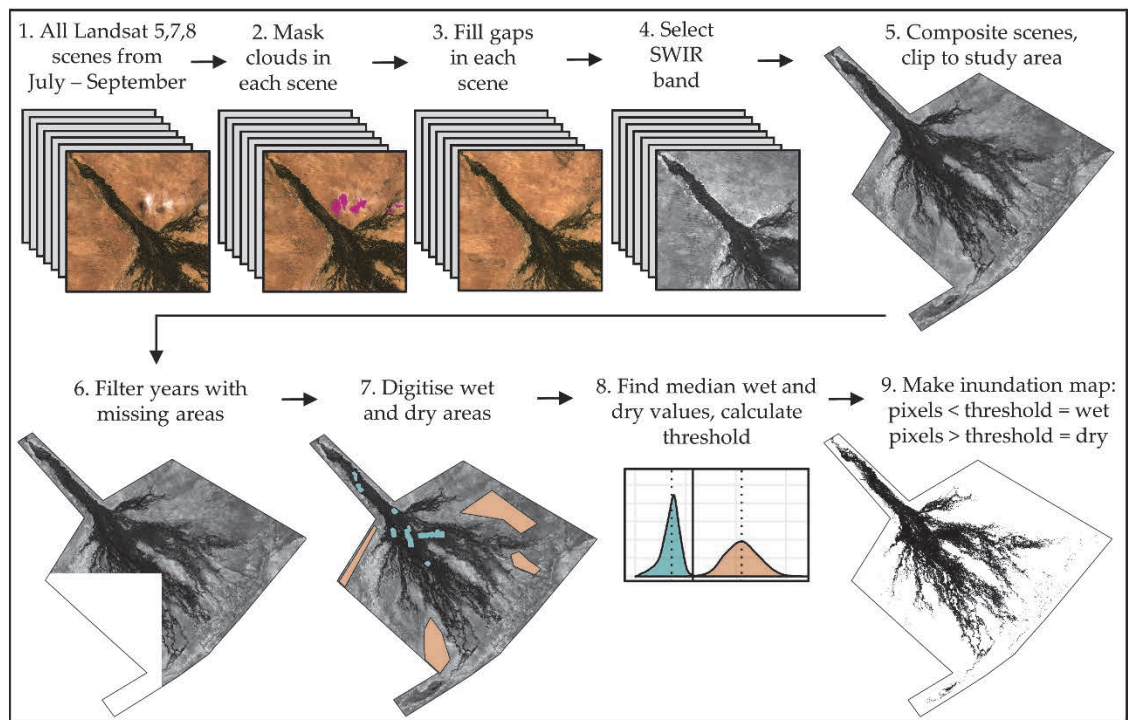
Figure 2.2. Schematic displaying the process of creating an annual inundation map. Steps are detailed in text.

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2.2.3 Validating inundation maps (image-based accuracy assessment)

Gathering in situ data for historical time series is difficult, and in many cases these data simply do not exist. To enable validation for at least some of the time series, we used a visual interpretation approach to generate reference data. Although this method can be subjective, it is a generally accepted approach, particularly when historical data are limited (Strand et al., 2002; Iwao et al., 2006; Wolski & Murray-Hudson, 2006b; Luedeling & Buerkert, 2008; Silvestri & Omri, 2008; Montesano et al., 2009; Bastin et al., 2013; Olofsson et al., 2014). We validated the accuracy of three sets of inundation maps (produced using 0.25, 0.3, and 0.35 in Equation 1) by visual assessment of true colour versions of the Landsat composites used to make the inundation maps, and high-resolution satellite images. The inundation maps were created without filling masked pixels, and only comprised a subset of the years (2000–2016). High resolution imagery taken between July and October was accessed via Google Earth's historical imagery function and the Digital Globe collection (obtained from the DigitalGlobe Foundation). Given that the study area (Figure 2.1) included large tracts of permanently dry areas (i.e. the Kalahari Desert) which we predicted would rarely be misclassified (Wolski et al., 2017), we used an amended area for the validation, removing some of the larger dry areas (Supplementary Figure S2.2). Using this amended area, fifty sample points (Supplementary Figure S2.2) were randomly generated using the sampleRandom function (raster package (Hijmans, 2019)) in R (R Core Team, 2018). For each year, the same 50 sample points were visually assigned as inundated or dry on the Landsat and high-resolution imagery before progressing onto the next year. This prevented the assessors from making classifications based on a sample point's previous inundation history. The classification (inundated or dry) of each sample point was extracted from the relevant inundation map and an error matrix created. Overall accuracy (the sum of the diagonal entries (correctly classified points) divided by the total sampled points), producer's accuracy (the diagonal entry divided by its respective column total), and user's accuracy (the diagonal entry of each row divided by its respective row total) were calculated.

2.2.4 Validating inundation maps (in situ data accuracy assessment)

To validate the accuracy of the classification method, we carried out a field examination of inundated and dry regions within one Landsat scene (scene 175/73, 25 July 2018). Owing to accessibility and safety constraints, we only sampled from the Abu Concession

(Supplementary Figure S2.3) where inundated areas could be accessed by field personnel by wading (within 100 m of dry land). Sampling points were chosen using a random stratified sampling approach, where inundated and dry were the stratification levels. The sampling area was created in QGIS (QGIS Development Team, 2018) by outlining islands that were accessible by vehicle, applying a 100 m buffer, and clipping the inundation map to this shape. The raster was imported into R (R Core Team, 2018) and 55 points in each stratum were randomly selected (Supplementary Figure S2.3) using the sampleStratified function (raster package (Hijmans, 2019)), which were then exported and uploaded to a handheld Garmin GPSMAP® 64 GPS. This number of sample points was chosen to ensure that if some points were inaccessible (e.g. vegetation too thick to drive through, unsafe to wade into water, wildlife within close proximity) the recommended minimum number of 50 (Olofsson et al., 2014) could still be obtained. Data collection occurred within two days of the sensor's collection of the scene (25–27 July 2018), with each point classified as either inundated (standing water) or dry based on which class occurred over the majority of the 30 m x 30 m area centred on each point. Where the proportion of each class was approaching equality, the point was classified but was also noted as an uncertain classification. The classification for each sample point was extracted from the inundation map created from the Landsat scene and an error matrix was created. Overall accuracy, user's accuracy, and producer's accuracy were calculated as above.

2.3 Results

The extent and distribution of the peak inundation varied annually (Figures 2.3 and 2.4), with the smallest inundation extent occurring in 2019 (3,487 km^2) and the greatest in 2011 (10,109 km^2) (Figures 2.4 and 2.5). The average inundation extent was 6635 km^2. The SWIR$_{threshold}$ values ranged from 1306 (2014) to 1637 (2003) (Supplementary Figure S2.1), emphasising the importance of calculating this variable individually for each composite. On average, estimates of inundation extent were 692 km^2 smaller than those from previous studies, which used MODIS (250 m and 500 m spatial resolution) and NOAA AVHRR (1000 m spatial resolution) imagery, with a maximum difference of 2373 km^2 (Figure 2.4).
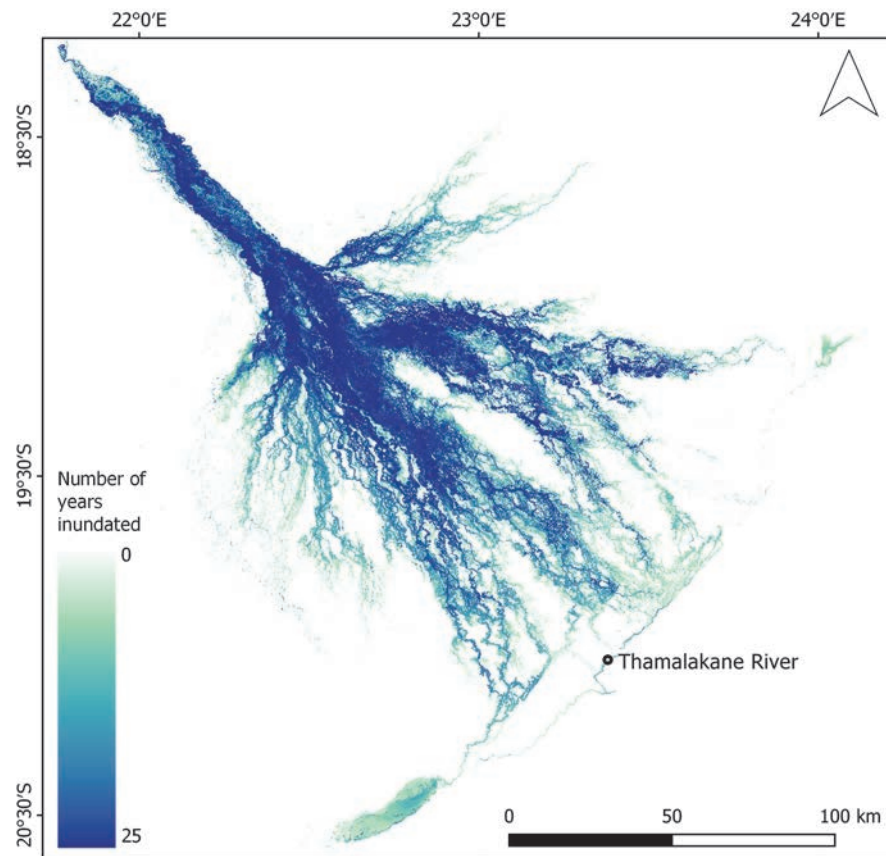
Figure 2.3. Summed annual inundation map for the time series (30-year span, 25 individual flood maps) showing the inter-annual variation in peak flood distribution.
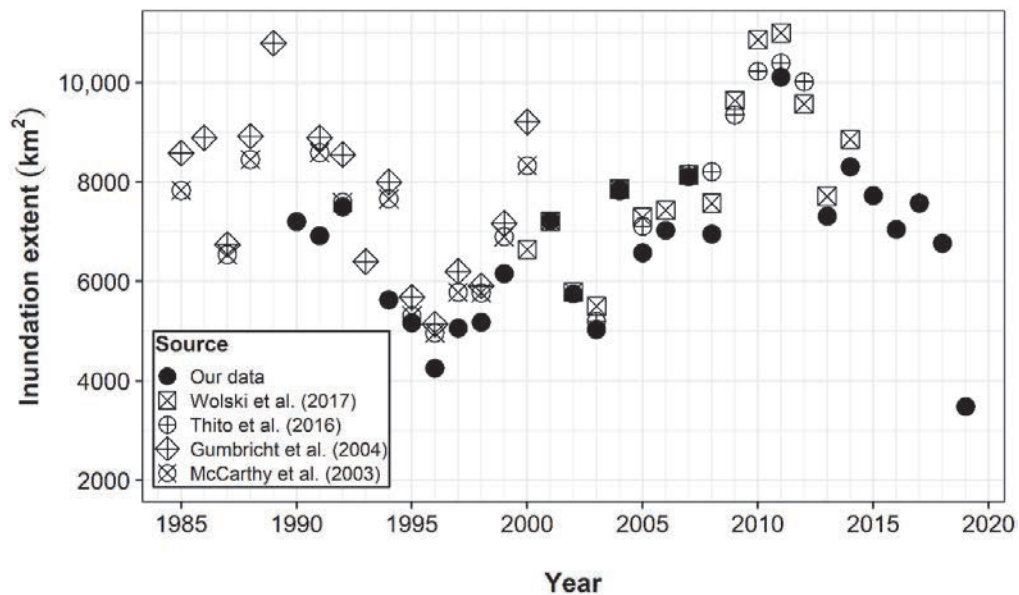
Figure 2.4. Annual (July–Sept) inundation extent (km^2) of the Okavango Delta from our data and other studies. Inundation maps from other studies were developed using imagery predominately from MCD43A4 (500 m spatial resolution) (Wolski et al., 2017), MOD09Q (250 m spatial resolution) (Thito et al., 2016), and NOAA AVHRR (1000 m) (McCarthy et al., 2003; Gumbricht et al., 2004b). Note: inundation extents from other studies were taken from tables and figures (using http://www.graphreader.com/) for the same months as those used in this study.

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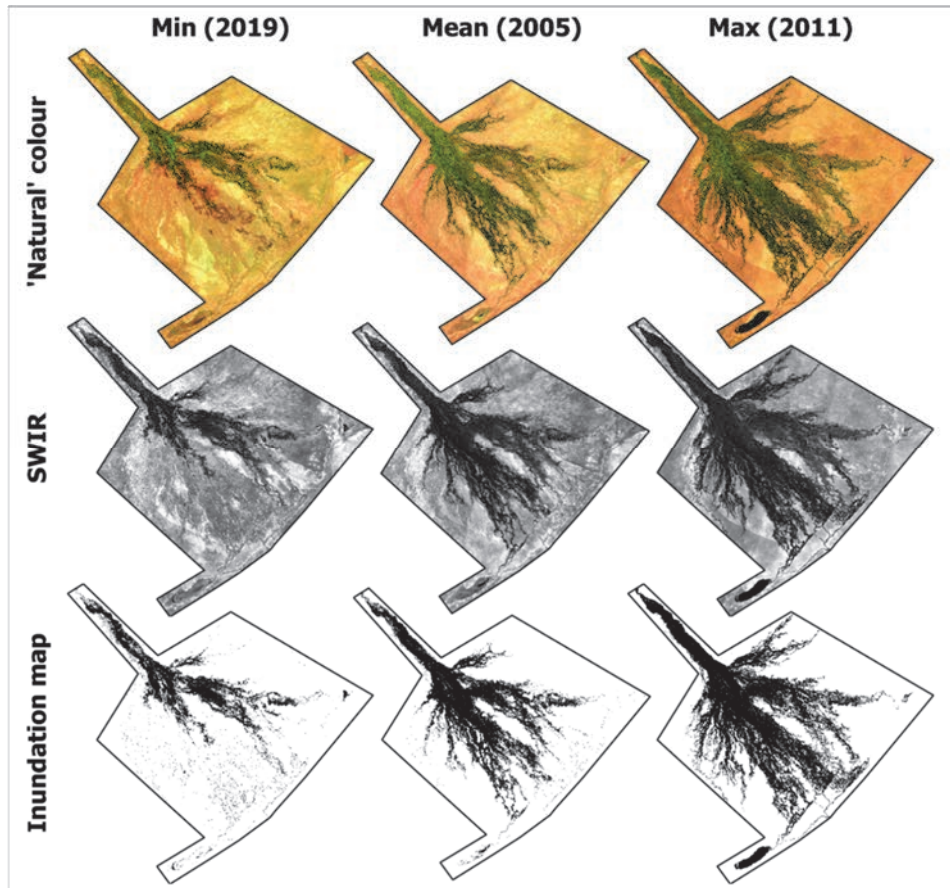
Figure 2.5. 'Natural' colour composite (SWIR, near infrared, green bands), SWIR band composite, and inundation map (black area is inundated) for years with minimum, mean, and maximum flood extent. In 2019, inundated pixels in the southwest of the map are likely misclassified. Note: flood extent in 2005 was within 100 km^2 of average flood extent.

2.3.1 Validating inundation maps

Using the true colour Landsat composites, a total of 691 points were visually classified; fifty points per year, except for years without inundation maps and 2010 and 2011, where five and four validation pixels were masked, respectively. There were fewer points (123) visually classified using the high-resolution imagery owing to a lack of available data. For inundation maps created using a multiplier of 0.3, based on the visual assessment of Landsat composites, the inundation maps had few misclassified pixels (1.9%), but this was slightly higher based on the visual classification of high-resolution imagery (4.1%) (Table 2.1). Inundation maps created using a value of 0.25 had slightly lower overall accuracy and using a value of 0.35 had almost identical overall accuracy (Supplementary Table S2.1). Misclassified points were located predominately on the boundary of inundated and dry areas and where there was high inter-annual variation in inundation (Supplementary Figure S2.2).

Out of the 110 sample points that were generated for the in situ validation, we classified 106 (four were inaccessible). The inundation map had an overall accuracy of 91.5% (nine sample points were misclassified) (Table 2.1, Supplementary Figure S2.3). Of these nine misclassified points, seven were noted as uncertain in the field as they had approximately equal areas of inundation and dry. There was an additional uncertain point that was correctly classified. When these uncertain points were removed, overall accuracy increased to 98.0% (Table 2.1).

Table 2.1. Error matrices and overall accuracy of inundation maps using image-based accuracy assessment (Landsat and high-resolution imagery) and in situ points. Note: values in square brackets are based on points noted as 'uncertain' being removed.

		Landsat		Hi-res visual interp.		In situ	
		Dry	**Wet**	**Dry**	**Wet**	**Dry**	**Wet**
Map	**Dry**	526	10	82	3	45 [44]	1 [0]
	Wet	3	152	2	36	8 [2]	52 [52]
Overall accuracy		98.1% (678/691)		95.9% (118/123)		91.5% (97/106) [98.0% (96/98)]	

Producer's accuracy – Landsat, dry = 99.4% (526/529) and wet = 93.8% (152/162); high-resolution imagery, dry = 97.6% (82/84) and wet = 92.3% (36/39); in situ, dry = 84.9% (45/53) [95.7% (44/46)] and wet = 98.1% (52/53) [100% (52/52)]
User's accuracy – Landsat, dry = 98.1% (526/536) and wet = 98.1% (152/155); high-resolution imagery, dry = 96.5% (82/85) and wet = 94.7% (36/38); in situ, dry = 97.8% (45/46) [100% (44/44)] and wet = 86.7% (52/60) [96.3% (52/54)]

2.4 Discussion

Our study details the longest ever time series of peak flooding extents for the Okavango Delta at a high spatial resolution (30 m), demonstrating the remarkable inter-annual variability of this system; the largest inundation extent recorded was almost three times that of the smallest (Figures 2.4 and 2.5). There are also inter-annual variations in the spatial distribution of inundation (Figures 2.3 and 2.5), driven by the volume of water discharged into the system, but also factors such as sedimentation, channel blockage from vegetation, and avulsion (McCarthy et al., 1992; Gumbricht et al., 2004b; Wolski & Murray-Hudson, 2006a; Thito et al., 2016). On the basis of the maps produced in this study, the 2019 flood event represents the smallest inundation since 1985, being around 769 km^2 smaller than the previous record in 1996 (Figure 2.4). Estimations of inundation extent going back to 1934 calculated the lowest inundation to be approximately 5100 km^2 (Gumbricht et al., 2004b). Our estimate of inundation extent in 2019 was 3483 km^2, making it the smallest flood in the last 85 years. This exceptionally low flood is likely driven by a multi-decadal (16–20 years) rainfall cycle in Southern Africa (McCarthy et
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al., 2000; Tyson et al., 2002; Gumbricht et al., 2004b), being 14 years since the previous dry year. The Delta is also at risk of drying owing to increases in temperature and evaporation and decreases in rainfall and river flow due to climate change and water abstraction and damming (Murray-Hudson et al., 2006; Milzow et al., 2009b).

The annual inundation extent estimates in our study were systematically smaller than previous studies but showed a similar trend (Figure 2.4). The most likely cause for this effect is our use of higher resolution imagery, an effect that is also evident in other study systems when comparing estimates from different sensor resolutions (Moody & Woodcock, 1994; Hlavka & Livingston, 1997; Loboda & Csiszar, 2004; Ozdogan & Woodcock, 2006). Broad spatial resolution imagery (as used in existing studies) increases the number of mixed pixels, and can lead to overestimations of the size of the inundated areas (Milzow et al., 2009b; Danaher & Flood, 2014), which we reduced by using Landsat images. Another potential cause for smaller estimates is our use of three-month composites rather than individual consecutive images, concealing the time of true maximum inundation, although our use of median values should be robust to this effect.

Accuracy assessments of Delta inundation maps have generally not included in situ data (Murray-Hudson et al. (2015) is an exception), instead using comparisons to high resolution aerial orthomosaics (Wolski & Murray-Hudson, 2006b), other inundation maps (Murray-Hudson et al., 2015; Thito et al., 2016; Wolski et al., 2017), or hydrological observations (Gumbricht et al., 2004b; Wolski et al., 2017). The overall accuracy of the method used in this study as determined by the image-based assessment (95.9–98.1%) is comparable to these other studies, being predictably higher for the Landsat composites than the independent high-resolution images, as these are the true colour version of the images on which the inundation maps were based. Also contributing to the reduced accuracy, high-resolution images covered a slightly longer time period (July–October) than that was used to make the inundation maps (done to increase available data), and were individual images, as opposed to composites, meaning they may have occurred before/after the full extent of the flood. Although only a subset of the maps (2000–2016) were validated, Supplementary Figure S2.1 provides further evidence that the thresholding method can accurately detect the boundary between inundated and dry pixels, with non-validated and validated years following a similar pattern.

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The overall accuracy from in situ data validation (91.5%) was slightly lower than from the image-based assessment, although not so (98.0%) when we removed points we had flagged as uncertain in the field. These were points that were approximately half inundated and half dry (i.e. a mixed pixel) and had remaining moisture in the soil (i.e. were muddy) where the flood had recently receded (but which we classified as dry as there was no standing water) (Supplementary Figure S2.3). In situ data collection in this area is difficult owing to logistics, accessibility, and safety issues, particularly during the high flood period (McCarthy, 2002; McCarthy et al., 2003; Wolski & Murray-Hudson, 2006b; Milzow et al., 2009b); so, while our in situ validation was small in scale, it represents a rarely conducted true accuracy assessment of Delta inundation mapping. In addition, given that the sampling area was centred on small islands and edges of the floodplain, it fittingly represents the boundary between dry and inundated areas, the area where most classification errors are likely to occur (Wolski et al., 2017) (Supplementary Figure S2.2), and which was under-represented in the sample points of the image-based accuracy assessment. Therefore, the high accuracy within this sampling area suggests the overall Delta wide classification is likely to be reliable, confirmed by the image-based validation.

In addition to inaccuracy caused by mixed pixels, we noted, as did Wolski et al. (2017), the presence of some true misclassification when using this method. Misclassifications are unlikely to significantly impact estimates of total flood extent but may be important if the maps are used for spatial analyses. Visual inspection of our maps suggests riparian woodland vegetation is sometimes misclassified as inundated area, a known problem in the Delta where these classes can have overlapping spectral signatures (Wolski & Murray-Hudson, 2006b) and where riparian woodland can saturate Landsat pixels (Ringrose et al., 2003). A potential solution to minimise this would be filtering out pixels that are discontinuous from the larger inundated area (Wolski & Murray-Hudson, 2006b), although for the sake of simplicity we have not attempted to do this. Misclassifications can also occur where there is a small difference between the SWIR value of the dry and inundated areas used for the threshold calculation, typically during the wet season (Wolski et al., 2017), which this study did not measure. The anomalously low flood level in 2019 meant it was difficult to get suitable training data that were consistent with the other maps. Therefore, dry pixels within the permanent water polygon increased the range

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of SWIR$_{wet}$ values (Supplementary Figure S2.1). This may have led to a higher level of misclassification (Figure 2.5).

Choosing a sensor is a compromise between spatial and temporal resolution and the computational time and power required to process the images. Google Earth Engine allowed us to take advantage of high-resolution images with minimal effort; all images are called directly to the software without downloading and functions (e.g. cloud masking) can be automated. In an ecosystem as complex as the Delta, broad spatial resolution maps may have restricted utility (Gumbricht et al., 2004b). Using 500 m spatial resolution imagery, Wolski et al. (2017) noted that some important terminal rivers of the Delta were not well represented on their inundation maps as they were narrower than the resolution of the imagery. However, by using Landsat imagery, the mosaic of floodplains and islands are well represented and rivers that are important indicators of the hydrology of the Delta, as well as essential to local communities (e.g. the Thamalakane River), are clearly mapped (Figure 2.3).

2.5 Conclusions

Wolski et al. (2017) developed a simple method (thresholding of the short wave infrared band) to accurately classify inundation in the Okavango Delta using broad spatial resolution (500 m) satellite imagery, noting the method was suitable for automation, but also cautioning that creating inundation maps using Landsat imagery was "laborious … making creation of a consistent, long time series of inundation maps difficult". In this paper we have shown that periodic, accurate inundation maps can be created using relatively high-resolution imagery (Landsat) suitable to capture the complexity of this important ecosystem, by utilizing Google Earth Engine, a cloud-based platform. We provide the longest time series (1990–2019) of inundation maps for the peak flood season at a relatively high spatial resolution (30 m) to date. The inaccessibly of remote sensing methods and processing capability have prevented wide-spread adoption of its use by non-experts. We anticipate that the methods/code and the data produced in this paper can be used and adapted by land managers, researchers, and other stakeholders, who require access to accurate high-resolution inundation maps. Further, the classification method is likely to be suitable for mapping inundation in other regions, with only minimal adaptation of the methods and code presented here.

Chapter 3: Temporal and spatial patterns of hippo populations in the Okavango Delta, Botswana

3.1 Introduction

Conservation of threatened species depends upon reliable estimates of their population size (Jachmann, 2001) and temporal trends (Stalmans et al., 2019). Examining what factors dictate their spatial distribution provides insights into habitat use and resource requirements (Timbuka, 2012; Stears et al., 2019). This can allow predictions of how changes in land and water use may affect future habitat suitability and conservation of species (Nuñez, 2017). A species' habitat use is often described using data collected from individuals or small groups over relatively short periods and small spatial scale. Investigating habitat use at a landscape-scale can provide valuable information, but requires data covering entire ecosystems, which is often difficult to obtain.

The common hippopotamus (*Hippopotamus amphibius*), or hippo, occurs in rivers, lakes and wetlands across sub-Saharan Africa (Eltringham, 1993b). Current understanding of their habitat use is based on generally small-scale studies of riverine and lacustrine populations (e.g. Attwell, 1963; Pienaar et al., 1966; Laws, 1968; Field, 1970; Olivier & Laurie, 1974; Viljoen & Biggs, 1998; Prinsloo et al., 2020; Stommel et al., 2016; Stears et al., 2019), with little published understanding of large-scale habitat use or population trends in extensive river and wetland ecosystems. Hippos are listed as Vulnerable on the IUCN Red List, threatened by habitat loss, poaching for meat and ivory, drought, disease, and human wildlife conflict (Eltringham, 1993b; Lewison & Carter, 2004; Timbuka, 2012; Lewison & Pluháček, 2017). The IUCN assessment reports the status of hippo populations in countries as: in decline (16 countries, including Botswana), stable or increasing (13 countries) and those with unknown population trends (nine countries, Lewison & Pluháček, 2017). Detailed analyses of such temporal variations is critical to reporting on the status of hippos and factors affecting their populations (Kanga et al., 2011).

Hippos occupy ecosystems where water is available for diurnal resting sites and there is sufficient surrounding grass (Karstad, 1984; Eltringham, 1993b; Viljoen & Biggs, 1998;

Timbuka, 2012; Klingel, 2013; Stommel et al., 2016; Prinsloo et al., 2020). In rivers, hippos are usually concentrated in areas of permanent, still water (e.g. bends) at relatively shallow depths, from which they can venture out to graze (Karstad & Hudson, 1984; Klingel, 1991a; Viljoen & Biggs, 1998; Chomba, 2013; Prinsloo et al., 2020). In inundated floodplains, hippos primarily rely on sources of open water, such as lagoons and channels (Chase et al., 2015). Hippos usually feed on terrestrial grasses, generally reliant on extensive grasslands (Laws, 1968b; Olivier & Laurie, 1974b; Scotcher et al., 1978; Caro, 1999), but also utilise available woody, riparian, and floodplain habitats (Brugière et al., 2006; Harrison et al., 2008; Stears et al., 2019; Prinsloo et al., 2020). Floodplains may be important to hippos given the dynamic seasonal and annual availability of water and grass (Attwell, 1963; Brugière et al., 2006; Harrison et al., 2008; Wilbroad & Milanzi, 2010). Such variability may be driven by a combination of local rainfall or upstream rainfall providing flows for rivers that inundate floodplains.

Hippo populations are highly vulnerable to changes in the distribution of water and vegetation. Scarce viable waterbodies and poor grazing from low rainfall/flow periods can drive declines or population crashes, with increasing mortality and slow breeding (Attwell, 1963; Sayer & Rakha, 1974; Viljoen & Biggs, 1998; Lewison, 2002). Contrastingly, when resources are widely available, hippo populations increase (Sayer & Rakha, 1974; Marshall & Sayer, 1976; Smuts & Whyte, 1981; Karstad & Hudson, 1984; O'Connor & Campbell, 1986; Lewison, 2007). Consequently, the availability of water and grass are critical and highly vulnerable to anthropogenic changes, threatening hippo populations (Nuñez, 2017). For example, water abstraction in the historically perennial Great Ruaha River in Tanzania reduced the river to isolated pools during the dry season, reducing habitat, driving hippos from the area, and causing overcrowding (Stommel et al., 2016; Stears et al., 2018). Such changes may increase mortality through increased intra-specific aggression and disease transmission (Attwell, 1963; Olivier & Laurie, 1974b; Timbuka, 2012). Around the world, the diversion of upstream water from rivers significantly impacts wildlife and human communities downstream (Lemly et al., 2000; Kingsford et al., 2006; Stears et al., 2018). Such degradation will be exacerbated by climate change, with changing rainfall and increasing temperatures and evaporation reducing habitat for hippos (McClain, 2013; Nuñez, 2017).

The Okavango Delta (the Delta) in northern Botswana is an internationally significant wetland extending over 40,000 km^2 (Gumbricht et al., 2004a), listed as a Wetland of International Importance under the Ramsar Convention (Ramsar, 2014) and a World Heritage site (UNESCO, 2014). Hippo populations are of particular conservation significance in this large ecosystem as they are functionally important, maintaining the expansive floodplains by creating paths that change the distribution of water and slow aquatic vegetation from closing off channels (McCarthy et al., 1998b). Further, hippos' unique grazing style creates 'lawns', beneficial to other herbivores (Eltringham, 1999; Verweij et al., 2006; Kanga et al., 2013). Their use of both aquatic and terrestrial landscapes also transfers nutrients from land to water (excrement), important for aquatic food webs (McCauley et al., 2015; Subalusky et al., 2015; Dawson, 2019). Despite their importance to the Okavango Delta, little is known about the size or status of the hippo population or their use of habitat.

The Delta primarily depends on an annual flooding event, with water from tributaries in the high rainfall areas in the highlands of Angola accumulating into the Okavango River, then flowing through Namibia and discharging into the Delta in Botswana (Figure 3.1), with inflow greatest in April/May (Gumbricht et al., 2004b; Wolski et al., 2008; Milzow et al., 2009a). The flood waters slowly move down the Delta, with peak flood extent in July–September (Gumbricht et al., 2004b; Tooth & McCarthy, 2007). This annual flood event is asynchronous with local rainfall (Wolski & Murray-Hudson, 2008), leading to complex water and vegetation interactions. Human mediated reductions to flow and flooding regimes to the Delta and Okavango River, upstream in Botswana, Namibia and Angola, as well as climate change, will fundamentally alter the availability of water and food for hippos in the Delta (Murray-Hudson et al., 2006; Milzow et al., 2009b, 2010; Nuñez, 2017). Our aim was to examine temporal and spatial patterns of hippo populations in the Delta using aerial survey data (1996–2018), to improve understanding of long-term trends of hippos and their habitat use. This information may be used to assess potential impacts of reductions in flow and changes to rainfall and flooding patterns on hippo populations.

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3.2 Methods

3.2.1 Aerial surveys of hippos

We used data from 13 years (1996, 1999, 2001–2006, 2010, 2012–2014, and 2018) of dry season aerial surveys over northern Botswana (including the Delta) by Elephants Without Borders (EWB) and the Department of Wildlife and National Parks (DWNP). Detailed methodology is available (Department of Wildlife and National Parks 1996, 1999, 2001, 2002, 2003, 2004, 2005, 2006, 2012, 2013; Chase 2011; Chase et al. 2015, 2018) but briefly described here. Different areas were surveyed each year; therefore, we restricted our analyses to the area that was intersected by all surveys, which included most of the Delta (Figure 3.1). Surveys were completed across different strata generally over a period of 1–3 months (Supplementary Table S3.1) following a stratified strip-transect sampling method (Norton-Griffiths, 1978). On average, 4.92% (range 4.40–5.92%, DWNP) and 18.19% (range 16.87–20.65%, EWB) of the study area was surveyed each year (sampling intensity varied in different strata and years, Supplementary Table S3.1). DWNP surveys' strata were generally larger than EWB survey strata. Each stratum was surveyed using a light aircraft, flying parallel regularly spaced transects, about 300 ft above ground level, at 167–180 km/hr. Observers scanned for all large herbivores (including hippos), recording the number of animals seen and their GPS location (observers did not record zero counts). Large groups were photographed during EWB surveys to verify or correct the numbers of animals seen by observers (Chase, 2011; Chase et al., 2015, 2018), recommended for improved accuracy of hippo counts (Jachmann, 2001; Bouché, 2008). The hippo population was estimated for each stratum by dividing the total number of hippos counted in transects by the searched transect area, then extrapolating for total stratum area. We calculated annual estimates of hippos in the Delta by summing the strata estimates, correcting for the proportion of the strata that fell within the study area (Supplementary Table S3.1). For the spatial distribution of hippos, we considered counts within the study area with GPS records (Figure 3.1), excluding 1996 and 1999 surveys because data were not available. We did not correct for non-detection errors in our analyses, though acknowledge their likely presence, particularly for smaller pods (Tracey et al., 2005; Ransom, 2012). Multiple independent counts of the same group (mark-recapture/double count) or recorded perpendicular distances (distance sampling) are required to calculate detection probabilities (Marsh & Sinclair, 1989; Laake et al., 2008; Fuentes et al., 2015), neither which were available to us.
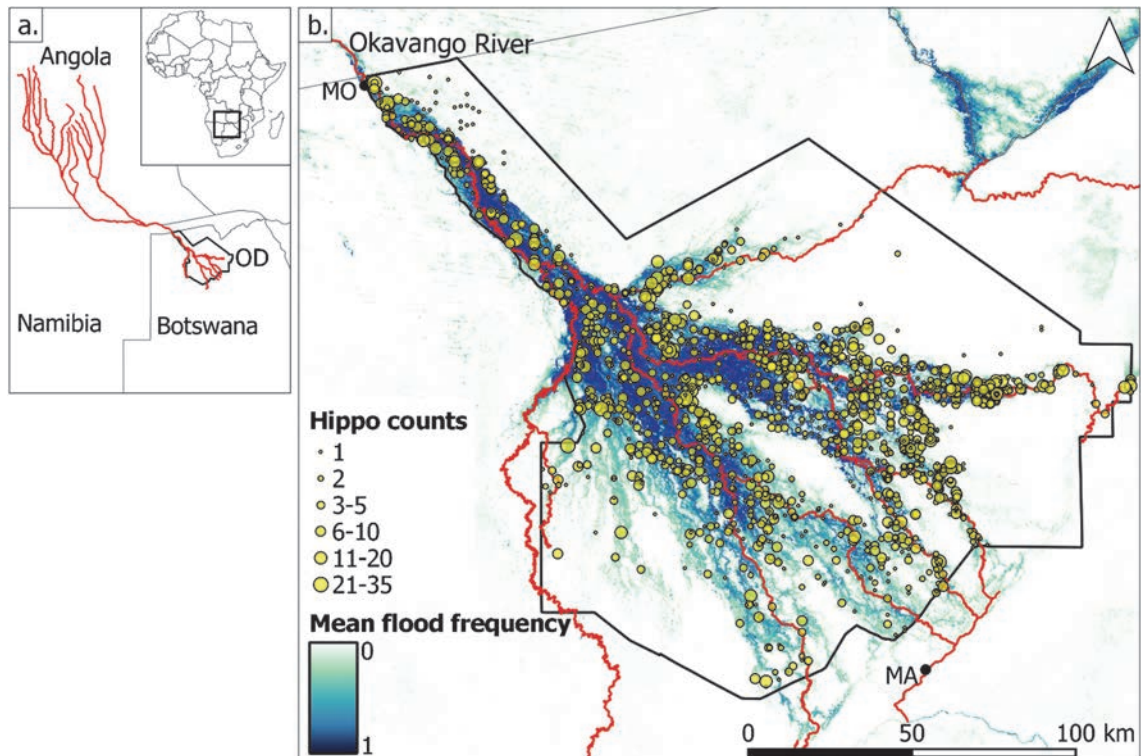
Figure 3.1. a. Location of the Okavango Delta (OD) and its main tributary and distributary rivers (red lines), flowing from Angola to Botswana and b. the Okavango Delta showing mean flood frequency (1989–2019; 0 was never flooded, 1 was permanently flooded), different numbers of hippo counts, with the black line showing the common area surveyed by Elephants Without Borders and Department of Wildlife and National Parks, showing where inflow was measured at Mohembo (MO) on the Okavango River, and rainfall at Maun (MA).

3.2.2 Flooding and vegetation distribution

The Delta is a complex mosaic of perennial channels surrounded by permanent swamps, smaller channels, lagoons, floodplains (secondary and tertiary), islands, grasslands, and woodlands (Ramberg et al., 2006; Department of Environmental Affairs, 2008; Milzow et al., 2009a). We captured this complexity with three environmental datasets to explain the distribution of hippos: flood maps (all inundated areas), surface water maps (open water), and mapped vegetation communities. We briefly describe the methods used to create the datasets here but see Supplementary Text S3.1 for more details on approach.

We created flood maps using a short wave infrared thresholding technique on Landsat scenes (30 m resolution, see Inman & Lyons (2020)), capturing the spatial extent of flooding during each aerial survey ('flood extent'). We also captured long-term flood patterns by creating maps showing flood extent for every two month period (January/February, March/April, May/June, July/August, September/October, and November/December, 1989–2019) and calculating a mean flood map 'flood mean'

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(Figure 3.1), with its variance 'flood variance'. We also captured surface water extent at the time of each aerial survey (30 m resolution) ('water extent') and a map of long-term occurrence of surface water ('water history'), showing the percentage of time that water occurred monthly between 1984–2018, from the Joint Research Center Global Surface Water Mapping project collection (Pekel et al., 2016). We also created a vegetation map using supervised classification of Sentinel-2 imagery (20 m spatial resolution), with 667 field-collected vegetation points (70% used to train the classifier and 30% used to evaluate performance) (data from Bennitt et al. 2014). Points were collected for seven vegetation classes, classified based on woody and grass species composition (Bennitt et al., 2014), and resampled into five classes (floodplain, grassland, riparian woodland, mixed shrubland, and low woodland). This accounted for temporal changes in the vegetation since the points were collected (e.g. primary and secondary floodplain were combined) (Bennitt et al., 2016) and reduced complexity where it was predicted hippos would be unlikely to use the habitat extensively (mopane and acacia woodland combined).

To examine habitat correlates for hippos we extracted corresponding flood, water, and vegetation values for each hippo count, sampling at three scales around each count. These reflected varying levels of habitat use: immediate diurnal living space (≤ 175 m), the average distance within the observers' view from transects for the eleven aerial surveys; lower range estimates of nocturnal foraging extent (≤ 1 km, O'Connor and Campbell 1986; Onyeanusi 2004), and; upper range estimates of nocturnal foraging extent (≤ 3 km, Pienaar et al. 1966; Lock 1972; Mackie 1976; Karstad 1984). We sampled data using QGIS and the buffer and zonal statistics functions (QGIS Development Team, 2018), calculating the predominant vegetation class and the mean value for water and flood maps within the three buffers around each hippo count.

3.2.3 Statistical approach

We calculated the trend in the hippo population over time, fitting a linear growth model (Equation 1) to the Delta-wide hippo population estimates (log transformed), including year as a continuous explanatory variable and survey organisation with two levels (EWB or DWNP), along with their interaction, expressed as:

$$Annual\ growth = \left(e^{(Coef \cdot year)} - 1\right) * 100 \text{ (Equation 1)}$$

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We then fitted a linear model associating Delta-wide hippo population estimates (log transformed) with the following explanatory variables: cumulative local annual rainfall (between June of survey year back to previous July), which included the wet season (October–April), recorded at Maun (Figure 3.1, Department of Meteorological Services 2018; Okavango Research Institute, 2019); cumulative annual inflow into the Delta (between October of survey year back to previous November, reflecting a hydrological year), measured at Mohembo on the Okavango River (Figure 3.1, Okavango Research Institute 2019); survey year and; aerial survey organisation (EWB or DWNP). To account for potential effects of previous environmental conditions on the Delta's hippo population, we included lagged annual rainfall and inflow one to five years before each survey year. We also included averages of annual rainfall and inflow of the survey year (year 1) and the previous years (2, 2–3,…2–5) to capture longer-term trends in rainfall and inflow. In total, there were 24 explanatory variables, combinations of these three variables, and survey year and organisation (Supplementary Model S3.1). We explored the full model space by examining all possible combinations of explanatory variables using the 'dredge' function in the 'MuMIn' package (Barton, 2018). To avoid overfitting, we limited model size to four explanatory variables for any one model (12,950 models). We used an information-theoretic approach to identify best-fitting models by considering models within $\Delta AICc \leq 2$ of best-fit model. We considered multi-collinearity among explanatory variables by computing variance inflation factors (VIF) for the top selected models, with VIF < 5 considered acceptable (Graham, 2003; Weisberg & Fox, 2011). Model fit was visually examined via diagnostic plots (residuals vs. predicted values and QQ-Plots), with the 'simulateResiduals' function (DHARMa package; Hartig, 2019). Given the small sample size we compared adjusted and predicted R^2 values for the top selected models to consider if there was overfitting, where values within 0.2 of each other are generally considered acceptable (Ferdosian & Camões, 2017; Stat-Ease Inc., 2020). We used a model averaging approach, weighted by model AICc scores, to quantify the average association between hippo estimates and explanatory variables using the 'model.avg' function (MuMIn package; Barton, 2018).

For habitat use by hippos, we fitted a model relating counts to the variables sampled at the three scales (≤ 175 m, ≤ 1 km, and ≤ 3 km): four static variables, 'vegetation class', 'flood mean', 'flood variance', and 'water history', and two temporally variant variables

specific to each aerial survey year, 'flood extent', and 'water extent', as well as year, and survey organisation (EWB or DWNP). Location was not included in the model as there was no significant spatial autocorrelation, tested by examining variograms and using Moran's I test via the 'testSpatialAutocorrelation' function on the global model (DHARMa package; Hartig, 2019). We analysed the data using a zero truncated negative binomial generalized linear model, using the glmmTMB function (glmmTMB package; Brooks et al., 2017), given there were no zero counts. Water extent and water history were square root transformed to fit a more Gaussian distribution. Visual examination of the data indicated potential non-linear relationships for the flood and water variables, and therefore both linear and non-linear (2nd order orthogonal polynomial) relationships for these variables were included in the model. We explored the full model space (35 explanatory variables) (Supplementary Model S3.2), limiting to four explanatory variables for any one model (59,535 models), and selected and averaged among plausible models. Of the top selected models, we only considered those where all explanatory variables were significant. This removed six models with 2nd order polynomial water variables, where the linear portion of the polynomial was significant, but the 2nd order polynomial was not (linear versions of these variables were represented in other top selected models). We confirmed a lack of multi-collinearity and spatial autocorrelation in the selected models. All statistics were conducted using the R computing environment (R Core Team, 2018). Means were reported with standard deviations.

3.3 Results

3.3.1 Hippo estimates

Population estimates for the common surveyed area in the Delta (Figure 3.1) averaged 7,192 hippos for EWB surveys and 2,336 hippos for DWNP surveys. The lowest estimate was 1,243 hippos in 1996 (the first year of data, DWNP) and the highest estimate was 9,665 hippos in 2018 (the most recent survey, EWB) (Figure 3.2, Supplementary Table S3.1). Hippo population estimates increased significantly in the Delta over time ($p = 0.002$), with EWB's estimates significantly higher than DWNP's ($p = 0.032$) (Figure 3.2). Average annual rate of population growth varied between 8.02% (EWB surveys) and 6.33% (DWNP surveys), although these rates were not significantly different ($p = 0.737$). When all data were pooled, average annual rate of population growth was 9.14%.

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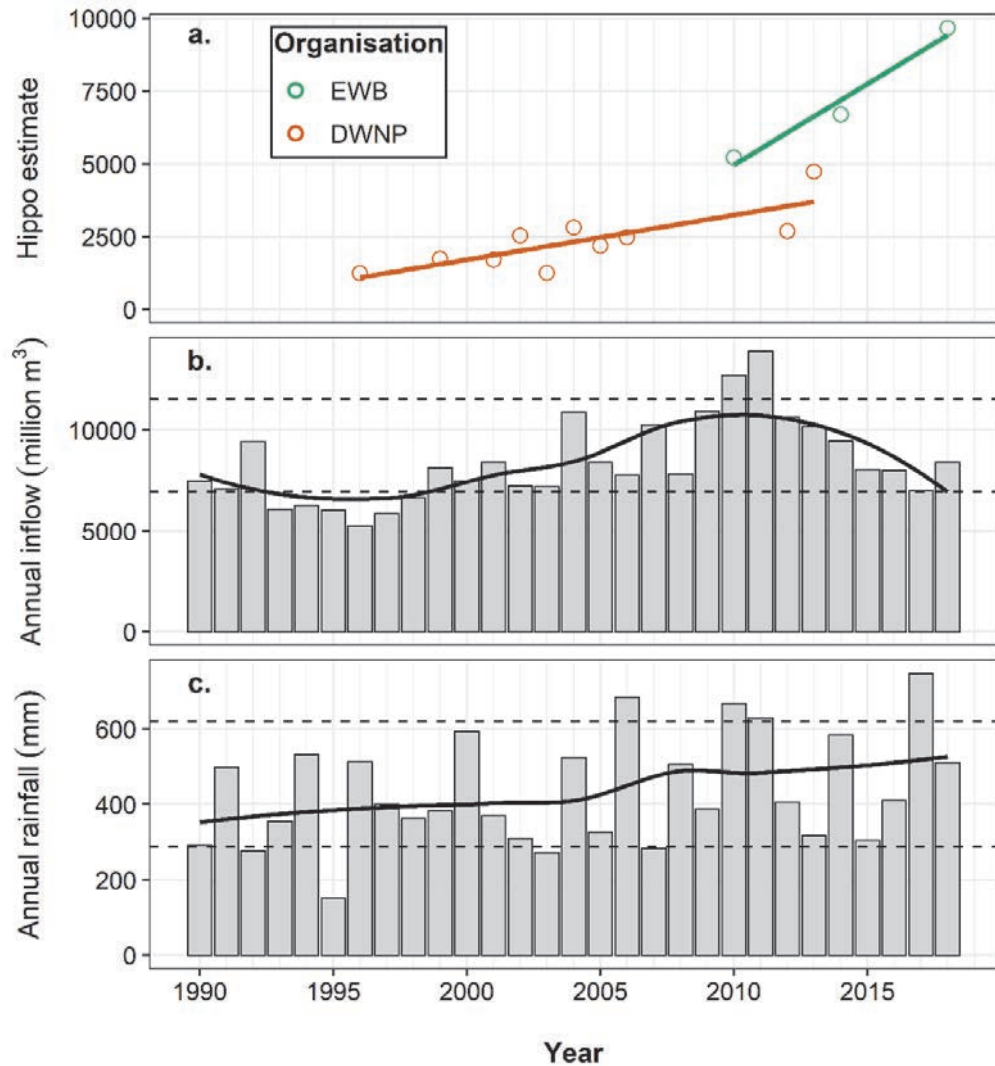
Figure 3.2. a. Hippo estimates (circles; linear regression, lines) in the Okavango Delta from aerial surveys flown by Elephants Without Borders (EWB) and Department of Wildlife and National Parks (DWNP), in relation to b. annual inflow into the Delta from the Okavango River and c. rainfall (see Figure 3.1 for locations), with solid lines representing LOESS smoothed regressions and dashed lines representing mean ± 1 SD, using records since 1934 (inflow) and 1922 (rainfall).

Annual inflow and rainfall varied among years (Figure 3.2). Based on records from 1934 to 2018, annual inflow into the Delta from the Okavango River averaged 9,245 ± 2,284 million m^3 (range 5,274–16,012 million m^3). The first year of aerial surveys (1996) had the lowest inflow on record (5,274 million m^3), in the middle of a six-year period of low floods (1993–1998). Since 1999, annual inflow steadily increased, reaching high levels in 2010 and 2011 (2011 was the fourth highest flood on record) before declining. Annual rainfall in the Delta was more variable than inflow (Figure 3.2) but averaged 454 ± 166 mm (range 151–1190 mm, 1922–2018), with a positive

increasing trend since surveys began. In 1995, the year before aerial surveys began, the lowest rainfall since 1922 was recorded.

Two possible models (ΔAICc $\leq$ 2) were identified as best explaining variation in the Delta-wide hippo population estimates, and included organisation, survey year, and inflow two years prior to the survey (Table 3.1). These models had adjusted R^2 values of 0.846 and 0.866, with little difference (<0.2) between adjusted R^2 and predicted R^2 (Table 3.1), suggesting models were not overfit. As above, the population estimates were significantly and positively related to year ($p = 0.003$) and the relationship between population estimates and organisation was significant ($p = 0.020$), with EWB having higher estimates than DWNP (**Error! Reference source not found.**Table 3.2). There was some evidence of a negative relationship with inflow two years prior ($p = 0.052$) (**Error! Reference source not found.**Table 3.2), though strong associations between this variable and both year and organisation suggest the association was not likely driven by ecological process.

Table 3.1. Linear models with ΔAICc $\leq$ 2, that best explain variation in Delta hippo population estimates in relation to rainfall, inflow, survey year, and the two organisations which flew the surveys (Elephants Without Borders and Department of Wildlife and National Parks).

Log(Estimate) ~	logLik	AICc	ΔAICc	Weight	Adjusted R^2	Predicted R^2
Year + Org	2.23	8.55	0.00	0.11	0.866	0.828
Year + Flow2YearLag	1.35	10.31	1.76	0.04	0.846	0.790

Table 3.2. Model averaged (conditional average) coefficients and standard errors of the variables included in the two best models (ΔAIC $\leq$ 2) explaining the variation in Delta hippo population estimates in relation to rainfall, inflow, survey year, and survey organisation. RI is the relative importance of the variables.

Log(Estimate) ~	Est	Adj SE	z	RI	*p* value
Intercept	-143.9801	50.866	2.83	-	0.005
Year	0.0760	0.025	2.99	1.00	0.003
Flow2YearLag	-0.0001	<0.001	1.94	0.29	0.052
Organisation (DWNP)	-0.5430	0.233	2.33	0.71	0.020

3.3.2 Habitat associations

Hippos were clustered within the floodplains of the Delta, roughly aligning with the main river channels (Figure 3.1). However, hippo groups were offset from the permanently flooded areas immediately surrounding the Okavango River in the panhandle and the

main channels in the central Delta. Towards the terminal sections of the Delta, hippos tended to occur along the channels where the adjacent areas were seasonally, and less extensively, flooded. There was little evidence that hippos occurred outside flooded areas, except some single hippos in areas near the panhandle, presumably in pans that filled during the wet season and where water had persisted. Two possible models (ΔAICc $\leq$ 2) best explained the spatial variation in hippo counts (Table 3.3). Long-term variation in flooding ($\leq$ 1 km) (2nd order polynomial), organisation, and water extent at time of survey ($\leq$ 175 m) were included in both models, with the fourth predictor as water extent at time of survey at $\leq$ 3 km (model 1) and $\leq$ 1 km (model 2) scales.

Table 3.3. Zero truncated negative binomial generalized linear models with ΔAICc $\leq$ 2, that explain variation in hippo spatial counts in relation to flood variance and water extent at different scales and survey organisation.

Count ~	logLik	AICc	ΔAICc	Weight
Org + (FloodVariance1km)^2 + WaterExtent175m + WaterExtent3km	-3491.7	6997.5	0.00	0.64
Org + (FloodVariance1km)^2 + WaterExtent175m + WaterExtent1km	-3492.3	6998.6	1.13	0.36

EWB recorded significantly larger hippo pods than DWNP ($p < 0.001$) (Figure 3.3, Table 3.4). There was a significant non-linear relationship ($p = 0.001$, second-order polynomial) between long-term variation in flooding at $\leq$ 1 km and hippo counts, with the number of hippos in a pod increasing with variance before plateauing and slightly declining at the highest variance (Figure 3.3, Table 3.4). There was a significant positive linear relationship between hippo counts and surface water extent at the time of aerial surveys (water extent) at $\leq$ 175 m ($p = 0.002$) (Figure 3.3, Table 3.4) and a negative relationship between hippo counts and water extent at $\leq$ 1 km ($p = 0.050$) and $\leq$ 3 km ($p = 0.025$).

Table 3.4. Model averaged (conditional average) coefficients and standard errors of the variables included in the two best models (ΔAIC $\leq$ 2) explaining the variation in hippo spatial counts in relation to flood variance and water extent at different scales and survey organisation. RI is the relative importance of the variables.

Count ~	Est	Adj SE	z	RI	p value
Intercept	0.557	0.113	4.95	-	<0.001
Organisation (DWNP)	-0.328	0.086	3.82	1.00	<0.001
poly(FloodVariance1km, 1)	8.841	1.559	5.67	-	<0.001
poly(FloodVariance1km, 2)	-5.057	1.565	3.23	1.00	0.001
WaterExtent175m	1.024	0.332	3.08	1.00	0.002

WaterExtent3km	-1.314	0.586	2.24	0.64	0.025
WaterExtent1km	-0.996	0.507	1.96	0.36	0.050
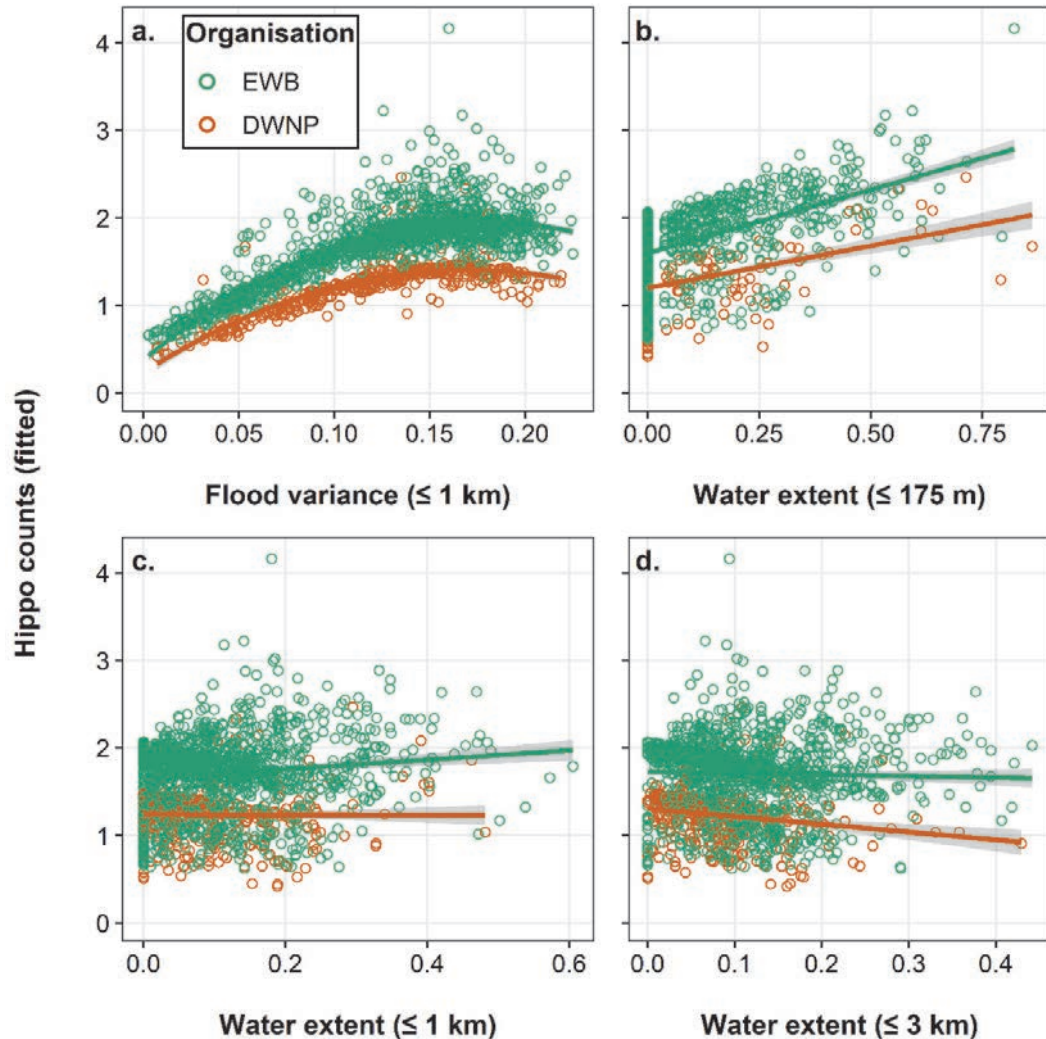
Figure 3.3. Relationships between hippo counts, from Elephants Without Borders (EWB) and Department of Wildlife and National Parks (DWNP), and a. flood variance at ≤ 1 km (0 is no variation, 1 is complete variation) and b. water extent at ≤ 175 m (0 is no water, 1 is complete water), c. ≤ 1 km, and d. ≤ 3 km. Data represent predicted hippo counts from the model-averaging of the top ($\Delta AIC \leq 2$) zero truncated negative binomial generalised linear models, with grey shading representing standard error.

3.4 Discussion

The Okavango Delta is one of the world's hotspots of biodiversity, reflected in its status as a Wetland of International Significance and on the World Heritage List. Its significant hippo population underlines this importance. In 2018, there were an estimated 12,576 hippos in the Delta and surrounding areas, representing 95% of Botswana's hippo population (Chase et al., 2018), and ranking the country third behind Tanzania and Zambia (Lewison & Pluháček, 2017), two long established hippo strongholds. Our

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matching estimate in 2018 of 9,655 hippos (EWB estimate, Figure 3.2) was lower, reflecting our restricted study area (Figure 3.1), which excluded the southern and western extents of the Delta and the Linyanti and Kwando River systems. There were generally higher estimates from EWB surveys than from DWNP surveys (Figure 3.2), probably from a combination of higher survey intensity (Supplementary Table S3.1) and adjusting undercounts of pods with camera data. Clumped distributions of animals, such as hippos, are generally more accurately sampled by increasing sampling intensity (Caughley, 1974; Jachmann, 2001). The Okavango Delta supports a significant proportion of the world's population of hippos (115,000–130,000, Lewison and Pluháček (2017)), challenging reported estimates of 500 and 1,600 hippos in respective dry and wet seasons (Lewison & Pluháček, 2017), estimates first made in 1993 (Eltringham, 1993b). Further, we identified an increasing trend in numbers (Figure 3.2), contrasting some other hippo populations in Africa (Kujirakwinja, 2010; Scholte & Iyah, 2016; Stalmans et al., 2019).

Before the first aerial survey in 1996, the Delta had recently experienced several drought years and an extended period of low flooding (Figure 3.2) (Mogotsi et al., 2013; Byakatonda et al., 2018; Inman & Lyons, 2020). Scarce grazing and water potentially caused a severe decline in the Delta's hippo population (Scotcher, 1978; Viljoen, 1995; Timbuka, 2012). Subsequently, increased inflow and rainfall prevailed probably allowing hippo populations to re-establish, given their rapid growth when resources are abundant (Attwell, 1963; Sayer & Rakha, 1974; O'Connor & Campbell, 1986; Kanga et al., 2011; Stalmans et al., 2019). However, significant statistical associations with water and rainfall availability were not observed in the top selected models, overridden by the strong annual trend and associations with organisation. The positive temporal trend likely reflects a general abundance of resources over the past two decades, which has supported sustained population growth. The rapid growth in hippo populations in the Delta underscores the importance of resource availability which can be highly variable, reflected in other ecosystems (e.g. Luangwa River, Zambia (Attwell, 1963)). The independently timed drivers of local rainfall and inflows may have underpinned this growth, allowing relatively constant availability of forage and water, which promotes hippo populations (Harrison et al. 2008; Timbuka 2012).

Local rainfall (October–April) (McCarthy, 2006; Milzow et al., 2009a; Wolski et al., 2017) provides essential foraging outside the months of the Delta's peak flooding (July–September) for populations to survive throughout the year. Additionally, dependency on flooding (reflected by inflow) is critical as this creates lagoons and stimulates growth of vegetation for foraging hippos as flood waters recede (Attwell, 1963; Brugière et al., 2006; Harrison et al., 2008; Bonyongo, 2009).Hippos are an obligate aquatic species and therefore are confined to areas which are flooded (Figure 3.1). Without high availability of water and grass, hippo populations in the Delta can crash (Smuts & Whyte, 1981; Lewison, 2007), as they probably had done before the aerial surveys began. Similarly, a very low flood in 2019, the lowest on record (Inman & Lyons, 2020) with a below-average rainfall year, has likely caused significant reductions in the hippo populations, with high mortality recorded anecdotally (Tebele, 2019). We did not account for other factors in our modelling, which could potentially also contribute to the growth in hippo populations. These include reduced competition from other grazers (Karstad, 1984), increases in grazing areas with land use change (Kanga et al., 2011), and conversion of woodland to grassland with increasing elephant populations (Naylor et al., 1973; Marshall & Sayer, 1976; Norton, 1988; Kanga et al., 2011). Further, hippos may have emigrated down the river from Angola and Namibia (Figure 3.1) and from other areas subject to high human pressure and habitat degradation, as reported in other countries (Scotcher, 1978; Zisadza et al., 2010; Kanga et al., 2011; Stommel et al., 2016).

Reflecting their aquatic lifestyle, hippo distribution was strongly associated with water and flooding at all spatial scales measured (≤ 175 m, ≤ 1 km, and ≤ 3 km). At a fine scale (≤ 175 m), large open water (e.g. large lagoons) provided important diurnal resting sites, with sufficient territorial space for bull hippos (Karstad, 1984; Chomba, 2013; Stommel et al., 2016). Water depth is also an important driver of hippo distribution and would have been a valuable predictor in our modelling, but was not available (Clough, 1967; Bruton, 1978; Barklow, 1997; Blowers et al., 2012; Klingel, 2013; Prinsloo et al., 2020). Some hippo counts did not coincide with surface water presence in the Delta (Figure 3.3), probably primarily reflecting accuracy issues of the surface water maps or delayed recording of GPS locations during surveys, misaligning counts with surface water data.

Hippos most associated with areas that varied in their flooding regime, particularly the seasonal swamps and intermittently flooded areas in the terminal parts of the Delta (Figure 3.1). This probably reflected increased access to more extensive areas of a broad variety of habitat types (e.g. floodplain, islands, and lagoons) (Attwell, 1963; Wilbroad & Milanzi, 2010). Contrastingly, they occurred in low numbers in areas which were always dry, but also in areas that were constantly flooded (e.g. the permanent swamp - the area surrounding the main channels) (Figure 3.1). This avoidance of areas of expansive water was also reflected in the negative relationship with open water extent at one and three-kilometre scales (Figure 3.3, Table 3.4). This could be because hippo movement is restricted by deep water and thick papyrus vegetation in the middle of the expansive wetland (McCarthy, 2002; Milzow et al., 2009a) with little access to dry land for grazing. Hippos sometimes consume aquatic vegetation, but probably not as a main food source (Taylor, 1975; Hoven, 1978; Mugangu & Hunter, 1992; Harrison et al., 2008; Klingel, 2013; Mekonen & Hailemariam, 2016; Prinsloo, 2016). Access to large grasslands is often reported as a primary driver of hippo distribution (Laws, 1968b; Olivier & Laurie, 1974b; Scotcher et al., 1978; Caro, 1999; Wilbroad & Milanzi, 2010; Chomba, 2013), though this was not reflected in our analyses, with vegetation class not included in any of our top-ranking models (Table 3.3). This may be because our vegetation classes were not sufficiently detailed spatially or temporally or perhaps because hippos in the Delta utilise a broad range of terrestrial habitats for grazing when sufficient grass is available (Scotcher et al., 1978; Karstad, 1984; O'Connor & Campbell, 1986; Harrison et al., 2008). Factors driving hippo distribution probably vary seasonally as grazing and water switch in availability (Pienaar et al., 1966; Olivier & Laurie, 1974a; O'Connor & Campbell, 1986; Brugière et al., 2006; Kanga et al., 2011), not assessed here given aerial survey data were collected during only one season.

Their dependency on water means that anthropogenic threats of climate change and water development threaten hippo populations considerably. Climate change models predict increases in temperature and evaporation and decreases in rainfall over southern Africa, increasing drought intensity and frequency (Niang et al., 2014; Moses & Hambira, 2018). These climate change scenarios will reduce habitat for hippos in the Delta (Nuñez, 2017), as reduced local rainfall will limit grazing and lower rainfall in Angola will lead to reduced inflow into the Delta, causing drying. Further, hippo habitat is highly sensitive

to reductions in water through water abstraction, with diversion of stream flows at relatively low rates (enough to meet just 1% of potential irrigation needs) reducing habitat by 37% over 50 years (Nuñez, 2017). Angola's waterways are currently underutilised, with high potential for future development (Weinzierl & Schilling, 2013), which could accelerate declines in hippo populations (Nuñez, 2017) and threaten the ecological character of this important wetland. Along the Limpopo River in South Africa, water extraction reduced habitat for hippos, forcing them into manmade sources of water (weirs), where they concentrate in large numbers that can rapidly deplete grazing resources (Jacobsen & Kleynhans, 1993). Further, when these threats combine, and habitat loss (through reduced inflows) is coupled with rainfall variability (predicted with climate change), the risk of declines in hippo population becomes two to five times higher (Lewison, 2007). Owing to these sensitivities, the status of hippo populations can be used as an indicator of the prevalence of these environment changes.

3.5 Conclusion

The Okavango Delta is a wetland of immense dimensions, biodiversity, and dynamism, which is reflected in its significant hippo population. The value of this species for the ecosystem, being functionally important for creating and changing water flows in the Delta, should not be underestimated. Apart from the size of the population, hippos in the Delta are subject to minimal direct human disturbance (e.g. poaching, hunting, and culling) (Central Statistics Office, 2005; Barnett & Patterson, 2006; Statistics Botswana, 2015, 2017), allowing the population to rapidly increase when environmental conditions were favourable (Attwell, 1963; O'Connor & Campbell, 1986; Wilbroad & Milanzi, 2010; Zisadza et al., 2010; Mackie et al., 2012; Stalmans et al., 2019). Hippos are dependent on water, which exposes their vulnerability to potential impacts of climate change and proposed upstream water abstractions (Murray-Hudson et al., 2006; Milzow et al., 2009b, 2010). Altered flow regimes would degrade hippos' habitat, reducing the size of lagoons (Zisadza et al., 2010), seasonal swamps, and intermittently flooded areas (Milzow et al., 2010). Hippos provide a responsive indicator to large scale changes in habitats of one of the world's most significant ecosystems, requiring ongoing and frequent surveys to monitor hippo populations and therefore ecosystem condition.

Chapter 4: Drone-based counting and ageing of hippos

4.1 Introduction

Much of the current Africa-wide population data on hippos originates from aerial surveys, which can be inaccurate (Karstad & Hudson, 1984; Smart, 1990; Eksteen, 1993; Stoner et al., 2007; Kujirakwinja, 2010). Reliable and accurate spatial and temporal data on abundances and demographics of hippo populations are essential for effective conservation (Eltringham, 1993a; Alonso & Nordin, 2003; Lewison & Pluháček, 2017) but hippos are inherently difficult to count because of their aquatic lifestyle and behaviour. They are also among the more dangerous animals in Africa (Durrheim & Leggat, 1999; Dunham et al., 2010; Chomba et al., 2012), limiting effectiveness of on-land and water methods of counting (Klingel, 2013).

Hippos are usually surveyed from the air (Viljoen, 1995; Viljoen & Biggs, 1998; Zisadza et al., 2010; Prinsloo et al., 2020), but also from boats and land (Chomba, 2013; Scholte et al., 2016; Prinsloo et al., 2020); each method has advantages and disadvantages. Aerial surveys cover large areas (Kujirakwinja, 2010) but with limited time to scan waterbodies and count hippos, given their speed. Also, aircraft noise may cause hippos to submerge (Bouché, 2008), contributing to underestimation (Timbuka, 2012). Aerial surveys are costly and logistically difficult, resulting in long intervals between surveys (Michez, 2006; Hodgson et al., 2013; Vermeulen et al., 2013; Linchant et al., 2015). Slow, low-flying microlight aircraft or helicopters capturing images may overcome some of these challenges (Jachmann, 2002) but remain costly and potentially logistically difficult, often still causing disturbance. Even counts from land which tend to be more accurate (Kujirakwinja, 2010) given hippo pods can be observed for a long period of time, cannot identify the true number of hippos in a pod, even a small one, without marked or recognised individuals. This is because hippos in the water continually surface and submerge, and individuals are not easily distinguishable (Klingel, 2013). Accuracy improves when hippos rest in aggregations in shallow water ("rafting") (Olivier & Laurie, 1974b) or on land, but still some individuals are inevitably obscured by others (Delvingt, 1978). Although land counts are the most accurate method for counting hippos (Karstad & Hudson, 1984; Tembo, 1987; Eksteen, 1993; Kujirakwinja, 2010; Balole-Bwami et al., 2014), they still have the potential to underestimate (Bere, 1959; Perry, 2015), and all

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counts should be considered a minimum, rather than a true count of hippos in an area (Ansell, 1965a; Scotcher, 1978; Eksteen, 1993). Land counts can also be dangerous and difficult or impossible to do where hippo pods are in remote or not easily accessible areas (Scotcher, 1978; Michez, 2006). Such difficulties compound when assessing demographic composition of hippo pods.

Drones (unmanned aerial systems/vehicles or remotely piloted aircraft) are an increasingly effective means for monitoring animals, including birds (Francis et al., 2020), turtles (Schofield et al., 2017), dugongs (Hodgson et al., 2013), and cetaceans (Koski et al., 2009). They usually have low impact, are relatively low cost, have consistent flight paths, allow remote operation away from wildlife, and enable monitoring of areas inaccessible by land or boat (Watts et al., 2010; Hodgson et al., 2013; Christie et al., 2016; Schofield et al., 2017). Hippos were counted, including their demographic composition, in pods in the Democratic Republic of Congo using relatively expensive technology and sophisticated methods (Lhoest et al., 2015; Linchant et al., 2018), but without comparing drone counts to a current survey method. Drone height and weather affected hippo detection, based on surveys only done in the early morning (Linchant et al., 2018). However, time of day is critical, given hippo behaviour varies throughout the day (Karstad & Hudson, 1986; Ngog Nje, 1988; Timbuka, 2012; Mekonen & Hailemariam, 2016).

Field measurements of restrained or immobilised animals can be used to determine body size (Bell et al., 1997; Allan et al., 2019), however for some species these methods are unfeasible. Alternatively, photogrammetry (measurements from images) is a viable way to collect these data (Berger, 2012) and recently has been extended to drone images (Christiansen et al., 2016; Allan et al., 2019; Burnett et al., 2019). Orthomosaics (images that are geometrically corrected to uniform scale) are preferred for photogrammetry as they have reduced distortion (e.g. Allan et al., 2019), however measurements from single images are also acceptable, especially when animals are unlikely to remain stationary (Bell et al., 1997; Berger, 2012; Christiansen et al., 2016; Burnett et al., 2019). If an animal is not fully exposed and a body measurement cannot be accurately taken, other body measurements may be used to estimate the missing value when the correlation between them is high (Berger, 2012). Body measurements can be used to predict the ages of animals and also to develop body condition indices, though demographic groups

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should be analysed separately as their body proportions can differ (Christiansen et al., 2016). Given there is a known relationship between their body length and age (Ansell, 1965b; Pienaar et al., 1966; Laws, 1968a; Skinner et al., 1975; Martin, 2005), hippos seem an ideal candidate for drone photogrammetry.

This chapter focussed on using drones to monitor and investigate the structure of hippo populations. The specific aims were:

- Compare drone and land surveys - Trial the use of a relatively low-cost drone, testing its effectiveness to estimate hippo numbers, the percentage of hippos that could be assigned to age classes, and numbers of juveniles, subadults, and adults, comparing these estimates to counts from land. Also test how time of day and survey height affected these counts.

- Compare drone and aerial surveys - Use the optimal time of day/survey height flight parameters from the first aim to test the effectiveness of the drone to estimate hippo numbers compared to aerial surveys.

- Age, sex and assess body condition of hippos - Accounting for the difficulty in obtaining full body length measurements, expand our investigation to other body measurements, determining which measurements are most correlated with total length, and therefore age. Investigate the possibility of differentiating between adult females and males on drone images and assessing body condition and its seasonal variations.

4.2 Methods

This study was conducted within the Abu Concession of the Delta. All statistics were conducted in R version 3.5.2 (R Core Team, 2018). Following all regression analyses, we examined plots of distributions of residuals against linear predictors and Q–Q plots of the normal distribution to test the assumptions of homogeneity of variance and normality of data. These assumptions were met in all cases. Means are reported ± standard error.

4.2.1 Drone specifications

The drone used was a multirotor DJI Phantom 4™ (1380 gram, 4K-quality video, 12.4 MP photo, aperture of f/2.8 (DJI, 2016)). The camera was controlled and stabilised by a three-axis gimbal, and the drone controlled by a GPS-stabilised system. All videos and

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images were captured with automatic ISO and shutter speed, allowing variation for neutrally exposed images. Sensor width was 6.2 mm and camera focal length was 3.61 mm (VIZf/x, 2016). The Phantom 4's height is calculated relative to the altitude of the launch location using barometric sensors. Therefore, the drone was launched in an area with similar altitude to the target area to ensure the correct flight height was achieved.

4.2.2 Comparing drone and land surveys

We conducted land and drone counts over a lagoon (-19.41725°E, 22.56815°S, 2.4 ha), with a resident hippo population (Figure 4.1) over seven days (7, 8, 11, 13 and 14 November 2017 and 2 and 3 December 2017).
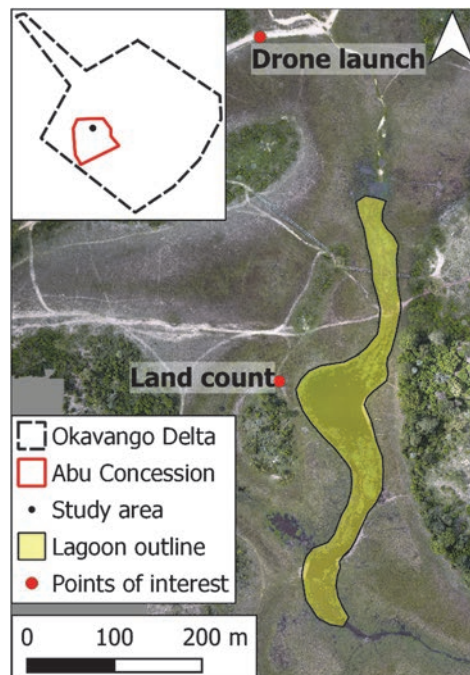
Figure 4.1. Lagoon where hippos were counted in the Abu Concession, within the Okavango Delta in Botswana, showing where the drone was launched, and land counts were done.

4.2.2.1 Drone surveys

The drone was programmed to fly (5.4 km/hr) in transects over the lagoon, calculated and controlled using the Drone Harmony app (www.droneharmony.com) and run through a smartphone, whilst continuously recording video. The lagoon was outlined using the satellite imagery provided on the app, and routes automatically calculated to ensure the entire lagoon was captured on video, with a horizontal overlap of 20%, with the camera facing directly downward (gimbal angle of -90°). Video was chosen rather than still images to increase the likelihood of noticing hippos that were momentarily surfacing, as

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well as improving our ability to capture hippos in a suitable posture for measuring (as done for cetaceans in Burnett et al., 2019).

We flew the drone at three heights sequentially in descending order (120 m, 80 m, 40 m), given 120 m was the height least likely to cause disturbance. The drone was launched and landed out of visual range of the hippos (Figure 4.1), avoiding disturbing them, only returning after two flights to change the battery. It took 30–40 minutes to complete the drone surveys. Given differential coverage of the lagoon, routes varied from backwards and forwards (east-west) across the lagoon (at heights 40 m and 80 m) to one path down the centre, north-south (at height 120 m). Surveys were conducted four times a day (early morning 6:30–7:30 [EM]; late morning 10:00–11:00 [LM]; early afternoon 13:30–14:30 [EA]; late afternoon 17:00–18:00 [LA]), evenly dividing diurnal hours from an hour after sunrise to an hour before sunset, when there was maximum visibility. This resulted in twelve drone surveys per day (one at each height [120 m, 80 m, 40 m] at each time of day [EM, LM, EA, LA]), for seven days. Therefore, we completed a total of 84 drone counts (28 per height, 21 per time of day). The 84 flight videos were reviewed in random order to prevent assessors recalling numbers/measurements from the previous survey, which could bias their assessments of the current survey video. When reviewing the videos, we also checked for behaviours indicating the hippos were disturbed by the drone.

4.2.2.2 Land surveys

We also counted hippos from a vehicle on land adjacent to the lagoon with two observers (15 minutes), in the same location each time (Figure 4.1) where all hippos could be observed, immediately following the last drone flight for each time of day. Therefore, we completed four land counts per day (EM, LM, EA, LA), for seven days, resulting in a total of 28 land counts. In conjunction with the drones counts, this equated to a total of 112 surveys. We noted any behaviours indicating hippos were disturbed by our presence, including submerging in water, vocalising, yawning, and charging (Barklow, 2004; Klingel, 2013).

4.2.2.3 Measurement for ageing

Ground sampling distance (GSD, i.e. pixel size) was calculated based on the equation:

$$GSD = \frac{sensor\ width * flight\ height}{focal\ length * image\ width}$$

Calculated GSDs may be inaccurate due to an inability to obtain exact camera dimensions, individual variation in cameras, the assumption of zero camera tilt, and inaccuracies in the height reported by the drone (Burnett et al., 2019). Measuring an object of known length is a standard way of assessing the accuracy of calculated GSD and correcting for it if needed (Burnett et al., 2019). We measured a 30 cm x 30 cm tile photographed by the drone at two heights (30 m and 20 m; the lowest height we could fly the drone over hippos) on two different dates (20 November 2017 and 14 August 2018), with the tile in the centre of the images. An additional source of error occurs when the target object is not centred in the image, as edge pixels are subject to distortion. To determine the significance of this distortion, during the November flight, we photographed and measured the tile in three additional positions (corner, bottom, and midway between corner and centre). To measure the tile on the drone images, GSD was calculated separately for each image, with image width set as 4000, and flight height obtained from the photo's metadata using ExifTool. Images were imported into ImageJ (Rasband, 2009), the 'set scale' function used to input the GSD for that image and the 'straight line' function used to measure the length of the tile. These values were then compared to the known size of the tile.

To measure the body lengths of hippos from the drone images we used the 'snapshot' function of VLC media player (VLC Media Player, 2014) to obtain still images of each hippo visible on each video. Individual images were imported into ImageJ (Rasband, 2009), the 'set scale' function used to input the GSD for that image (1.79 cm/pixel for drone images at 40 m, 3.58 cm/pixel at 80 m, and 5.37 cm/pixel at 120 m) and the 'straight line' function used to measure the length of each hippo from the tip of the snout to the base of the tail. This length was then used to assign each hippo to three age classes (juvenile, subadult, and adult), with no differentiation between males and females, based on the known relationship between body length and age (Martin, 2005). Hippos < 184 cm were less than two years old and classed as juveniles; hippos 184–233 cm were two to four years old and classed as subadults, and hippos > 233 cm were classed as adults. If the entire body was not visible (e.g. the hippo was partially submerged), but the visible section exceeded 233 cm, then it was classed as an adult. Other partially submerged hippos, where the snout and base of the tail were not visible, were classed 'unknown'. For land counts, hippos were similarly assigned into the three age classes. Hippos judged as less than 1/2 the length of the largest hippo (typically the dominant male (Laws, 1968a;

Skinner et al., 1975)) were classed as juveniles; subadults were between 1/2 and 2/3 the length of the largest hippo; and adults were over 2/3 the length of the largest hippo. Based on the proposed maximum hippo body length of 359 cm (Martin, 2005), the land count classes aligned well with the drone classes, with the distinction between juveniles and subadults calculated as 179.50 cm (compared to 184 cm) and between subadults and adults as 239.30 cm (compared to 233 cm). The use of visual assessment often resulted in difficulty assigning ages (Olivier & Laurie, 1974b), and when an individual was close to the boundary between two age classes or could not be confidently identified, it was assigned as unknown.

4.2.2.4 Analysis

We tested the effect of survey height (including land counts), time of day, and their interaction on total hippo count (model 1), percentage of hippos assigned to age classes (number of juveniles, subadults, and adults divided by the total count for each drone/land survey; model 2), and counts of juveniles, subadults, and adults (models 3–5). 'Height' had four levels (land count and drone heights 40 m, 80 m, 120 m) as did 'time of day' (early morning [EM], late morning [LM], early afternoon [EA], and late afternoon [LA]). Height and time of day were defined as fixed effects, with survey date as a random effect. Attempts to include a more complex random effects structure led to inadequate convergence in the models and so we adopted a simple random effect structure. For model 1, we used a linear mixed model (count data were normally distributed), for model 2 a generalized linear mixed-effect model, with family Binomial and weights equal to the total number of hippos for each count, and for models 3–5 generalized linear mixed-effect models, with family Poisson, and a zero inflation variable (count data included zeroes and were non-normally distributed). We checked for serial autocorrelation in the residuals of all models by comparing models with AR(1) covariance structures to models assuming uncorrelated residuals, using likelihood ratio tests (LRT, anova function). All modelling was conducted using the glmmTMB function (glmmTMB package (Brooks et al., 2017)), with the significance of the fixed effects, their interaction, and the random effect, determined by comparing full and reduced models using LRT (anova function). Differences among the levels of the effects were tested using post hoc pairwise comparisons, based on estimated marginal means, using a Tukey adjustment with the emmeans package (Lenth, 2019). We determined the maximum number of hippos seen

for each day (from any drone or land count), investigating how counts compared to this daily maximum, as another measure of accuracy, given that hippos generally do not move out of lagoons during diurnal hours (Eltringham, 1999). The actual number of hippos in the lagoon was unknown and difficult to estimate given their behaviour, therefore true accuracy could not be calculated.

4.2.3 Comparing drone and aerial surveys

On 3 August 2018, we flew the drone over 17 lagoons with a surface area greater than 0.001 km^2 (at the time of survey) that occurred within a designated site of interest (see Chapter 5 for details on determining which lagoons met these criteria). The lagoon boundaries were imported into the Drone Harmony app, which automatically calculated the flight routes for each lagoon based on a height of 40 m (optimal height as determined by Section 4.2.2). The app settings from Section 4.2.2 were used, except horizontal overlap was reduced to 10% and flights were conducted at a speed of 10 km/hr or 3 m/s. The drone flew the pre-programmed transects whilst recording video. The drone was launched and landed at positions that were out of sight of the lagoons to avoid disturbance to the hippos if there were any present. Where practical, several lagoons were surveyed from the same launch position. Based on the optimal time of day (late morning to early afternoon) determined in Section 4.2.2, we tried to fly between 10:00 and 14:30. However, due to the proximity of three lagoons to tourist lodges, it was only permissible to survey these in the late afternoon. Videos were reviewed for number of hippos and were watched as many times as necessary to achieve an accurate count.

For the aerial survey, a small fixed-wing plane flew over the same lagoons at a target speed of 180 km/hr and a target altitude of 300 feet (91.4 m) above ground level between 11:35–11:45am on the same day as the drone surveys. The lagoon locations were exported as a GPX file and the optimal route between them calculated using the DNR Garmin Sampling Extension in ArcMap (DNR Garmin Extension, 2002; ESRI, 2012). As the plane approached each lagoon, the observers counted the hippos and recorded the GPS location. The observers also scanned for hippos outside the designated lagoons. This aerial survey method replicated standard wildlife aerial survey protocols conducted within Africa and was completed by an experienced aerial survey team (Chase et al., 2018). We tested the effect of survey method (drone or aerial) on hippo count by fitting a generalized

linear model (family Negative Binomial) with lagoon and survey method as fixed effects using the manyglm function of the mvabund package (Wang et al., 2012), using bootstrap resampling with 9999 resamples.

4.2.4 Ageing, sexing, and assessing condition with body measurements

For this analysis, we used drone survey data obtained in Chapter 5 (see chapter for details on video acquisition). As with Section 4.2.2, we used the 'snapshot' function to obtain still images of every hippo visible in each video, by looking for instances where: most of the hippos' body was visible, the hippo was in a 'natural' resting position (stretched out with its head parallel to the water and head, neck, and body in straight alignment), and in the centre of the image. We calculated GSD for each image with height set as 40 m, and image width as 3840 or 4096 pixels (dependent on video settings used). The set scale and straight-line functions of imageJ were used to take seven body measurements: back length (base of tail to neck fold), neck length (neck fold to back of ears), head length (back of ears to end of snout), body width (widest part of back), neck width (widest part of neck), forehead width (widest part between eyes and ears), and snout width (widest part of snout) (Figure 4.2). We only measured when the body part was clearly visible and were confident that measurements would be accurate. We tentatively assigned the sex of some adult hippos based on their spatial relationship with conspecifics. Hippos that were solitary (either alone in a lagoon or > 100 m from another hippo) were assigned as adult males (Olivier & Laurie, 1974a; Skinner et al., 1975; Owen-Smith, 1988), and hippos with juveniles resting on them as adult females (Dibloni et al., 2010).
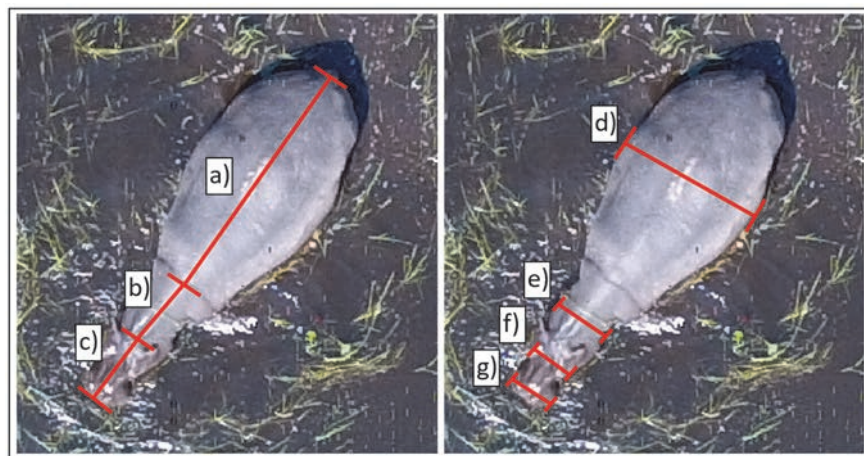
Figure 4.2. Seven body measurements taken from drone images: a) back length (base of tail to neck fold), b) neck length (neck fold to back of ears), c) head length (back of ears to end of snout), d) body width (widest part of back), e) neck width (widest part of neck), f) forehead width (widest part between eyes and ears), and g) snout width (widest part of snout).

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4.2.4.1 Multiple imputation

The resulting dataset had numerous missing measurements, where hippos were partially submerged, or image quality was insufficient to take either some or all measurements. Missingness patterns were investigated using the md.pattern function and multiple imputation (MI) by chained equations was conducted to impute missing values using the mice function (MICE package, van Buuren & Groothuis-Oudshoorn, 2011). We used a predictive mean matching method and set the number of multiple imputations as 70 and number of iterations as 50. The MI were inspected using the densityplot and plot functions. All seven body measurements were used as predictors for all other variables. Hippos with no measurements (i.e. completely submerged but still identifiable as hippos), as well as hippos that had two or less measurements, were excluded from imputation. However, hippos with only back length and/or body width measurements were retained, given these were strong predictors of total length on their own. The imputations were averaged to obtain one complete dataset. Averaging the results of MI is generally not recommended as it reduces the level of variation when performing regression (van Buuren, 2018), therefore the averaged dataset was used only when examining the total length for each hippo, whereas all imputations were considered for regression. Hereafter, we refer to "measured data" and "imputed data" to differentiate between the original dataset of actual measurements (with missing values) and the imputed dataset (with missing values imputed).

4.2.4.2 Analysis

The total length of each hippo was calculated by adding the back, neck and head lengths together. For both measured and imputed data, hippos were assigned ages based on their total length. Martin (2005) provided this relationship separately for male and female hippos (referred to as *sex-dependent* age/length relationship), where both sexes have the same total length for the first eight years and then diverge (with males being larger than females of equivalent age) (Supplementary Table S4.1). Unable to differentiate between adult males and females, we averaged the total lengths (referred to as *averaged* age/length relationship) (Supplementary Table S4.1). The difference in the size of the sexes increases with increasing age, therefore averaging is likely to result in ageing errors only in older adults, and only adding a maximum error of four years. Based on the given ages, hippos were assigned to three age classes (juveniles, subadults, and adults) as in Section 4.2.2.

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The data likely represent repeated measurements of the same individuals, though a lack of individual identification restricted our ability to account for this in the analyses. We calculated the amount of variation (R^2) in total length that was explained by each of the seven body measurements by fitting linear regression models (lm function) separately for each measurement for both the measured and imputed data (using the pool function on all imputations). Body measurements were log transformed to achieve normality.

To determine if male and female hippos had significantly different body proportions, linear regression models were fit separately for each of the seven measurements, with total length as an explanatory variable (to control for the fact that male hippos are larger overall). For this analysis, we used only measured data from hippos that were assigned as adult males and females based on spatial relationships. To account for multiple testing, p values were adjusted using the p.adjust function (method = "BY"), which controls the false discovery rate (Benjamini & Yekutieli, 2001)

There are numerous ways to assess body condition in animals, though indices should be length normalized given body measurements scale with overall body size (Christiansen et al., 2016; Burnett et al., 2019). We used the ratio of body width to total length (BW:TL ratio) to assess hippo body condition, only using measured (not imputed) data. There were insufficient data to analyse the body condition of juveniles, subadults, or adult females and males, so analyses were conducted only on non-sexed adults. We examined how body condition varied seasonally (the three seasons outlined in Chapter 1), by fitting a linear model with BW:TL ratio as the response variable and season as the explanatory variable. We repeated this analysis using ratios calculated for the other body width measurements (neck width, forehead width, snout width).

4.2.4.3 Validating methods

To test the validity of using body length measurements from drone images to assign ages, we applied the method to hippos of known age class/sex. On 14 August 2018, we visually assigned all hippos within a lagoon (same lagoon as Section 4.2.2) into three age classes (juveniles, subadults, and adults). In addition, adults were classified as females if a juvenile was resting on them and were tentatively recorded as females if a subadult was resting on them (Dibloni et al., 2010). Adult males were identified by their large size,

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particularly in relation to their neck and head. In addition, one adult male at this location had been observed out of the water giving a clear view of its genitals and could from then on be identified by a noticeable scar on its neck.

Once the visual assessment was complete, we took drone images of each hippo. Using the same methods as earlier, we calculated the seven body measurements for each hippo, calculated total length, and assigned an age and age class to each hippo using the *averaged* age/length relationship, as well as the *sex-dependent* age/length relationship where possible. The age classes assigned from drone images were then compared to those we assigned in the field. In addition, we identified potential males from the drone images, by examining if their snout and neck widths were larger than those seen in the adult females from the previous analysis. We also tested the accuracy of multiple imputation by randomly removing body measurements from the validation dataset using the sample function, based on the percentage that each body measurement was missing from the main dataset. This incomplete validation dataset was then joined to the original measured dataset and multiple imputation rerun using the same inputs as before. Ages and age classes were assigned based on the imputed body lengths.

4.3 Results

4.3.1 Comparing drone and land surveys

The number of hippos counted in the lagoon averaged 9.18 ± 0.25 (range 1–14, $n = 112$ counts). We use daily maximum counts to describe the population because of emigration and immigration between surveys days: first two days (14 hippos), following two days (12 hippos), following two days (10 hippos), and last survey day (9 hippos). The pod consisted of one juvenile, two subadults, with adults ranging in number from eleven on the first survey day to six on the last day, based on daily maximum counts of each age class. All hippos remained in the water during the surveys. The drone's low impact sound was audible at 40 m (with decreasing noise level at higher altitudes) but hippos were not observed to be disturbed by the drone at any height, with no obvious changes in behaviour observed on the videos. The hippos were slightly disturbed by the presence of the vehicle during land counts. The hippos did not charge the vehicle or behave aggressively, but if they were near the edge of the lagoon when the observers arrived, they became vigilant and sometimes moved away from the observers. Their disturbance response varied with

their activity, responding most when they were already active (e.g. the early morning), whereas if they were resting when we approached, they seldom moved.

Summary tables of the fitted models are shown in Supplementary Tables S4.2–S4.6. There was no significant interaction between height of survey and time of day on total hippo count ($\chi^2(9) = 11.276$, $p = 0.257$), so we omitted the interaction from subsequent analyses. Hippo count varied significantly with height ($\chi^2(3) = 12.180$, $p = 0.007$) and time of day ($\chi^2(3)= 38.384$, $p < 0.001$, Figure 4.3). Hippo count was also significantly negatively related to survey date ($\chi^2(1) = 64.757$, $p < 0.001$); fewer hippos were counted in subsequent days of the survey. Counts at 40 m were significantly higher than counts at 120 m ($p = 0.004$), identifying on average 17.6% more hippos (Figure 4.3a). Also, 10.6% more hippos were counted at 40 m than during land counts, although this was not significant. The average number of hippos detected at 80 m was the same as the number of hippos counted from land, but numbers of hippos detected at 120 m were 5.9% less than during land counts. Early morning counts were significantly lower than at all other times of day (late morning, $p < 0.001$; early afternoon, $p < 0.001$; late afternoon, $p < 0.001$), with no significant differences among the other times of day (Figure 4.3b). There were 22.4–26.0% fewer hippos counted during early morning counts, compared to other times of the day. The inclusion of an AR(1) covariance structure did not improve model fit ($\chi^2(2) = 3.548$, $p = 0.170$), so was omitted from the model.
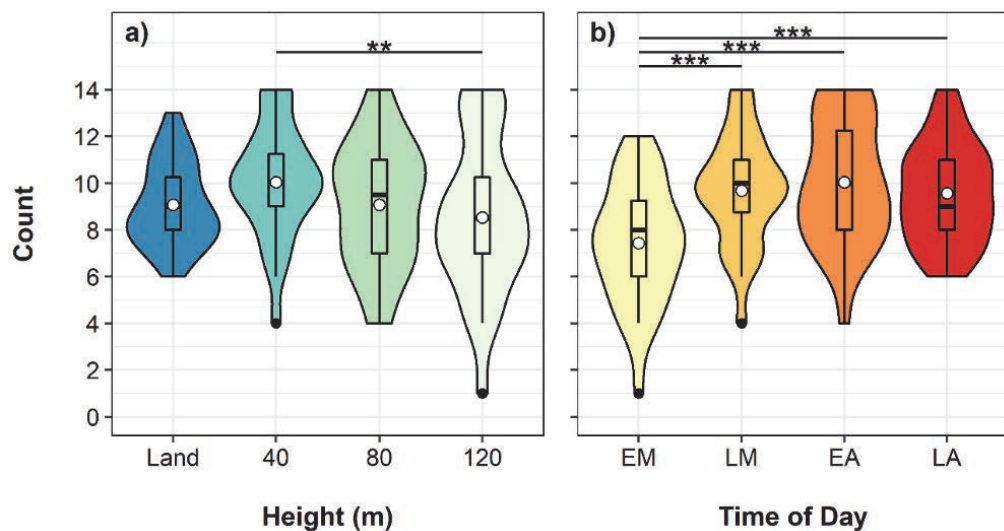
Figure 4.3. Violin and boxplot (mean, circle) showing variation in total hippo counts for a) land and three drone heights (40 m, 80 m and 120 m) and b) time of day (EM – early morning, LM – late morning, EA – early afternoon, LA – late afternoon). Significant post hoc pairwise comparisons identified by asterisks.
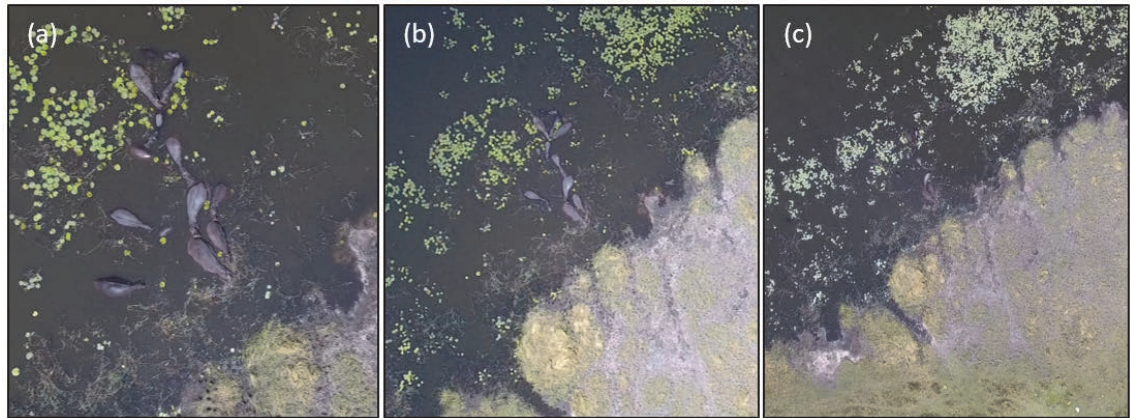
Figure 4.4. Snapshots taken from videos at a) 40 m, b) 80 m, c) 120 m in early afternoon. Note the increasing difficulty in detection with increased altitude due to low resolution, and resting posture of hippos with their bodies exposed, allowing easy detection.

Our daily maximum counts occurred at all times of the day, although there were more in the middle of the day: early morning (3), late morning (6), early afternoon (9), and late afternoon (3, Figure 4.5, Table 4.1). Eighteen daily maximum counts were drone counts: 40 m (10), 80 m (3), and 120 m (5), along with three land counts (Table 4.1). The count with the greatest difference from the daily maximum was a 120 m drone count in the early morning (71.4% less hippos than daily maximum).
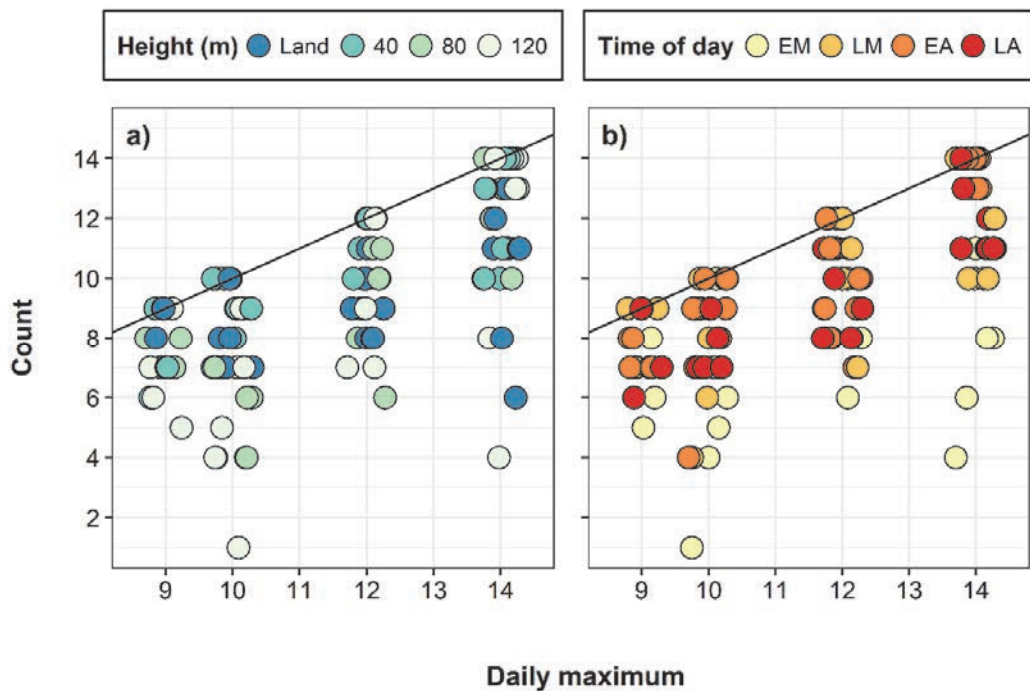
Figure 4.5. Relationship between daily maximum hippo count (a proxy of the true count) and counts at a) different heights and b) times of day (EM – early morning, LM – late morning, EA – early afternoon, LA – late afternoon). The black line indicates the points where counts equalled the daily maximum count. Points were jittered along the x axis.

Table 4.1. Mean counts of hippos (± SE) and number of times counts matched the daily maximum (Daily max) for each time of day and height combination. Sample size was seven for each count.

Time of Day	Height	Mean count	Daily max
Early Morning	Land	7.3 ± 0.3	1
	40 m	9.0 ± 1.1	2
	80 m	7.7 ± 1.0	0
	120 m	5.7 ± 1.1	0
Late Morning	Land	9.7 ± 0.7	0
	40 m	10.7 ± 0.7	4
	80 m	8.7 ± 1.2	0
	120 m	9.6 ± 0.9	2
Early Afternoon	Land	9.7 ± 0.7	1
	40 m	10.7 ± 1.0	4
	80 m	10.3 ± 1.0	2
	120 m	9.4 ± 1.4	2
Late Afternoon	Land	9.6 ± 0.5	1
	40 m	9.7 ± 0.8	0
	80 m	9.6 ± 0.8	1
	120 m	9.4 ± 1.2	1

Tile measurements obtained from drone images ranged from 29.83 cm to 30.14 cm (actual size 30 cm). The most imprecise measurement, with an error of 0.17 cm, occurred when the tile was not centred in the image. This measurement was the only value less than the actual size of the tile (all other measurements were > 30 cm). Measurements taken of the tile in the same position at the same height but on different days (approximately nine months apart) had differences of 0.11 cm (at 20 m) and 0.05 cm (at 30 m).

The percentage of hippos that were assigned to age classes was significantly related to the interaction between height and time of day ($\chi^2(9) = 17.100$, $p = 0.047$, Figure 4.6). Land counts and counts at 40 m assigned similar numbers of hippos to age classes and this did not differ with time of day. In the early morning, land counts assigned more hippos to age classes than counts at 80 m ($p = 0.013$) and 120 m ($p = 0.003$), with counts at 80 m and 120 m having significantly fewer hippos assigned to age classes in the early morning compared to the early and late afternoon (all $p < 0.05$). By late morning, all survey heights assigned similar numbers of hippos to age classes. The height and time of day survey with the highest average percentage of hippos assigned to age classes was land counts, in the late afternoon (66.8% of hippos), compared to the lowest average of 3.6% from surveys at 120 m in the early morning. The inclusion of AR(1) covariance structure significantly improved model fit ($\chi^2(2) = 18.760$, $p < 0.001$), and was retained in the model, indicating a temporal pattern in the percentage of hippos that could be aged.

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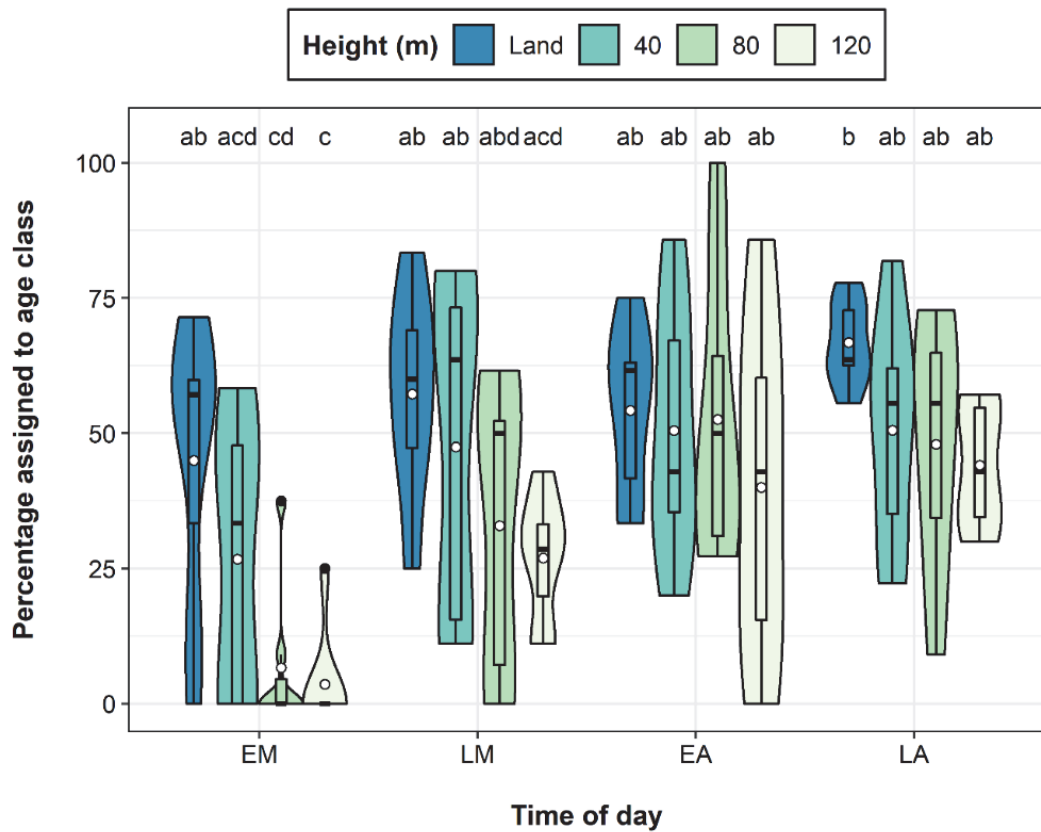
Figure 4.6. Violin and boxplot (mean, circle) showing significant interactive effect of height and time of day (EM – early morning, LM – late morning, EA – early afternoon, LA – late afternoon) on percentage of hippos assigned to the three age classes (juvenile, subadult and adult). Significant post hoc pairwise comparisons identified by letters.

There was no significant interaction between height and time of day on the number of observed juveniles ($\chi^2(9) = 7.994$, $p = 0.535$) or subadults ($\chi^2(9) = 12.640$, $p = 0.180$) and so we omitted the interaction from subsequent analyses. The number of juveniles and subadults observed in images was significantly related to height (juveniles, $\chi^2(3) = 19.172$, $p < 0.001$; subadults, $\chi^2(3) = 24.151$, $p < 0.001$, Figure 4.7a), with land counts providing significantly higher counts than counts at 40 m (subadults, $p = 0.021$), 80 m (juveniles, $p = 0.045$) and 120 m (juveniles, $p = 0.016$; subadults, $p = 0.007$). For juveniles, land counts were higher than counts at 40 m, although this was close to, but not below, the 0.05 significance level ($p = 0.072$). This was also true for subadults with land counts and counts at 80 m ($p = 0.055$). There were no significant differences among the other drone heights. The number of juveniles counted was not related to time of day ($\chi^2(3) = 3.158$, $p = 0.368$) but number of subadults was ($\chi^2(3) = 10.896$, $p = 0.012$, Figure 4.7b). Early morning counts of subadults were significantly lower than counts in the late afternoon ($p = 0.033$), with no significant differences among the other times of day. There was no

effect of survey date on the number of juveniles or subadults. We were unable to include AR(1) covariance structures in the models due to lack of convergence.
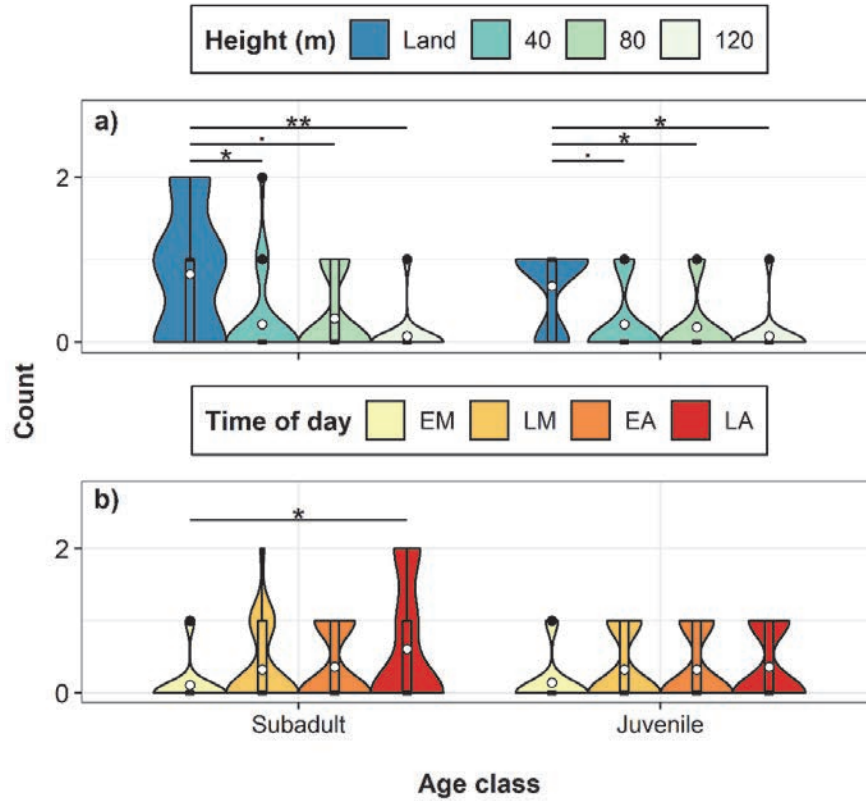
Figure 4.7. Violin and boxplot (mean, circle) showing variation in counts for juvenile and subadult hippos for a) height and b) time of day (EM – early morning, LM – late morning, EA – early afternoon, LA – late afternoon). Significant post hoc pairwise comparisons identified by asterisks, near significant ($0.075 > p > 0.05$) comparisons identified by dots.

The number of observed adults was significantly related to the interaction between height and time of day ($\chi^2(9) = 24.854$, $p = 0.003$, Figure 4.8). The number of adults counted from the land and at 40 m did not significantly change with time of day, but for the other heights, fewer adults were counted in the early morning compared to late morning (120 m, close to, but not, significant; $p = 0.067$), early afternoon (80 m, $p = 0.010$; 120 m, $p = 0.009$), and late afternoon (80 m, $p = 0.030$; 120 m, $p = 0.008$). From late morning onwards, and particularly in the afternoon, all surveys (land counts and drone counts at 40 m, 80 m, and 120 m) counted similar numbers of adults. There was no effect of survey date on the number of adults. The inclusion of an AR(1) covariance structure significantly improved model fit ($\chi^2(2) = 6.228$, $p = 0.044$), suggesting a temporal pattern in the number of adults counted, likely due to the emigration of adults from the lagoon over the survey period.
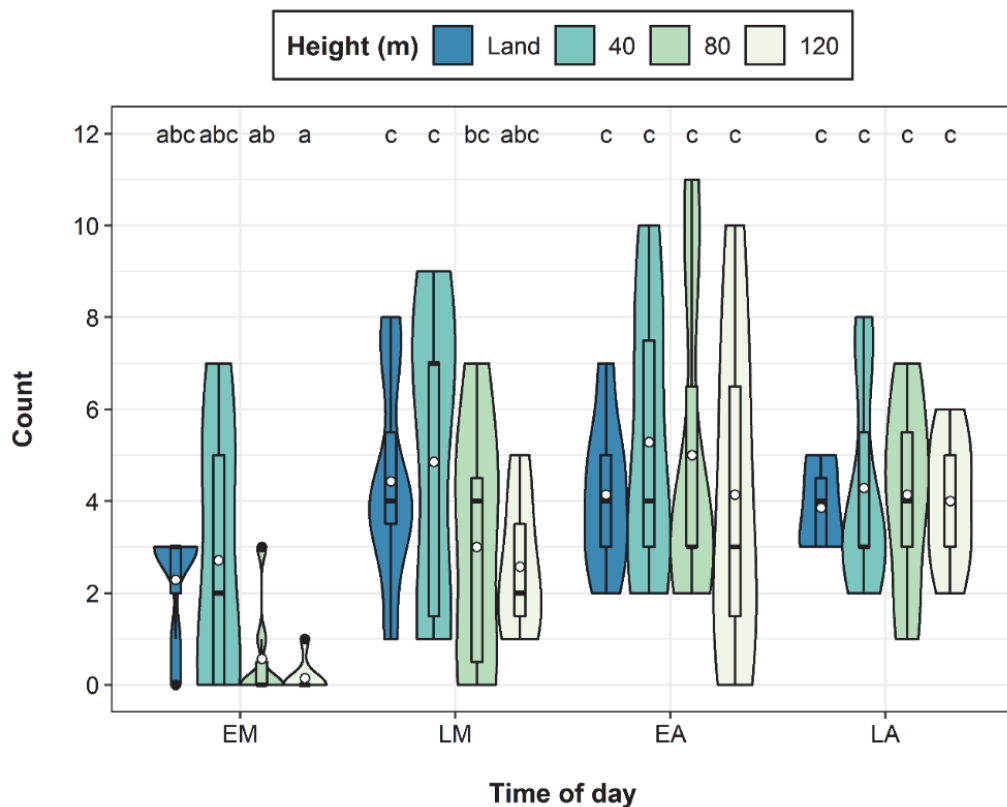
Figure 4.8. Violin and boxplot (mean, circle) showing significant interactive effect of height and time of day (EM – early morning, LM – late morning, EA – early afternoon, LA – late afternoon) on adult hippo counts. Significant post hoc comparisons identified by letters. Note: the difference between counts at 120 m EM and 120 m LM was close to, but not, significant ($p = 0.067$).

4.3.2 Comparing drone and aerial surveys

Of the 34 lagoons in the area of interest, 17 had surface areas greater than 0.001 km^2 and were surveyed. Drone surveys were conducted between 12:03–13:59, except for the three lagoons close to tourist lodges, which were flown between 16:42–17:50 (Table 4.2). In total, 46 hippos were counted during drone surveys, compared to 29 during aerial surveys (Table 4.2). Hippos were detected in seven lagoons. The drone survey counted the same number of hippos, or more, than the aerial survey in four of the five lagoons that both the drone and aerial survey detected hippos in. A solitary hippo in 'Lagoon 25' was seen by the drone survey but missed by the aerial survey, and conversely, a solitary hippo was spotted by aerial survey in 'Lagoon 33' but was undetected by the drone survey. The largest count discrepancy occurred in 'Lagoon 30', where the drone survey counted 16 hippos and the aerial survey saw five. The difference in numbers of hippos counted in lagoons between the survey methods was close to, but not below, the 0.05 significance level ($p = 0.074$) (Supplementary Table S4.7). No hippos were observed outside the surveyed lagoons during the aerial survey.

Table 4.2. Counts from drone and aerial surveys and drone survey times for each lagoon.

Lagoon	Drone	Aerial	Drone time
1	5	9	13:10
2	1	1	12:03
3	0	0	12:07
4	0	0	12:25
5	8	2	12:24
7	0	0	12:11
11	15	11	12:32
13	0	0	12:29
16	0	0	12:52
18	0	0	17:50
22	0	0	13:27
25	1	0	13:35
28	0	0	13:57
29	0	0	13:59
30	16	5	16:42
31	0	0	17:01
33	0	1	12:47
Total	**46**	**29**	

4.3.3 Ageing, sexing, and assessing condition with body measurements

In total, 576 hippos were detected in drone videos. We were unable to take any of the seven body measurements for 11.8% of these hippos. For the remaining 508 hippos, the number of body measurements able to be taken varied: 2.8% of hippos had one measurement, 10.1% had two measurements, 25.5% had three measurements, 9.9% had four measurements, 13.5% had five measurements, and 7.8% had six measurements. We were only able to take all seven body measurements for 18.6% of hippos. Back length was the measurement most often missing (68.7%) followed by body width (65.7%), neck length (44.1%), neck width (43.9%), snout width (26.6%), head length (9.6%), and forehead width (6.3%) (Table 4.3). There were 141 hippos for which back, neck, and head length measurements were available and therefore total length could be calculated. After removing hippos with no measurements (68) and hippos with too few measurements (57), 451 hippos were included in the imputation. Density plots suggested relatively good fit of the imputed data, though imputed values for back length, body width, neck length, and neck width showed some shifting distribution patterns to lower values compared to the measured data (Supplementary Figure S4.1). For both datasets (measured and imputed), total length was most strongly correlated with back length followed by body width (Table 4.3; Figure 4.9). The order of the remaining measurements varied between the measured and imputed datasets, though neck width and length were the poorest predictors of total length for both datasets (Table 4.3; Figure 4.9).

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Table 4.3. Percentage of each body measurement missing and variation in total length (R^2) explained by each measurement (all log transformed) for measured and imputed data.

Variable	% missing	R^2 measured	R^2 imputed
log(Back length)	68.7	0.95	0.95
log(Neck length)	44.1	0.61	0.72
log(Head length)	9.6	0.67	0.77
log(Body width)	65.7	0.83	0.84
log(Neck width)	43.9	0.63	0.72
log(Forehead width)	6.3	0.70	0.75
log(Snout width)	26.6	0.71	0.76
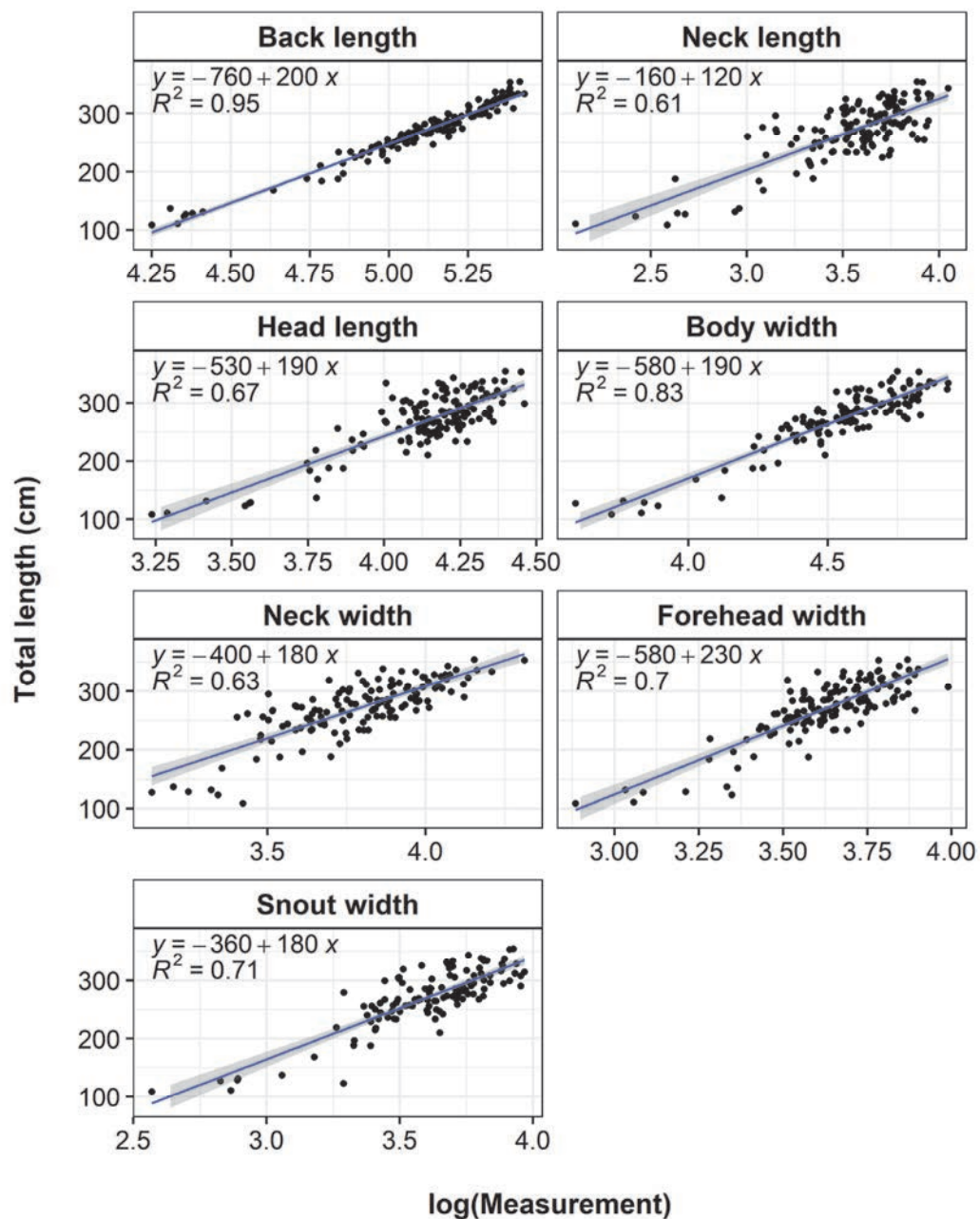
Figure 4.9. Linear relationships between body measurements (log transformed) and total length for measured data.

Hippo length ranged from 109–354 cm (Figure 4.10), which corresponds to the full hippo age range (< one year old to 45 years old), using the *averaged* age/length relationship (Martin, 2005). Of the 141 hippos for which total length could be calculated from the measured data, 5.7% were juveniles, 7.8% subadults, and 86.5% adults (Figure 4.10). Using the imputed data, calculating age classes for the 451 hippos, this changed to 13.3% juveniles, 14.4% subadults, and 72.3% adults (Figure 4.10).

Age class	Measured	Imputed
Juvenile <2 years	8 (5.7%)	61 (13.5%)
Subadult 2-4 years	11 (7.8%)	66 (14.6%)
Adult >4 years	122 (86.5%)	324 (71.8%)
Total	141	451
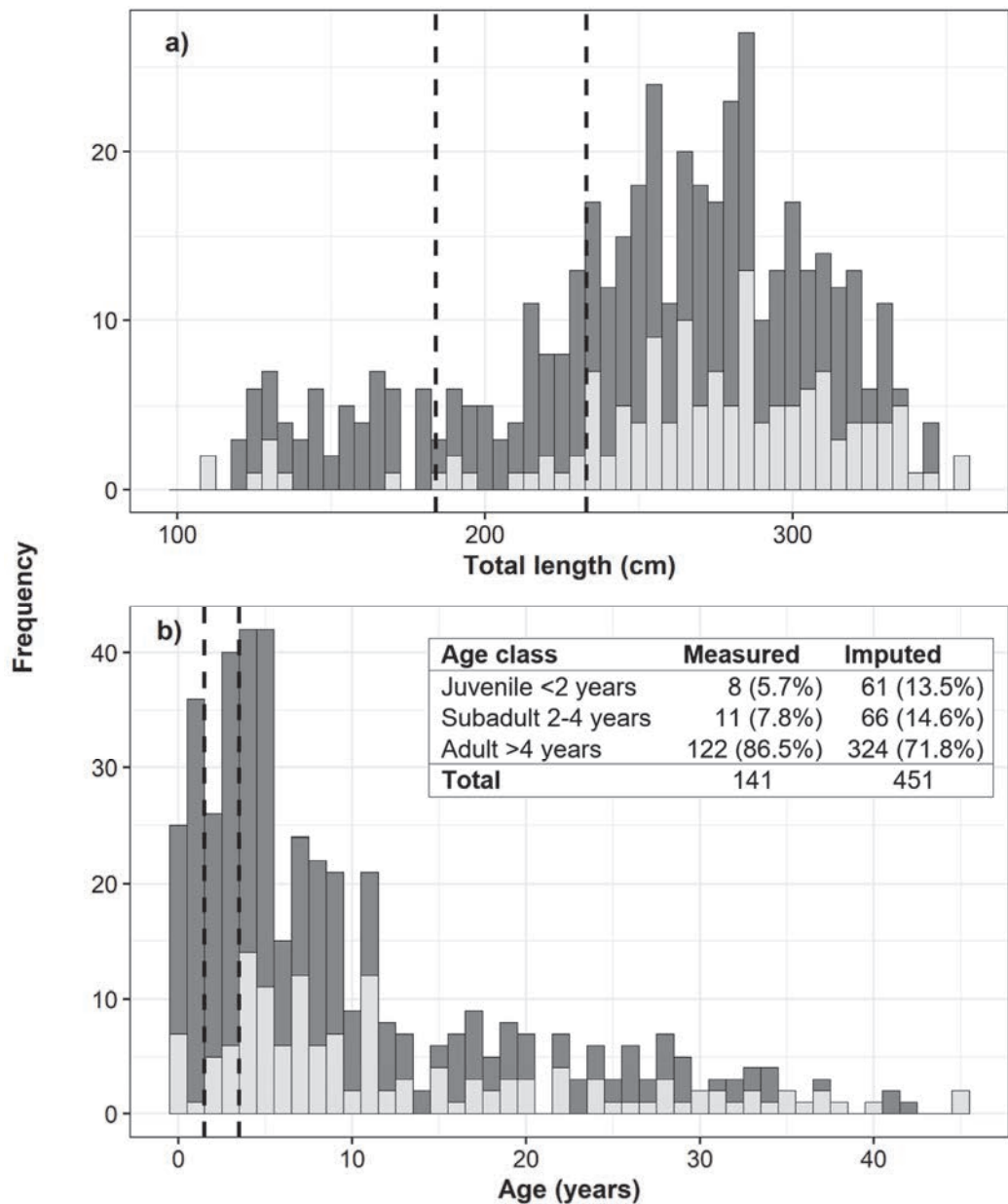
Figure 4.10. Frequency histogram of a) total length and b) age for measured data (light grey) and imputed data (dark grey) and table of number and percentage of hippos in each age class. Vertical lines indicate age classes.

Of the 53 hippos that were assigned as adult males (28) and females (25) based on their spatial relationship with other hippos, 13 males and nine females were missing at least one length measurements and therefore had to have values imputed; they were all correctly classified as adults based on the imputed values. All seven body measurements were obtained for 24 (45.3%) of the adult male and female hippos. After accounting for total length, male hippos had significantly wider necks (t_{23} = 4.114, BY adjusted p = 0.006) and snouts (t_{22} = 3.977, BY adjusted p = 0.006) than female hippos (Figure 4.11). There were no significant differences in back length, neck length, head length, body width, or forehead width (all $p > 0.05$) between the sexes after controlling for total length (Figure 4.11). The average neck width of female adult hippos was 43.4 cm ± 1.25 (range 33.2–58.1 cm) compared to 55.7 cm ± 1.64 (range 40.6–74.5 cm) for males. Average snout width for female adult hippos was 36.7 cm ± 0.79 (range 30.6–44.9 cm) compared to 43.2 ± 1.00 (range 33.2–51.6 cm) for males. The mean total length for adult females was 282.0 cm (range 233.6–338.4 cm) and 317.3 cm (range 283.5–354.4 cm) for adult males.

Based on these results, we tentatively assigned hippos in the complete dataset as adult males if their necks or snouts were one standard deviation wider than the largest female measurement (for neck width this equated to 64.38 cm and for snout width as 48.82 cm), or were larger than the upper length measurement of females (343 cm; Martin, 2005). This resulted in 23 hippos being assigned as male, of which 17 were 'new' males (i.e. has not been assigned as males based on their spatial relationships to other hippos). None of the hippos that were assigned as male based on their size were assigned female based on their spatial relationships. Analysing these data with a factor analysis would allow the relationships among all body measurements (and how they relate to sex) to be investigated, though is outside the scope of this work. The two largest hippos (aged 45 years) were assigned as adult males; and using the *sex-dependent* age/length relationship their ages reduced to 42. Adult males were on average 20 years old, with the youngest seven years old and the oldest 42 years old. Adult females were on average 12 years old (range 4–38).
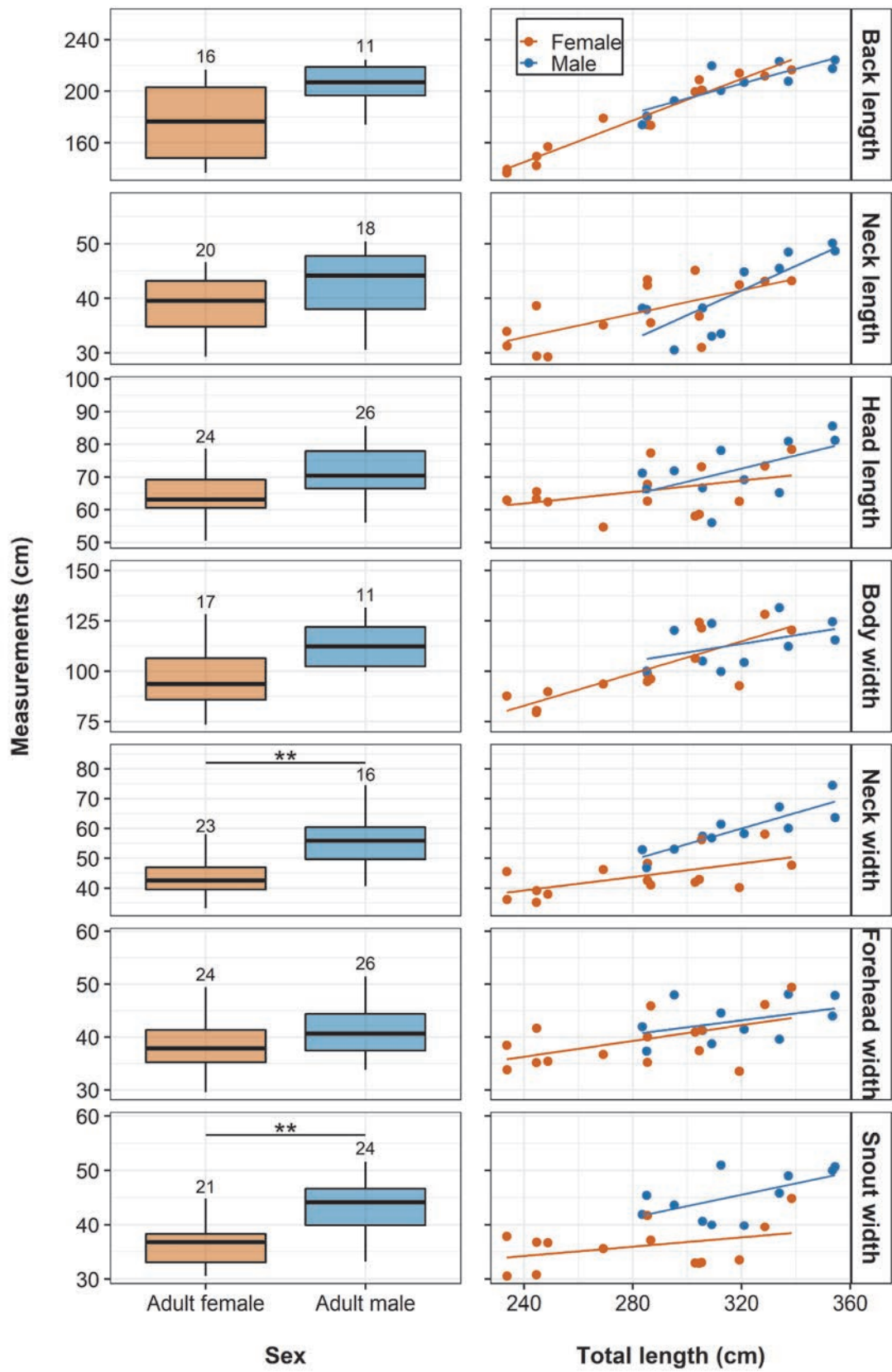
Figure 4.11. Body measurements and linear relationship between body measurements and total length of adults based on sex.

Adult body condition (BW:TL ratio) varied significantly with season ($F_{2,104} = 8.303$, $p < 0.001$), being lower (i.e. leaner) in the wet season (low flood) than the dry season (high flood) ($p < 0.001$) and dry season (med-low flood) ($p = 0.034$) (Figure 4.12). The other width ratios did not significantly change with season: neck width to total length ratio ($F_{2,114} = 1.036$, $p = 0.358$), forehead width to total length ratio ($F_{2,119} = 1.714$, $p = 0.185$), and snout width to total length ratio ($F_{2,104} = 1.356$, $p = 0.262$).
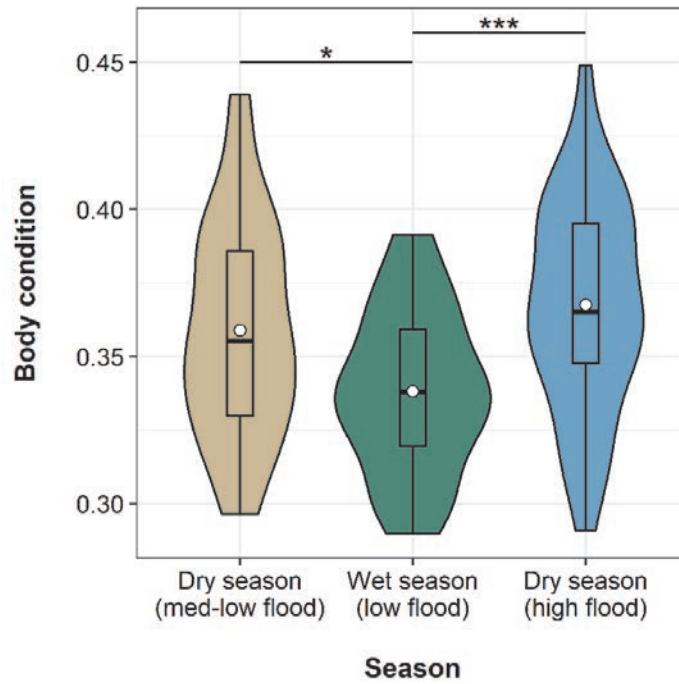
Figure 4.12. Boxplot (mean, circle) showing seasonal changes in adult hippo body condition (body width:total length). Significant post hoc pairwise comparisons identified by asterisks.

For the validation, we visually assigned age classes to all eleven hippos that were in the lagoon (Table 4.4). We identified seven adults (one male, two females, two likely females, and two unknown), two juveniles, and two subadults. The age classes calculated from measurements from the drone images matched those we had visually assigned for all hippos (Table 4.4). The ages calculated based on the *averaged* age/length relationship ranged from < one to 38, and reassigning these based on the *sex-dependent* age/length relationship changed them by a maximum of three years. Two adults were flagged as potential males based on drone measurements , one had both a neck and snout wider than the above-mentioned threshold value and was also visually confirmed as an adult male. The other had a wider snout, but not neck, than the threshold value and while we were not able to visually confirm it as an adult male at the time, four days after we noted there were

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two adult males in this pod (personal observation). After randomly removing body measurements (in order to validate the reliability of the multiple imputation method), three hippos retained their back, neck, and head length measurements, so total length was unaffected (i.e. the imputed values are the original measured values). The remaining eight hippos had new total lengths imputed, and this changed their assigned ages by a maximum of two years. Of these, seven hippos remained within the correct age class, but one subadult had an imputed age of one (true age was two years old) and was therefore was incorrectly reassigned as a juvenile.

Table 4.4. Total length, age, age classes, and sexes assigned using visual assessment, measured data from drone images, and from imputation. Note that imputed length, age, and age class are absent for hippos 1, 4, and 7 as randomly removed values did not affect back, neck, or head length for these hippos. Hippo 8 was the only hippo misclassified using imputed data.

Hippo	Total length (cm)		Age			Age class		
	Measured	Imputed	Measured (average)	Measured (sex-dependent)	Imputed	Visual	Measured	Imputed
1	338.87		38	35		Adult male	Adult (potential male): neck width > 64.38 cm (70.3 cm) snout width > 48.82 cm (50.0 cm)	
2	317.82	313.73	27	-	25	Adult	Adult (potential male): snout width > 48.82 cm (49.2 cm)	Adult
3	296.80	296.15	16	17	16	Adult female	Adult	Adult
4	295.40		15	16		Adult female	Adult	
5	323.25	323.58	30	33	30	Adult (likely female)	Adult	Adult
6	300.06	299.49	18	19	17	Adult (likely female)	Adult	Adult
7	264.11		7	-		Adult	Adult	
8	194.68	178.71	2	-	1	Subadult	Subadult	Juvenile
9	184.62	196.97	2	-	2	Subadult	Subadult	Subadult
10	134.26	135.17	<1	-	<1	Juvenile	Juvenile	Juvenile
11	121.86	122.90	<1	-	<1	Juvenile	Juvenile	Juvenile

4.4 Discussion

4.4.1 Comparing drone and land surveys

We showed that by flying a relatively cheap drone at 40 m, as long as not in the early morning, reasonable estimates of hippo numbers and demographics were achievable. Although we were unable to estimate true accuracy for the drone counts, they were equal to or better than land counts, considered the most accurate method for counting hippos (Karstad & Hudson, 1984; Tembo, 1987; Eksteen, 1993; Kujirakwinja, 2010; Balole-Bwami et al., 2014). Both methods may still underestimate hippo numbers, which cannot be confirmed barring further testing where individuals can be recognised. Further, the models used may inadequately represent the random variation in the data, and results could be improved with larger sample sizes. The effectiveness of flying at a reasonably low height reflects the increased video resolution with decreasing height; at higher heights it is difficult to distinguish and count individual hippos (Figure 4.4). Land counts were possibly more accurate in our site than would be experienced elsewhere because the pod was reasonably habituated to humans and vehicles, given regular visits by tourists. Disturbance of less habituated hippos is likely (Attwell, 1963; Ansell, 1965a; Onyeanusi, 2004), leading to poorer land counts. Further, with increasing pod size and waterbody size land surveys become increasingly difficult, given uniformity of hippo appearance and diving behaviour (Klingel, 2013).

Encouragingly, the drone did not disturb the hippos, although the pod's proximity to an airstrip (1 km) may have habituated the hippos to aerial noises. We surveyed a relatively small pod (maximum 14 individuals), whereas hippo pods can sometimes number in their hundreds (Laws & Clough, 1966; Balole-Bwami et al., 2014). A larger pod size would still be relatively easy to survey using a drone, though it would take longer to count and differentiate demographic groups; time-consuming data processing is a drone cost (Linchant et al., 2015; Callaghan et al., 2018). Increasingly, such data processing could lend itself to automation through machine learning, which has already proven successful at identifying hippos on thermal infrared images (Lhoest et al., 2015), although it may be more difficult using RGB images, given the low colour contrast. Although hippos in larger congregations may be difficult to identify and track on video (Linchant et al., 2018), our video continuously recorded the lagoon, allowing detection of hippos which surfaced momentarily, easily missed on images.

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Measuring an object of known size from the drone showed remarkable consistency between the measured values and the true size, even when off centred. Inaccuracies may be due to unaccounted for variations in flight height or measuring imprecision. The latter would increase when measuring hippos, as the transition between hippos and the water is less distinct. Nevertheless, our results provide a high level of confidence in subsequent measurements of hippos using this technique.

The lower height of the drone allowed the demographic composition of the hippo pod to be effectively estimated, with no significant difference in the percentage of hippos assigned to age classes between land counts and counts at 40 m (Figure 4.6). We identified more juveniles and subadults from our land counts, probably because they were easier to see than from drone footage and were able to be visually assigned to age classes, even when they were partially submerged. This was reflected in the similarity between drone and land counts of adults, given their relatively larger size, and because we classified partially submerged hippos over a certain size as adults on drone images. In addition, the small sample size of juveniles (one) and subadults (two) may have reduced the statistical power of our analyses. Estimating demographic groups in the Democratic Republic of Congo pods had mixed success, with numbers of each age class varying for different flights over the same pod (Lhoest, 2015). This could reflect differential hippo submergence between flights, unsuitable survey time of day, and visual extrapolation of body sizes. Restricting measurements to fully visible hippos reduces the sample size of hippos that can be assigned to age classes, but this can be increased by surveying when hippos are more exposed, or through use of imputation as discussed below.

Early morning was an unsuitable time to effectively survey hippos. This is when hippos were active, continuously diving and surfacing, after returning to the water from nocturnal feeding (Timbuka, 2012; Mekonen & Hailemariam, 2016). This could also be a problem late in the day when there is high activity (Barklow, 2004; Mekonen & Hailemariam, 2016; Prinsloo, 2016), but was not detected because our drone surveys occurred before sunset. Our highest hippo counts were in the late morning and afternoon when hippos usually rested as a group during the middle of the day (Timbuka, 2012; Mekonen & Hailemariam, 2016), often in shallow water with most of their body exposed, making them easy to detect and distinguish (Figure 4.4). The overall highest hippo counts were

from drone flights at 40 m in the late morning and early afternoon, also having the greatest number of surveys which matched the daily maximum. Our avoidance of early mornings for hippo drone surveys runs counter to recommendations from surveys of Democratic Republic of Congo hippo pods (Linchant et al., 2018), although these did not test the effect of time of day. Instead, they argued for the advantages of minimising sun reflection, which we effectively reduced by recording video and surveying when they considered hippos most visible (Delvingt, 1978). Hippo behaviour may differ by region or habitat, we therefore recommend adapting the timing of surveys to when hippo are resting, which may vary in location and time, and could be determined through simple observations, examining existing literature, or local knowledge where possible. Importantly, our surveys also effectively tracked changes in the hippo pod over time, as adults emigrated from the lagoon as it dried, a typical response of hippos to changing water availability (Scotcher, 1978; Smart, 1990). Further, individual hippo detection probabilities could be calculated, which would allow population estimates with confidence intervals, though was not attempted here.

4.4.2 Comparing drone and aerial surveys

Drone surveys provide more accurate hippo counts than comparative aerial surveys. In one lagoon, we counted three times as many hippos using the drone than the aerial survey team detected. Aerial surveys of hippos are routinely flown at around 100 m above ground level at speeds of 160–180 km/hr (Olivier & Laurie, 1974b; Norton-Griffiths, 1978; Bhima, 1996; Kujirakwinja, 2010; Chase et al., 2018), with observers estimating hippo numbers. It is not surprising that these aerial surveys underestimate hippos compared to land (Marshall & Sayer, 1976; Karstad & Hudson, 1984; Balole-Bwami et al., 2014) and drone surveys. There are several clear advantages to drone surveys; they capture data at high resolution, given the relatively low flight height. The slower speed of the drone also increases viewing time and the video allows multiple viewings until an accurate count has been achieved, improving counts when hippos are diving and resurfacing. Further, their noise level is minimal, in contrast to aerial surveys which can disturb hippos and encourage them to submerge (Bouché, 2008). However, there are considerable advantages of the larger spatial coverage possible with aerial surveys, allowing access to areas inaccessible to vehicles and drones. In this study, the aerial survey was completed in approximately 10 minutes, whereas drone surveys took 50 minutes, not including time

spent travelling between launch locations and reviewing videos. Where financial resources are limited the compromise of spending additional time on cheap drone surveys may be acceptable, especially given the minimal training required to pilot small multirotor drones, as opposed to training and hiring an aerial survey team. Inexpensive drones offer considerable promise for effective surveys of hippo pods, although battery life (about 20 minutes flight time) and flight range limits coverage to relatively small areas. If lower accuracy counts are acceptable, flying at a higher altitude allows a larger area to be surveyed (Lhoest, 2015). The utility of drone technology is as an intermediate tool between lower accuracy, high cost, large scale aerial surveys and high accuracy but labour intensive land surveys (Jones, 2003).

4.4.3 Ageing, sexing, and assessing condition with body measurements

It was rare to obtain all seven body measurements for hippos, and the probability of obtaining a measurement varied with body part. Due to their common posture of resting with their head above water whilst submerging their body, head measurements were more frequent, although snout width was often missing. We were generally less confident taking 'width' measurements, and therefore irregularly recorded them, as there were fewer indicators that the body part was fully exposed. In contrast, all three length measurements had obvious indicators: the base of the tail, neck fold, ears, and nostrils. Therefore, missing length measurements are more likely related to hippo posture. There can be a high level of uncertainty and therefore inaccuracy associated with manual detection of the edge of an animals body, especially when water disturbance and turbidity distort the body outline (Christiansen et al., 2016; Burnett et al., 2019). We attempted to minimise this by only measuring hippos when we were confident their bodies were clearly exposed. There is generally good consistency between measurements taken of the same animal by different observers (e.g. sea lions, Hodgson et al., 2020; whales, Soledade Lemos et al., 2020), though it would be valuable to investigate this specifically for hippos, given the abovementioned lack of clear exposure. Back length had the highest correlation with total length, logical given it is the largest measurement included in the total length calculation, but it was also the measurement most often missing. Neck measurements had the lowest correlation (despite neck length's inclusion in the calculation of total length) probably because postural changes of extending and contracting the neck can change both the width and length significantly. Lhoest (2015) also suggested changes in posture and

body spread may have affected body measurements. Multiple imputation allowed us to increase the number of hippos that we could assign ages to threefold. Imputing body length measurements appears to be an acceptable compromise when data are limited. However, if accuracy and completeness are priorities, then multiple flights could be conducted until all lengths measurements for all hippos are obtained.

The body lengths we obtained from drone images fall within the range obtained from culled hippo (Pienaar et al., 1966; Laws, 1968a), providing support to their validity. Our results provide the first classification of the relative age structure of a hippo population (Figure 4.10) not taken from culled hippos, and comparing our results to these studies emphasises their underrepresentation of young hippos (Marshall & Sayer, 1976; Suzuki & Imae, 1996 in Eltringham, 1999). Examining the age classes from the measured data, most hippos were adults, with similar numbers of juveniles and subadults, but the relative percentage of both juveniles and subadults increased based on the imputed data. This shift suggests that younger hippos were disproportionately more likely to be missing measurements, probably given their smaller size and therefore likelihood of being more submerged (also noted when comparing drone and ground counts). The percentage of hippos in each age class, for both the measured and imputed data, fall within the range of values seen elsewhere and therefore seem reasonable (Olivier & Laurie, 1974b; Laker-Ojok, 1985; Tembo, 1987; Smart, 1990; Viljoen, 1995; Viljoen & Biggs, 1998; Brugière et al., 2006; Dibloni et al., 2010; Kanga et al., 2011; Perry, 2015). Further exploration of hippo demographic structure based on these data can be found in Chapter 5.

Male hippos are known for their large size (Klingel, 2013), and this was confirmed in our study, with all body measurements being, on average, bigger for males than females. However, only neck width and snout width were significantly larger once the effect of total size was accounted for. The largest adult male we measured (354.4 cm) was slightly smaller than the maximum size given for adult males (359 cm), as was the largest adult female (338.4 cm, maximum size 343 cm). Bulls spanned a wide age range (7–45 years old), and probably represent hippos that were ejected from pods, were not strong enough to defend territories, or were trying to establish a new territory (Karstad, 1984; Kayanja, 1989; Klingel, 2013). The smallest adult female (as determined by the presence of a juvenile) we measured was four years old (233.6 cm). This supports estimates of age of

puberty as being much earlier (three to four years; Dittrich L., 1976; Graham et al., 2002; Wheaton et al., 2006) than previously suggested (seven to fifteen years old; Laws et al., 1966; Sayer & Rakha, 1974). There were another eight adult females (with juveniles) younger than seven years old. Assigning hippos as male or female based on their spatial relationship to other hippos is not infallible. It is unlikely, though possible, that a male hippo could have a juvenile resting on them, and therefore be incorrectly assigned as female. Likewise, females may distance themselves from their pod prior to giving birth (Ansell, 1965a), which would have them incorrectly assigned as male. Furthermore, given we only assigned solitary hippos as male, and never hippos that occurred within a pod, we indirectly excluded dominant bulls. Peripheral males are smaller than their dominant counterparts (Skinner et al., 1975), suggesting our results are conservative in terms of difference between adult males and females. Further sampling could improve our understanding of the body size/sex relationship, increasing our confidence and ability to determine threshold values above which certain measurements must belong to an adult male. Efforts should be focussed to ensure visual confirmation of sexes, to remove the uncertainty of the current sexing method.

Examining seasonal variations in an animal's body condition allows assessment of how that animal is responding to changes in the environment, as well as its life history (e.g. reproduction) (Christiansen et al., 2016; Burnett et al., 2019). We expected hippos would be in better condition (greater BW:TL ratio) during the wet season, owing to more abundant and better-quality graze (Treydte et al., 2008; Hempson et al., 2015), however adult hippos were leanest in this season. This may be because the wet season is when most female hippos give birth (Laws & Clough, 1966), with poorer body condition potentially due to the cost of reproduction (e.g. lactation), a pattern consistent with that seen in mature whales (Christiansen et al., 2016). Further, hippos may have been wider in the other seasons due to the presence of large pregnant females. Seasonal changes were not apparent when examining indices for other width measurements (snout, forehead, neck), indicating these are not fat deposit areas, and emphasising BW:TL as a valid body condition index for hippos. Similar patterns have been noted in whales, where seasonal changes in condition were not homogenous across the body, with no evidence of a seasonal change for measurements not associated with fat storage (e.g. the head) (Christiansen et al., 2016).

There was excellent agreement when comparing hippos of visually assigned age class/sex to those assigned from drone images. The two confirmed females and two likely females had body measurements consistent with adult females, though these could also describe young males. The known adult male was identified as such from the drone images based on neck and snout measurements. Further, the random removal and subsequent imputation of values for the validation pod demonstrated the validity of the imputed data. One subadult was incorrectly reassigned as a juvenile, as imputation underestimated its total length. For the remaining hippos, the ages based on imputed total length varied from those based on measured length, though the variation was minimal ($\leq$ two years). Inaccurate ageing will mainly occur in adults, as small changes in length correspond to larger changes in age, though the age class of 'adult' is likely to remain.

4.5 Conclusions

Drones are increasingly valuable as a non-invasive monitoring tool for wildlife populations (Linchant et al., 2015; Christie et al., 2016; Lyons et al., 2019), including hippos. Our analyses show that drone data can provide accurate estimates of hippo pods, including their demographic structure. Importantly, they also provides a viable alternative to current survey methods, with low impact on hippos, offering further opportunities to survey in difficult to access areas (Scotcher, 1978; Karstad & Hudson, 1984; Balole-Bwami et al., 2014) and, just as critically, collect these data safely. Such data could be routinely collected in different systems, providing indices of abundances, temporal changes and tracking the long-term status of hippo populations, an imperative given their declining populations in many parts of Africa.

Chapter 5: Seasonal changes in hippo pod size, density, demographic composition, and distribution

5.1 Introduction

The habitat use and social groupings of a species can be affected by changes in the extent, distribution, and quality, and availability of the resources they require to survive (Timbuka, 2012). Investigating these changes gives insight into that animal's biology and ecology, their ability to adapt to more permanent changes in resources, as well as defining areas to prioritise for management (Fryxell et al., 2014). Hippos are a semi-amphibious animal, using waterbodies as daytime refuges (Klingel, 2013). Intuitively, their social dynamics and distribution within the environment will therefore be affected by changes in water availability. Yet, an examination of the literature shows that hippo studies often present data on social groupings (e.g. pod size) without accounting for water availability at the time of study.

Hippo social structure is detailed in Chapter 1, but in summary, hippos occur in pods of variable size and composition, with bulls exhibiting strong territoriality in the water (Karstad & Hudson, 1986; Klingel, 1991b; Eltringham, 1999). Some hippos are solitary, thought to be predominately bulls defending a territory with no conspecifics, but can also be females about to give birth (or have given birth and the calf is hidden) (Ansell, 1965a; Olivier & Laurie, 1974b; Marshall & Sayer, 1976; Bruton, 1978; Karstad, 1984; Klingel, 1991b). Even though there are no strong associations between hippos (except mother and calf), individuals normally return to the same aquatic resting sites following nocturnal feeding , resulting in generally consistent groups within an area (Olivier & Laurie, 1974b; Karstad, 1984; Klingel, 1991b).

The size of hippo pods is less a sociological parameter and more a response to environmental conditions (Klingel, 2013), with the amount of diurnal aquatic habitat observed to affect the number and size of hippo pods and the population density within an area (Olivier & Laurie, 1974b; Karstad, 1984; Klingel, 1991b). When water is limited, density increases as hippos consolidate into large pods into areas of remaining habitat. Hippo surveys are normally conducted at this time of year to take advantage of these

groupings for easier counting (Attwell, 1963; Harrison et al., 2008; Scholte & Iyah, 2016). In contrast, when water is abundant, density reduces as some hippos disperse, often into temporarily flooded wallows and pools (Attwell, 1963; Field, 1970; Karstad, 1984; Klingel, 1991b; Harrison et al., 2008; Zisadza et al., 2010; Perry, 2015; Stommel et al., 2016). Olivier & Laurie (1974) stated that "a true hippo group, which should be defined as the lowest common multiple of the population or minimal social unit, may only become evident when the population has been able to expand itself fully". Multi-tiered hierarchical social structures, with primary stable grouping nested within unstable groupings (which vary for example over seasons), have been identified in elephants (Wittemyer et al., 2005), gorillas (Morrison et al., 2019), and zebras (Rubenstein & Hack, 2004). It is also when water and grass are abundant (typically the wet season), that hippo births peak, though they can give birth throughout the year (Laws & Clough, 1966; Marshall & Sayer, 1976; Graham et al., 2002).

As discussed previously, the Delta is subject to large intra-annual variations in its water availability (Gumbricht et al., 2004b; Milzow et al., 2009a, 2009b; Thito et al., 2016), with peak flooding occurring asynchronously with the local wet season (Wolski & Murray-Hudson, 2008). Therefore, this ecosystem provides a unique environment in which to study the role of water availability on hippo pods. Further, the Delta is a large wetland where lagoons are the only source of open water in many areas, contrasting the riverine or lacustrine habitats that hippos have previously been examined in. The aim of this chapter was to examine how hippo pods (size, density, demographic composition, and distribution) change seasonally with varying water availability. It represents the first investigation of hippo pods in the Delta, providing baseline data on their pod dynamics and habitat choices in this wetland environment. We hypothesised that hippos would occur in smaller and less dense pods in the high flood season (the dry season). We also predicted there to be more newborns in the wet season, despite the low flood levels, due to greater grass availability.

5.2 Methods

5.2.1 Study area

The study area was a 13.83 km^2 section of floodplain within the Abu Concession (Figure 5.1). Where possible, the borders of the study area were aligned with natural boundaries

(e.g. the edges of islands), but the overall extent of the site was chosen as it could be surveyed year-round. This study was conducted between 22 November 2017 and 24 October 2018, occurring over the three seasons detailed in Chapter 1: dry season (med-low flood), wet season (low flood), and dry season (high flood). The dry season (med-low flood) data collection spanned two periods (end of 2017 and end of 2018), with the other seasons occurring between these two periods.
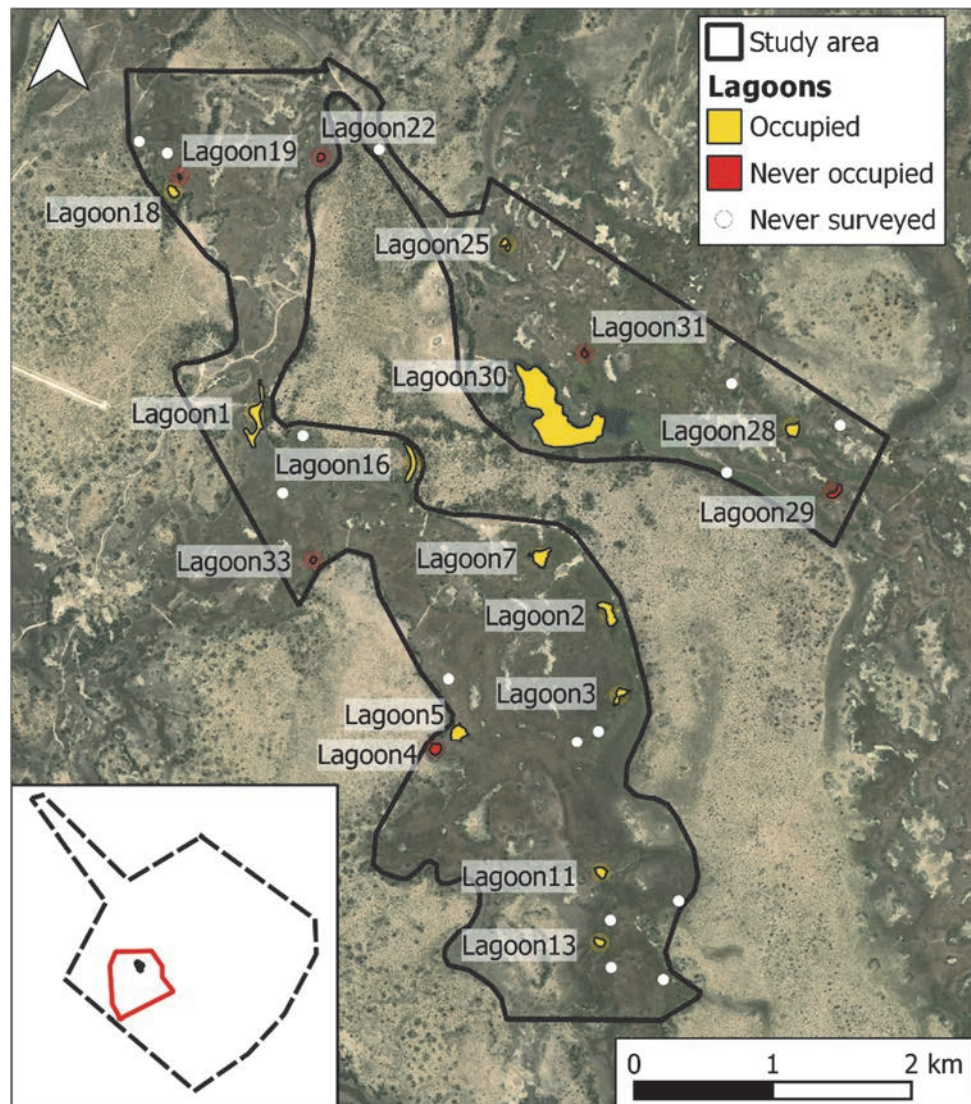
Figure 5.1. Study area and surveyed lagoons (yellow were occupied by hippos at least once; red were never occupied). White points are non-surveyed lagoons (< 0.001 km^2).

5.2.2 Mapping the study area

High resolution (5.1 cm/pixel) orthomosaics (orthorectified image mosaics) of the study area were created from drone images and used to identify and measure lagoons within the area. For each season, orthomosaics were created every three weeks (± one day), resulting

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in three orthomosaics for the wet season (low flood) and dry season (high flood) and four for the dry season (med-low flood) (two in 2017 and two in 2018). The drone used for this study is described in Chapter 4. Details of the collection of drone images and processing into maps can be found in Supplementary Text S5.1.

5.2.3 Hippo counts

Using the drone, lagoons within the study area were surveyed for hippos four times each season, each flight being two weeks (± one day) after the previous. To determine where to survey, we uploaded the most recent orthomosaic into QGIS (QGIS Development Team, 2018) and visually identified all lagoons. During the low flood period, lagoons were easy to identify as they were surrounded by dry floodplain. However, during the high flood season this distinction was less obvious, as most of the study area was flooded. Lagoons were considered distinct from the inundated floodplain as they were areas of open water not covered with aquatic vegetation.

We digitised all lagoons (creating a shapefile) and calculated their surface area. Lagoons with a surface area $< 0.001 \, \text{km}^2$ on the most recent orthomosaic were considered unsuitable for hippos and therefore not surveyed. Amoussou et al. (2006) reported they did not observe hippos' in lagoons $< 0.2 \, \text{km}^2$, therefore our size threshold to disregard lagoons is conservative. The lagoon outlines were imported into the DroneHarmony app, which was used to control the drone flight during surveys. The app calculated transects (as reported in Chapter 4) with a flight speed of 3 m/s, flight height of 40 m (based on optimal flight height for counting hippos described in Chapter 4; Inman et al., 2019), side overlap of 10%, and camera facing directly downward (gimbal angle of -90°). The optimal flight direction calculated by the app was used, except for two lagoons which were elongated and where flight direction was set east to west (Lagoon 1) and south-west to north-east (Lagoon 30) as shorter transects allow easier video review. The drone was operated at a minimum of 100 m from the edge of the lagoons, out of line of sight of the hippos, to avoid disturbing them. If several lagoons were in proximity, they were flown over in the same flight, otherwise the drone was landed and then relaunched closer to the next lagoon. The results of Chapter 4 and Inman et al. (2019) described the optimal time to count hippos as 10:00–14:30. Surveys were conducted between these times, except for lagoons located near tourist lodges (Lagoons 18, 19, 30, and 31) where flights occurred

as close to optimal times as possible, but varied with guest activities. For these four lagoons, drone counts were supplemented with a 15 minute ground count conducted by two observers and the greater count was used. We were unable to conduct this supplementary ground count for Lagoon 31 as it was inaccessible by vehicle.

After all surveys were completed, hippos in each video were counted and measured, and hippos assigned to ages (using imputed data where necessary) as described in Chapter 4. In addition, the position of hippos within lagoons were recorded such that hippos further than 100 m from other hippos were classed as in a different pod, so that it was possible for more than one pod to occur within a lagoon. This has been differentiated below as the "number of hippos in a pod (pod size)" and the "number of hippos in a lagoon". The cut off value of 100 m was taken from the average distance between hippo territories reported in other studies (Klingel, 1991b; Prinsloo, 2016). The sex of individuals was not considered in this chapter due to low numbers of each (see Chapter 4).

5.2.4 Analysis

5.2.4.1 Numbers of hippos in pods (pod size) / numbers of hippos in lagoons

We produced descriptive statistics and frequency distributions for pod sizes and numbers of hippos in lagoons and examined how these changed with season. We calculated values both with and without solitary hippos, to allow comparison of our results with other studies (which vary in their inclusion of solitary animals).

5.2.4.2 Effect of season and surface area on numbers of hippos in lagoons

We investigated how the number of hippos in lagoons was affected by season and lagoon surface area (km^2) (both fixed effects), and their interaction, by fitting a zero truncated generalised linear mixed effects model, with lagoon ID as a random effect to account for multiple flights over the same lagoon, using the glmmTMB function (glmmTMB package; Brooks et al., 2017). While we used the most recent orthomosaic to determine which lagoons to survey, to achieve a more accurate estimate of lagoon surface area on the date of the hippo survey, we calculated the rate of change in surface area between consecutive orthomosaics and extrapolated surface area based on how many days after mapping the hippo survey occurred.

5.2.4.3 Hippo density

Most studies describe hippo density in terms of length of a waterbody, however in the wetland ecosystem of the Delta this is not intuitive to calculate, as lagoons have no obvious length. Therefore, we provided estimates of hippo density in terms of surface area of lagoons (hippos/km^2).

5.2.4.4 Demographic composition of pods

We described the demographic composition of pods in terms of proportion of different age classes, further dividing juveniles into those 0–1 year old (neonates) and those 1–2 years old, and excluding solitary hippos. We investigated the factors affecting the demographic composition of pods by fitting a series of generalised linear models (family binomial, with weights set as the total number of hippos in the pods, glmmTMB function) for each demographic, with proportion of the demographic as the response variable, and season and total pod size, and their interaction, as fixed effects. Proportion was used as opposed to count, to account for overall more hippos in certain seasons.

5.2.4.5 Hippo use and movement between lagoons

We described lagoons that were used by hippos, how often they were occupied, and how the numbers of hippos using specific lagoons changed between surveys. Further, we analysed the effect of season on changes in numbers of hippos using lagoons by calculating the absolute difference between consecutive counts per lagoon (three differences calculated for wet season (low flood) and dry season (high flood) and two differences calculated for dry season (med-low flood)). The effect of season was tested by fitting a constant zero inflated negative binomial generalized mixed effects model (glmmTMB function), with the absolute count difference as the response variable, season as a fixed effect, and lagoon ID as a random effect to account for repeated observations of the same lagoons over time.

For all statistical tests, the significance of the effects was determined using the Anova function (car package; Weisberg & Fox, 2011). Estimates were obtained from the summary function and differences among the levels of the significant effects were tested using Tukey-adjusted post hoc pairwise comparisons using the emmeans and emtrends functions of the emmeans package (Lenth, 2019). Model fits were visually examined via

diagnostic plots (residuals vs. predicted values and QQ-Plots) with the simulateResiduals function of the DHARMa package (Hartig, 2019). These assumptions were always met, requiring no transformations. All statistics were conducted using the R computing environment (version 3.5.2) (R Core Team, 2018). Means are rounded to the nearest integer when discussing numbers of hippos and reported with standard errors.

5.3 Results

5.3.1 Summary of surveys

In total, 12 surveys were conducted over the study area: four in each season (Table 5.1). There were 34 lagoons identified in the survey area: sixteen were never surveyed (always had surface area < 0.001 km^2) and eighteen were surveyed at least once (Figure 5.1). Of these, eleven lagoons were flown in every survey (always had surface area > 0.001 km^2) whilst seven were only occasionally surveyed.

Table 5.1. Number of lagoons surveyed (i.e. had surface area > 0.001 km^2) and occupied by hippos, and number of hippos counted in the study area for the twelve surveys.

Survey date	Season	Lagoons surveyed	Lagoons occupied	Number of hippos
22/11/2017	Dry season (med-low flood)	17	4	46
05/12/2018	Dry season (med-low flood)	17	4	47
17/02/2018	Wet season (low flood)	16	3	59
03/03/2018	Wet season (low flood)	15	7	66
16/03/2018	Wet season (low flood)	14	3	59
31/03/2018	Wet season (low flood)	12	5	62
20/07/2018	Dry season (high flood)	18	5	46
03/08/2018	Dry season (high flood)	17	6	46
17/08/2018	Dry season (high flood)	17	5	41
30/08/2018	Dry season (high flood)	15	3	22
05/10/2018	Dry season (med-low flood)	15	4	24
19/10/2018	Dry season (med-low flood)	15	7	58

The average number of hippos counted in the study area was 48 ± 4.06, and the number of hippos varied between seasons, but also within seasons (Table 5.1). The number of hippos in the area was highest in the wet season (low flood) (62 ± 1.66), followed by the dry season (med-low flood) (44 ± 7.12), with the fewest hippos observed in the dry season (high flood) (39 ± 5.71). There were only two consecutive counts that had the exact same number of hippos (20 July 2018 and 3 August 2018). Lagoon 1 and Lagoon 30 were the only lagoons large enough to contain more than one pod. For Lagoon 1, this occurred four

times (three times in the dry season (high flood) and once in the dry season (med-low flood)), with a maximum of two pods. For Lagoon 30, this occurred in nine out of the twelve surveys (the exceptions were two surveys in the wet season (low flood) and one survey in the dry season (med-low flood)), with the greatest number of pods being five.

5.3.2 Numbers of hippos in pods (pod size) / numbers of hippos in lagoons

Overall average pod size was seven (10 when solitary hippos were excluded from the calculation) and this changed seasonally, being highest in the wet season (low flood), followed by the dry season (med-low flood) and lowest in the dry season (high flood) (Figure 5.2, Table 5.2). This pattern maintained for the number of hippos in lagoons, with an overall average of 10 (13 when solitary hippos were excluded) (Figure 5.2, Table 5.2).

Table 5.2. Average seasonal pod size, numbers of hippos in lagoons (calculated including and excluding solitary hippos), and hippo density within lagoons.

| Season | Pod size | | Number in lagoon | | Density |
	Incl. singles	Excl. singles	Incl. singles	Excl. singles	Hippos /km²
Dry season (med-low flood)	6 ± 1.5	10 ± 2.2	9 ± 2.4	12 ± 2.8	139 ± 53.4
Wet season (low flood)	12 ± 3.9	20 ± 5.8	14 ± 4.5	22 ± 6.3	154 ± 59.9
Dry season (high flood)	5 ± 0.8	6 ± 0.9	8 ± 1.3	9 ± 1.4	140 ± 47.7
Average	7 ± 1.2	10 ± 1.7	10 ± 1.7	13 ± 2.1	144 ± 31.0

Overall, the most frequent pod size and number of hippos in a lagoon was one (33.8% and 25.0% respectively), representing solitary hippos (Figure 5.2). For pod size, this was followed by pairs of hippos, with a general decrease in frequency for subsequent larger pods. However, for numbers of hippos in lagoons, there was a relatively equal frequency of pairs of hippos and pods up to 20, after which there was a reduction in frequency. In the dry season (med-low flood), there was a high proportion of solitary hippos, some within lagoons that contained other hippos (but that were separated by more than 100 m). This was also true of pairs of hippos, where no lagoon had only two hippos within it yet there were pairs of hippos within a pod. In this season, there were some large pods (up to a maximum of 31). In the wet season (low flood), the frequency pattern of pod size and numbers of hippos in lagoons were similar. There were many solitary hippos, numerous pairs of hippos, and the remainder occurred in large groups (maximum pod size 54). In

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the dry season (high flood), there was more variation in the frequency patterns of pod size and numbers of hippos in lagoons, particularly regarding solitary hippos, where there were fewer solitary hippos in lagoons compared to in pods. Compared to the other seasons, there was a more equal spread from solitary hippos up to a maximum pod size of 15, with no large pods.
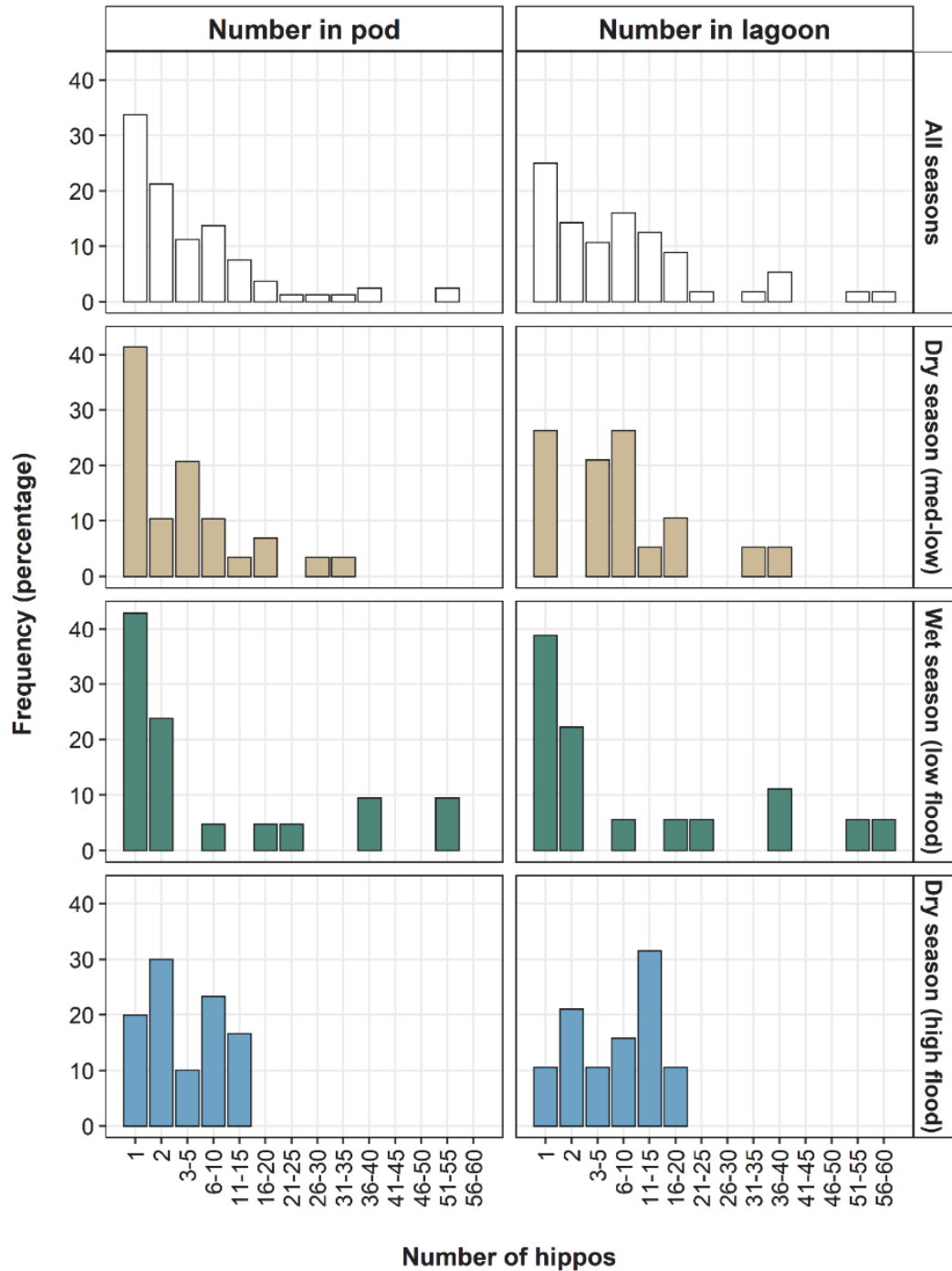
Figure 5.2. Frequency distribution of numbers of hippos in pods (pod size) and within lagoons. Note unequal division of bins to allow individual and paired hippos to be differentiated from pods.

5.3.3 Effect of season and surface area on numbers of hippos in lagoons

There was a significant interaction between season and surface area on the number of hippos in lagoons ($\chi^2(2) = 17.135$, $p < 0.001$) (Figure 5.3). The relationship between surface area and number of hippos was positive in all seasons, but the regression was significantly steeper in the wet season (low flood) than the dry season (med-low flood) ($p = 0.018$) and dry season (high flood) ($p < 0.001$), with some evidence of difference between the dry season (high flood) and dry season (med-low flood) ($p = 0.096$) (Figure 5.3). In the dry season (med-low flood), the greatest numbers of hippos occurred in larger lagoons, but some smaller lagoons also had moderate numbers. In contrast, in the wet season (low flood), hippo pods occurred in large groups in the largest lagoons, with solitary hippos occupying smaller lagoons than in other seasons. In the dry season (high flood), there was no obvious relationship between numbers of hippos within lagoons and surface area, with similar numbers of hippos occurring in both small and large lagoons. The smallest lagoon occupied by a hippo was 0.0016 km^2 (a solitary hippo) and the largest unoccupied lagoon was 0.1640 km^2, with the next largest being 0.0167 km^2.
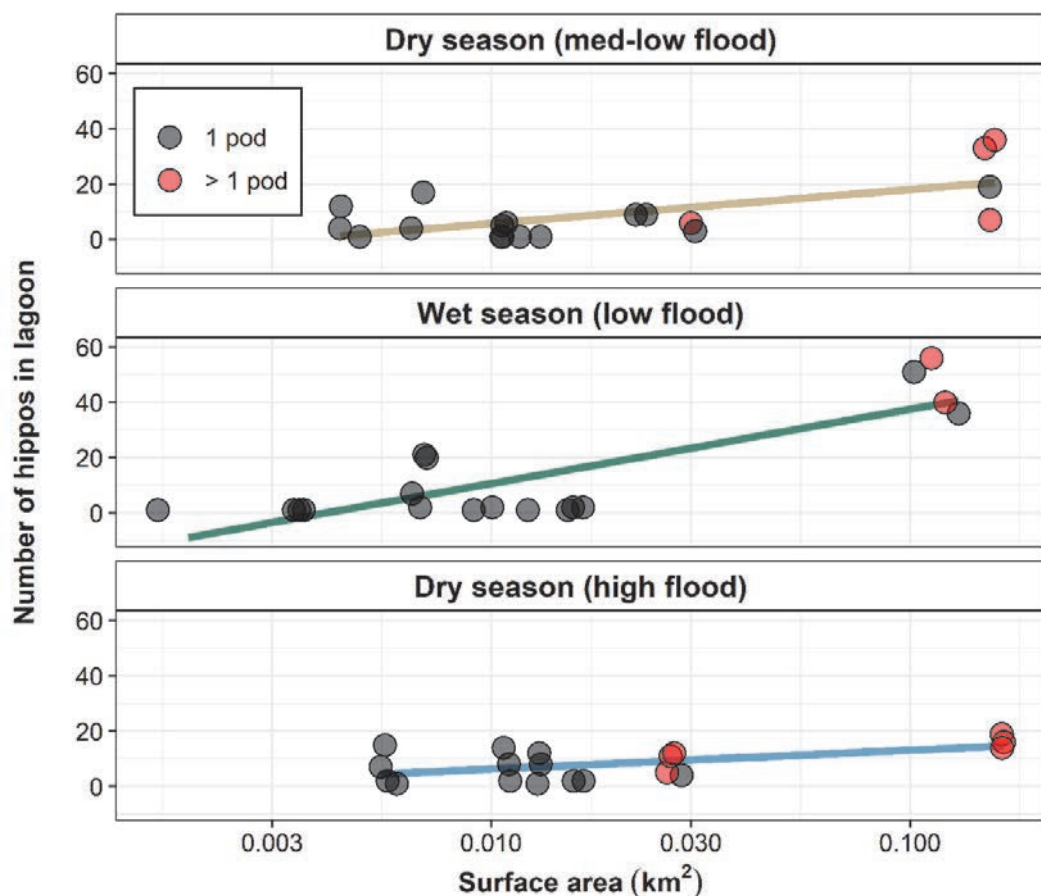
Figure 5.3. Relationship between surface area (log scale) and season on numbers of hippos in lagoons (colour of circles depicts number of pods in lagoons).

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5.3.4 Hippo density

The average density of hippos in lagoons was 144 ± 31.0 hippos/km^2 (Table 5.2). Density was lower in the dry season (med-low flood) (139 ± 53.4 hippos/km^2) and the dry season (high flood) (140 ± 47.7 hippos/km^2) and higher in the wet season (low flood) (154 ± 59.9 hippos/km^2) (Table 5.2). Given the overall study area was approximately 13.83 km^2, and on average 48 hippos were counted, this equates to an average 3.47 hippos/km^2 of floodplain.

5.3.5 Demographic composition of pods

The composition of an average hippo pod was 62.6% adults, 9.2% subadults, 7.7% juveniles [4.4% 1–2 years old, 3.2% 0–1 year old), with the remaining 20.5% as unknown. The proportion of adults was not significantly related to pod size ($\chi^2(1) = 0.306$, $p = 0.580$), season ($\chi^2(2) = 1.855$, $p = 0.396$), or their interaction ($\chi^2(2) = 0.333$, $p = 0.847$). The proportion of subadults and juveniles was significantly related to pod size (subadults, $\chi^2(1) = 8.873$, $p = 0.003$; juveniles, $\chi^2(1) = 4.828$, $p = 0.028$), with a higher proportion of both in larger pods. Season did not affect the proportion of subadults ($\chi^2(2) = 2.212$, $p = 0.331$) and juveniles ($\chi^2(2) = 4.139$, $p = 0.126$), nor did the interaction between season and pod size. There was no significant effect of pod size on the proportion of neonates ($\chi^2(1) = 0.721$, $p = 0.396$) but there was a significant effect of season ($\chi^2(2) = 6.047$, $p = 0.048$), with a higher proportion in the wet season (low flood) than the dry season (med-low flood) ($p = 0.043$), but not the dry season (high flood) ($p = 0.663$). All pods with 15 or more hippos were nursery groups (i.e. had juveniles or neonates). There were several smaller pods (< 15) that appeared to be non-nursery groups because they had no juveniles or neonates (some had subadults), but these also had unidentified hippos that may have been juvenile/neonates.

5.3.6 Hippo use and movement between lagoons

Of the eighteen lagoons that were surveyed, twelve were occupied by hippos at least once, and six were never occupied (Figure 5.4). The average surface area of the twelve occupied lagoons ranged from 0.003–0.146 km^2 (Figure 5.4) and from 0.001–0.004 km^2 for the six unoccupied lagoons (not shown in Figure 5.4). The least number of lagoons occupied during a survey was three (this occurred on 17/02/2018, 16/03/2018, 30/08/2018) and the most was seven (3/03/2018 and 19/10/2018) (Figure 5.4, Table 5.1). Zero counts were

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assumed for Lagoon 18 for two surveys (16/03/2018 and 31/03/2018) and Lagoon 25 for one survey (30/08/2018), as they were < 0.001 km^2 and therefore were not surveyed. There were no lagoons that were occupied in every survey, though Lagoon 1 and Lagoon 30 were occupied in all but one (Figure 5.4). For 11 out of the 12 surveys, Lagoon 30 had the most hippos.

There were no consecutive counts within a season where the number of hippos in specific lagoons remained the same. The largest change in the number of hippos in a lagoon in consecutive counts was 29, where the population in Lagoon 30 went from seven to 36 within two weeks in the dry season (med-low flood). The change in the number of hippos in lagoons between consecutive counts was significantly related to season ($\chi^2(2) = 8.036$, $p = 0.018$), being highest in the dry season (med-low flood) followed by the dry season (high flood), with lowest rates in the wet season (low flood). The rate of change was significantly different between the dry season (med-low flood) and the wet season (low flood) ($p = 0.020$).
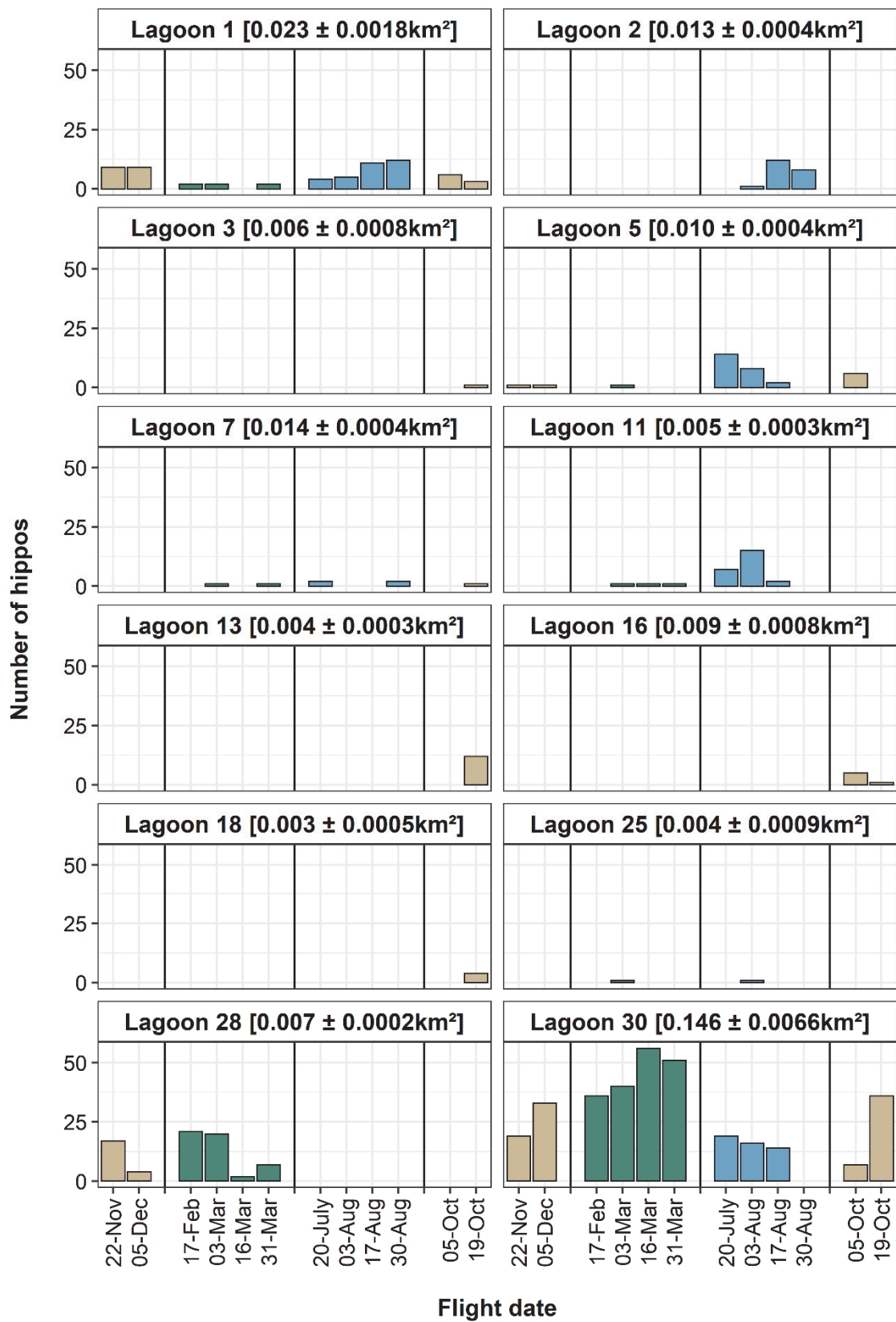
Figure 5.4. Counts of hippos in lagoons with average ± SE surface area of lagoons. Colours represent seasons: beige is dry season (med-low flood), green is wet season (low flood), blue is dry season (high flood).

5.4 Discussion

The results of this study show that hippos in the Okavango Delta exist in dynamic pods, with their size, density, demographic composition, and distribution varying both within and between seasons, following patterns reported elsewhere. During the low flood season, there were more hippos in the study area, and they occurred in larger pods and higher densities, being forced to consolidate on what minimal water was still available (Attwell, 1963; Karstad & Hudson, 1984; Stommel et al., 2016). There was a particular preference for larger lagoons in this season, as they acted as important refuges for large aggregations of hippos when other lagoons in the study area were rapidly drying (Laws & Clough, 1966; Pienaar et al., 1966; Field, 1970; Olivier & Laurie, 1974b; Karstad, 1984; Prinsloo, 2016; Stommel et al., 2016). As the majority of hippos abandoned these less-desirable lagoons, bulls were left alone in their territory, resulting in a higher proportion of solitary hippos in the low flood seasons (also observed by Viljoen, 1995; Brugière et al., 2006). As water reduces, hippos face a choice; they may move into a crowded lagoon with sufficient water, but that has potentially high levels of aggression and disease transmission, or remain in a drying lagoon and risk complete water depletion (Viljoen & Biggs, 1998; Timbuka, 2012). Further, bulls entering a new territory will have to become subordinate to another male (Karstad & Hudson, 1986). In this study it appeared that bulls preferred to remain in less desirable lagoons, perhaps as the mosaic landscape meant there was never a great distance to another lagoon. Further, the high percentage of solitary animals suggests that bulls prefer a solitary existence (also noted by Karstad & Hudson, 1986), though there were some bachelor groups.

When water was abundant, hippos remaining in the study area dispersed into lower density, smaller pods as predicted, having a more even distribution across a broader range and size of lagoons. Similar patterns of redistribution have been observed in other populations (Field, 1970; Olivier & Laurie, 1974b; Kayanja, 1989; Eltringham, 1999; Timbuka, 2012; Klingel, 2013). Further, there were multiple separate pods within some of the larger lagoons, potentially indicating the territorial structure of bulls within this wetland ecosystem. In small lagoons, the whole waterbody probably represents one territory, but if a lagoon is large enough it may contain multiple bull territories. In the high flood season, hippos never aggregated in the large pods (50 hippos) recorded in the low flood season, instead occurring in smaller pods (up to a maximum of 15). This

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suggests this is their preferred state (Attwell, 1963; Scotcher, 1978), probably because it leads to reduced touching/body contact, disease incidence, and aggression (Timbuka, 2012). Larger subadult males are particular likely to disperse when water is abundant, with home ranges three times larger than small subadults and dominant bulls in these seasons (Stears et al., 2019).

Given changes in hippo densities and groupings are mainly a result of redistribution between sections as the environment changes (Viljoen & Biggs, 1998), increases in immigration and emigration will tend to occur at times with the highest fluctuation in resources (Olivier & Laurie, 1974b; Timbuka, 2012; Stommel et al., 2016). In the Delta, the most dramatic change in resources occurs when the annual flood arrives, transforming the area from dry to flooded in a short period of time. This is when the greatest fluctuations in pods are likely to occur as the hippos use the abundant water to re-establish home ranges and territories. Another significant period of change in the Delta is the phase where the floodwaters begin to recede (represented in this study as the dry season (med-low flood)). This season had the highest measured rate of change compared to the other seasons, possibly because as the Delta began to dry, most hippos moved out of ephemeral lagoons. This season experiencing the highest rate of change provides further strong evidence of hippo pod dynamics being a mechanism of changing water availability. There was a lower rate of change in the dry season (high flood) and wet season (low flood), probably because the water level (whether high or low) was already established, staying relatively consistent throughout this period and hippos had already settled into their lagoons or moved. Not all the movements into/out of lagoons were a pattern consistent with changing water over the season. For example, in the dry season (high flood) the number of hippos in Lagoon 11 increased from one count to the next, before falling again in the next count. Compare this to Lagoon 1 in the dry season (high flood), which had a successive increase in hippos as the season progressed, as predicted.

Female hippos can have home ranges occurring over multiple bull territories, and there are no consistent relationships between hippos (except mother and calf), however its thought that most hippos return to the same general area after nocturnal feeding leading to generally consistent groupings in certain locations (Olivier & Laurie, 1974b; Karstad, 1984; Klingel, 1991b; Prinsloo, 2016). Further, a core group of hippos will normally

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remain together when migrating to new diurnal sites (Karstad, 1984). In this study, all seasons were characterised by near constant short time-frame changes of groupings within lagoons, further emphasising the dynamic nature of hippo pods (though our inability to recognise individuals reduced our ability to ascertain the extent of this). In other studies, large changes in the number of hippos in pools as seasons progress are predominately females or subadult males moving from pool to pool upstream trying to find a suitable permanent location as the river dries (Stommel et al., 2016; Stears et al., 2019), with dominant bulls retaining similar home ranges throughout the year, even with changes in water availability (Stears et al., 2019). Movement between lagoons to find long-term habitat may explain the results of this study, however a dispersal pattern was difficult to detect due to the mosaic nature of the landscape. Further, rather than returning to a general section of river, solitary grazing hippos may return to one of several lagoons within their home range, meaning home ranges appear more random and variable than riverine or lacustrine hippos, and are less likely to lead to consistent groups. Individuals would need to be tracked to understand hippo home ranges in the Delta. It is probably that hippos are taking advantage of the resources available at any point time, with their individual needs, rather than territories, dictating their lagoon choice (Karstad, 1984; Karstad & Hudson, 1986; Prinsloo, 2016).

Hippos are known to have high site selectivity, choosing daytime living spaces that have favourable combinations of resources (Olivier & Laurie, 1974b; Viljoen & Biggs, 1998; Timbuka, 2012; Stommel et al., 2016; Prinsloo et al., 2020). Therefore, it is unsurprising that in general, larger lagoons that provided more space contained more hippos, with small lagoons generally being empty or occupied by solitary animals (also reported by Stommel et al., 2016). Within the study area, Lagoon 30 was substantially larger than all other lagoons (six times the size of the next largest), and this was reflected in the number of hippos occupying it. The second largest (Lagoon 1) was also occupied most of the year, but with less hippos. Scotcher (1978) noted that where a pan was large and provided habitat year-long, there were minimal changes in the number of hippos using it. Despite remaining the largest lagoon (by surface area), hippo numbers in Lagoon 30 were not consistent. Perhaps it was too shallow or deep in certain seasons to provide habitat for all hippos, or other factors (e.g. human disturbance) may have discouraged some hippos using this lagoon.

There were notable exceptions to the positive relationship between lagoon surface area and number of hippos, with some small lagoons having relatively large pods (e.g. Lagoon 28) and vice versa (e.g. Lagoon 7). Further, there were lagoons of similar sizes (e.g. Lagoon 3 and Lagoon 28) and yet were not equally occupied by hippos. Unexpectedly high numbers of hippos in what appeared to be relatively small areas has been reported elsewhere (Clough, 1967) and even when there is sufficient habitat available, hippos will often remain in a small selection of pools, not always preferring the largest (Timbuka, 2012). Water depth and bank geomorphology can be important drivers of hippo habitat selection (Clough, 1967; Laws, 1968b; Olivier & Laurie, 1974b; Bruton, 1978; Scotcher, 1978; Klingel, 1991b, 2013; Viljoen & Biggs, 1998; Timbuka, 2012; Prinsloo et al., 2020), but were not investigated in this study. It is possible that some smaller lagoons were deep or had more favourable geomorphology and were therefore preferred by hippos. Further, grass availability and human disturbance may also be important for habitat selection (Karstad & Hudson, 1986).

As hypothesised, we recorded a higher proportion of neonates in the wet season, suggesting a spike in hippo births, also reported in Zambia, Uganda, and South Africa (Laws & Clough, 1966; Clough, 1967; Marshall & Sayer, 1976; Smuts & Whyte, 1981). In contrast to these countries, in the Delta, this is the season with the least water, suggesting birth timing is more related to the availability of nutritious graze. The higher number of neonates may be the reason there were more pairs of hippos in the wet season (low flood) and the following dry season (high flood), but rarely in the dry (med-low flood season), as female hippos are known to separate from the pod prior to giving birth and then for some weeks after remain separate with their calf (Attwell, 1963; Ansell, 1965a; Laws & Clough, 1966; Clough, 1967; Field, 1970; Olivier & Laurie, 1974b; Bruton, 1978; Karstad, 1984; Klingel, 1991b). This was also possibly why there was no significant relationship between pod size and proportion of neonates. In contrast, there were significantly more juveniles and subadults in larger pods, which has also been observed elsewhere (Stommel et al., 2016). These large nursery groups may provide protection for younger hippos (Chansa et al., 2011a). The relative abundance of juveniles can be used to assess population density, as hippo conceptions slow when conditions are unfavourable or a population is overcrowded (Attwell, 1963; Sayer & Rakha, 1974; Viljoen & Biggs, 1998; Lewison, 2002; Kanga et al., 2011). However, comparing values

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of juveniles from multiple studies is difficult due to the high level of variability in the methods used to classify juveniles, especially as the method is often not even specified. The proportion of juveniles we recorded (7.6%) is much lower than reported values for some populations (20–35%) (Olivier & Laurie, 1974b; Laker-Ojok, 1985; Brugière et al., 2006; Perry, 2015), although it is within range of that reported elsewhere (4–10%) (Tembo, 1987; Smart, 1990; Viljoen, 1995; Viljoen & Biggs, 1998; Dibloni et al., 2010; Kanga et al., 2011). Given that the population is growing (see Chapter 3), such a low proportion of young animals would imply a much higher adult survival rate that has been estimated (Lewison, 2007). There were approximately 20% of hippos in pods that could not be aged and we know that juveniles are easily missed during counting (Tembo, 1987), even using the drone (Inman et al., 2019), and therefore the data presented here are likely underestimates.

Hippo densities vary dramatically throughout their range, from < one hippo/km in very small hippo populations (Viljoen, 1980; Brugière et al., 2006) to densities as high as 45–55 hippos/km in areas renowned for their large populations (Queen Elizabeth National Park in Uganda, Luangwa River in Zambia) (Anon, 1954 in Attwell, 1963; Chansa et al., 2011). Here, we report density as hippos/km^2 and therefore are limited with estimates to compare to, relying on studies that provide the width of the surveyed area or the total surface area. The density we recorded in the Delta (139–154 hippos/km^2) appears to represent moderate hippo density, similar to values reported in the wet season in Mara River in Kenya (113–221 hippos/km^2) (Karstad, 1984). In the dry season, hippo density in the Mara River was as high as 518 hippos/km^2 (Karstad, 1984), whereas densities were lower in Sierra Leone (19 hippos/km^2) (Perry, 2015) and South Africa (1–77 hippos/km^2) (Prinsloo, 2016). However, comparing densities of hippos between regions may have limited value, as the available habitat varies with different ecosystems (Olivier & Laurie, 1974b; Karstad, 1984), and this difference can be particularly stark comparing a wetland to riverine or lacustrine ecosystems. Group size is probably a more useful index (Laws & Parker, 1968 in Olivier & Laurie, 1974), but even this is limited when comparing values taken when the amount of water at the time of data collection differed. The overall average pod size of hippos in this study was seven and ten hippos, including and excluding solitary hippos, respectively. This is within range (though slightly lower) of average pod size reported in other countries, with most between 8–13 hippos (Attwell,

1963; Ansell, 1965a; Laws & Clough, 1966; Field, 1970; Sayer & Rakha, 1974; Viljoen, 1980; Karstad, 1984; Karstad & Hudson, 1984; Ngog Nje, 1988; Zisadza et al., 2010; Prinsloo et al., 2020). In areas known to have small hippo populations, averages are lower (3–4 hippos) (Roth et al., 2004; Brugière et al., 2006) and during periods with exceptionally low water levels and in areas where crowding is known to occur, larger average group sizes (20–40 hippos) are recorded (Olivier & Laurie, 1974b; Kanga, 2011). The maximum pod size we recorded (54 hippos) was low compared to other studies, with maximum pod sizes of 100–200 hippos (Attwell, 1963; Laws & Clough, 1966; Clough, 1967; Olivier & Laurie, 1974b; Ngog Nje, 1988; Klingel, 1991b; Kanga et al., 2011; Stommel et al., 2016). Further, the average number of solitary hippos (assumed as bulls) we recorded (33.8% of the population) is higher than most records (2–10%) (Attwell, 1963; Ansell, 1965a; Viljoen, 1980; Smart, 1990; Brugière et al., 2006; Zisadza et al., 2010), although there are a few studies with similar values of 20–35% (Ngog Nje, 1988; Viljoen & Biggs, 1998).

5.5 Conclusions

In this study, hippo pods were moderate in size (with low maximum values) and density, and there were a high number of solitary hippos, all of which suggests hippos in the Delta are not subject to overcrowding or suppression. Nonetheless, the pods exhibited dramatic seasonal fluctuations, possibly due to the high variability of water in the Delta. The extent to which hippos disperse/consolidate in reaction to increases/decreases in water varies in different ecosystems, with rates of change related to the stability and general abundance of water (Karstad, 1984; Stears et al., 2019). For example, Taylor (1975) saw no large-scale seasonal changes of areas used by hippos, perhaps as a result of the less dramatic seasonal changes in water availability of lake systems (Olivier & Laurie, 1974b). Laws (1968b) reported that hippos take advantage of changed situations when they are beneficial, and this was observed during this study. Water availability is an apparent cause of distribution changes in a hippo population and given this, hippo research must consider season of data collection (Olivier & Laurie, 1974b).

Chapter 6: Hippo behaviour, diurnal and nocturnal activity budgets, social grouping, and habitat use

6.1 Introduction

Animal activity budgets describe a series of trade-offs, where time spent doing one activity necessarily restricts an individual's ability to perform another beneficial activity (e.g. Hamel & Côté, 2008). Investigating these activities, particularly how much time is dedicated to each, allows us to understand how and where an animal chooses to spend its time, giving insight into their energy requirements and preferred habitat (Timbuka, 2012; Prinsloo, 2016; Rimbach et al., 2016; Pęksa & Ciach, 2018; Fraser et al., 2019). Using this information, we can calculate carrying capacities, develop priorities for habitat protection, select suitable areas for reintroduction programs (Timbuka, 2012; Majolo et al., 2013; Stears et al., 2019), and even ensure appropriate habitats are provided to captive animals (Blowers et al., 2012). Examining how animals respond to different environmental conditions gives insight into their ability to adapt to manmade or natural changes to their habitat (Timbuka, 2012; Owen-Smith & Goodall, 2014; Rimbach et al., 2016; Pęksa & Ciach, 2018). A species' behaviour can vary due to a range of variables: population density, time of day, season, moon phase, climate/weather, resource availability, group composition, predation risk, inter-individual variation (e.g. personality), human disturbance, age, and sex (Timbuka, 2012; Majolo et al., 2013; Navarro-Castilla & Barja, 2014; Owen-Smith & Goodall, 2014; McQualter, 2016; Mekonen & Hailemariam, 2016; Rimbach et al., 2016; Pęksa & Ciach, 2018; Fraser et al., 2019). Sampling over a range of these factors allows a more comprehensive understanding of that species' activity budget; a species' behaviour should not be generalised from minimal data.

Our knowledge of hippo behaviour is limited, particularly regarding their activity budgets (Eltringham, 1993a). This is due to the difficulty in making extensive observations on them: they are primarily nocturnal, they are aquatic, dangerous, lack obvious individually identifiable features, and often inhabit difficult to access areas (Karstad, 1984; Barklow, 1997; Krueger, 1997; Eltringham, 1999; Lewison & Carter, 2004; Blowers et al., 2010; Timbuka, 2012; Maust-Mohl et al., 2015; Prinsloo, 2016). To date, our understanding of diurnal hippo activity budgets is taken from four observational studies (Bouché, 2004b;

Timbuka, 2012; Mekonen & Hailemariam, 2016; Prinsloo, 2016), conducted in the Ivory Coast, Tanzania, Ethiopia, and South Africa, with varying levels of sampling intensity and detail. In addition, the 24-hour behaviour of hippos in Kenya was derived from GPS tag movement data, although the explicit purpose of this work was not an activity budget study (Nuñez, 2017). Social behaviour is one of the better understood behaviours of hippos due to research undertaken in Uganda in the 1970s (Klingel, 1991a, 1991b, 2013), and there have been studies over short periods of the day or on specific social behaviours of interest (e.g. communication, aggression) (Karstad, 1984; Karstad & Hudson, 1986; Barklow, 2004; Blowers, 2008; Blowers et al., 2010; Maust-Mohl et al., 2015). In addition, there are incidental references to hippo behaviour in studies focussed on hippo populations (e.g. Viljoen & Biggs, 1998), ecology (e.g. Harrison et al., 2007), physiology (e.g. Luck & Wright, 1964), and anatomy (e.g. Laws et al., 1966).

What is lacking from most hippo activity studies is how behaviour changes over temporal and spatial scales, because the authors have tended to collect data during short periods of the year or used data aggregated across months, which omits potential seasonal variation (Bouché, 2004a; Mekonen & Hailemariam, 2016; Prinsloo, 2016; Nuñez, 2017), and/or have restricted their studies to a single pod (Prinsloo, 2016). Timbuka (2012) provides the most thorough investigation into hippo activity budgets, sampling five pods over a full year, analysing differences between the wet and dry seasons. This study focused on how hippos responded to variations in water availability, predicting how hippo may react to landscape-scale changes. Previous authors looked at different focal activities but all recorded resting, feeding, and moving (Timbuka, 2012; Mekonen & Hailemariam, 2016; Prinsloo, 2016; Nuñez, 2017). Timbuka (2012) did not record aquatic movement as an activity, despite its prevalence (Blowers et al., 2012; Mekonen & Hailemariam, 2016), Bouché (2004a) does not describe the activities he recorded, and Nuñez (2017) could not differentiate between the various aquatic activities. The observational studies all prioritised the detailed sampling of social behaviours (e.g. yawning, vocalisations, ear-flicking), which typically represents only a small portion of the activity budget of hippos. They further generalised the main activities: for example, all four studies recorded resting without specifying if it occurred in the aquatic or terrestrial habitat, resulting in a superficial understanding of hippo habitat use. Even though hippos are primarily nocturnal, most studies have not attempted to investigate hippos' nocturnal activity

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budgets (Timbuka, 2012; Mekonen & Hailemariam, 2016; Prinsloo, 2016), or their attempts to do so were unsuccessful (Bouché, 2004a). By extracting data from GPS tags, without the need to observe hippos directly, Nuñez (2017) was able to capture nocturnal behaviour. To understand and characterise fully hippo behaviour, food requirements, and ecology, it is necessary to study their nocturnal behaviour because the majority of their energetic activities occur at night (Bouché, 2004a; Lewison & Carter, 2004; Prinsloo, 2016).

The aim of this study was to describe the 24-hour activity budget of hippos and investigate how this changed temporally, spatially, and seasonally in variable landscapes. We aimed to improve upon the currently limited knowledge of hippo behaviour and activity budgets, including nocturnal activity, recording the spatial distribution of activities and noting social groupings associated with activities. We also provide the first hippo behavioural data for Botswana.

6.2 Methods

6.2.1 Study area

This study was conducted between 14 August 2017 and 11 October 2018 in five areas (Table 6.1); Abu1 (-19.4181°S, 22.5676°E) and Abu2 (-19.4186°S, 22.6046°E) within the Abu Concession; Chobe1 (-17.8282°S, 25.0293°E) and Chobe2 (-17.8339°S, 25.1025°E) within Chobe National Park; and Chobe3 (-17.7857°S, 25.1889°E) within the township of Kasane (Figure 6.1). Behavioural data were collected for each area over the three seasons described in Chapter 1: wet season (low flood), dry season (high flood), and dry season (med-low flood).

Abu1 occurred close to a well-used bridge and was frequently visited by tourists from nearby lodges. In contrast, Abu2 was not adjacent to a main thoroughfare so, whilst the lagoon was sometimes visited, this did not occur to such an extent as Abu1. In Chobe National Park, Chobe1 and Chobe2 were well visited by tourists. Chobe3 was located in the township of Kasane, on a section of river adjacent to an undeveloped plot of private land but was flanked to the east by farms and to the west by a shopping complex. At the beginning of the period of data collection, the property was unfenced and was frequented by people, but after fencing in October 2017, human visits to the property were rare.
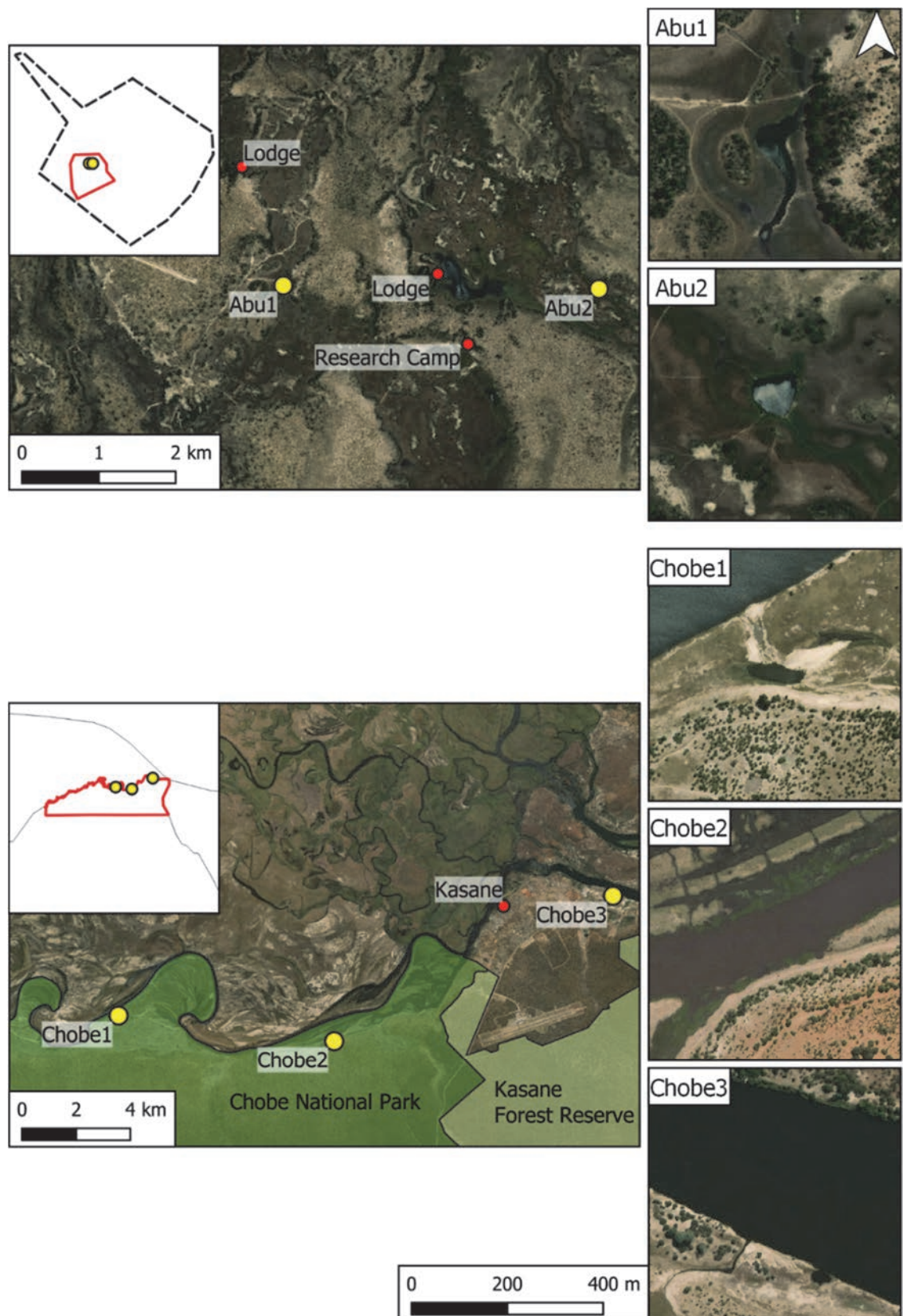
Figure 6.1. Study areas within the Abu Concession and Chobe District (Kasane township and Chobe National Park).

Table 6.1. Data collection dates, average daily temperatures (range in brackets) and total rainfall for each study area for each season. Weather variables correspond to exact dates of data collection.

Season	Region	Dates	Average max temp (°C)	Average min temp (°C)	Rainfall (mm)
Dry season (med-low flood)	Chobe	Aug–Oct 2017 Sept 2018	33.2 (28.6–36.6)	13.5 (6.2–21.2)	0.0
	Abu	Oct 2018	35.2 (34.4–36.0)	11.9 (8.9–16.0)	0.0
Wet season (low flood)	Chobe	Jan 2018	33.1 (28.4–36.4)	19.3 (17.2–21.3)	73.5
	Abu	Feb–Mar 2018	29.8 (23.0–33.5)	18.9 (16.6–20.9)	54.9
Dry season (high flood)	Chobe	Apr–May 2018	29.0 (27.4–30.5)	11.9 (7.6–17.9)	0.0
	Abu	Jul–Aug 2018	31.8 (28.2–36.1)	7.4 (3.2–11.8)	0.0

6.2.2 Behavioural data

6.2.2.1 Sampling technique and schedule

Wherever possible observations were collected in sessions spanning either a full day or a full night. Diurnal sessions began at, or soon after, sunrise and concluded before sunset, while nocturnal observations began just before sunset and concluded after sunrise. The exact start and end times of the sessions varied throughout the year with changing sunrise/sunset times. In Chobe, days were shortest in the dry season (high flood) (on average 06:36–17:59), followed by the dry season (med-low flood) (06:18–18:14), and then the wet season (low flood) (06:00–19:01). In Abu, days were shortest in the dry season (high flood) (06:54–18:16), followed by the wet season (low flood) (06:30–18:49), and then the dry season (med low flood) (06:05–18:30). Observations commenced ten minutes after arrival, the delay in recording to allow for any possible disturbance caused by the vehicle's approach to be minimised.

Observations were conducted from a vehicle in an advantageous position with a good field of vision, whilst remaining at a distance that did not disturb the hippos. For diurnal observations, it was rare that all hippos moved out of sight but when this occurred the vehicle was repositioned to afford "best view". Before sunset, the hippos were most often located in the water but, after sunset, hippos tended to move away in the water or leave the water either singularly or in small groups. Observations continued in the original position until the last of the hippos left the water or moved away. Hippos were then followed by vehicle keeping as many individuals in sight as possible.

Behavioural data were collected using the instantaneous scan sampling technique (Altmann, 1974) at five minute intervals for the whole session with the activity of all visible hippos recorded. Hippos were assigned one of nine mutually exclusive (i.e. no two could occur at the same time) activities (Figure 6.2, Table 6.2). Along with the activities, the age class and sex of each individual hippo was recorded, based on the descriptions given in Chapters 1 and 4. Age classes and sexes were only assigned when the observer was confident in the classification, otherwise the hippo was recorded as unknown. Therefore, each hippo was assigned to one of six categories: adult female, adult male, adult unknown, subadult, juvenile, or age unknown. In addition, every thirty minutes (including the first and last scan of the session), along with their activity, the observer recorded the position of hippos relative to each other. Hippos that were within three adult hippo lengths (approximately nine metres) of other hippos were recorded as being within the same close association ('group'), doubling the highest average inter-individual distance between hippos in a pod (Timbuka, 2012), and therefore allowing a generous estimate of grouping. Not all hippos were visible during every scan as they may have been submerged or moved out of the area. Bushnell Excursion binoculars (8 x 42, FOV 426 ft) were used to assist observation when hippos were out of close observational distance. To assist nocturnal observations, a handheld red-filtered spotlight and a night scope (Night Owl Explorer Pro^{TM} NOCX5) were used.

On land, hippos were often easily disturbed by the presence of the vehicle. This, as well as their tendency to disperse whilst grazing and the reduced visibility at night, resulted in most nocturnal observations occurring on less individuals. It was common for the observer to lose sight of all hippos at night. If this occurred, the observer would remain in the same location for at least two scans (i.e. ten minutes) to confirm the hippos were not underwater or behind vegetation. If it was believed there may still be hippos within the area (e.g. either from direct observation or hearing vocalisations or movement) the observer would remain in place until no further sign of hippos could be heard or seen. The observer would then drive to relocate them, starting in the area where they were last observed and expanding the search area until animals were found. When a hippo was located, the observer waited ten minutes to resume scans to ensure any disturbance was minimised. This process of losing sight of hippos and driving to locate new hippos was a common occurrence at night.

Table 6.2. Description and codes of activities assigned to all visible hippos.

Activity and code	Description
Resting deep aquatic (RDA)	Not moving, more than 2/3 of body submerged in water
Resting shallow aquatic (RSA)	Not moving, less than 1/3 of body submerged in water
Resting terrestrial (RT)	Not moving on land
Moving aquatic (MA)	Walking, porpoising, diving, or surfacing in the water without any other target activity (e.g. feeding)
Moving terrestrial (MT)	Moving on land without any other target activity (e.g. feeding)
Feeding aquatic (FA)	Consuming vegetation growing in water
Feeding terrestrial (FT)	Consuming vegetation growing on land
Social (S)	Any social behaviour included yawning, mating, fighting, playing, tail paddling, dung paddling. Vocalisations were noted but not recorded as an activity as it was difficult to distinguish which hippos were vocalising
Other (X)	Unknown behaviour or one that did not fit into other categories. A brief description was recorded
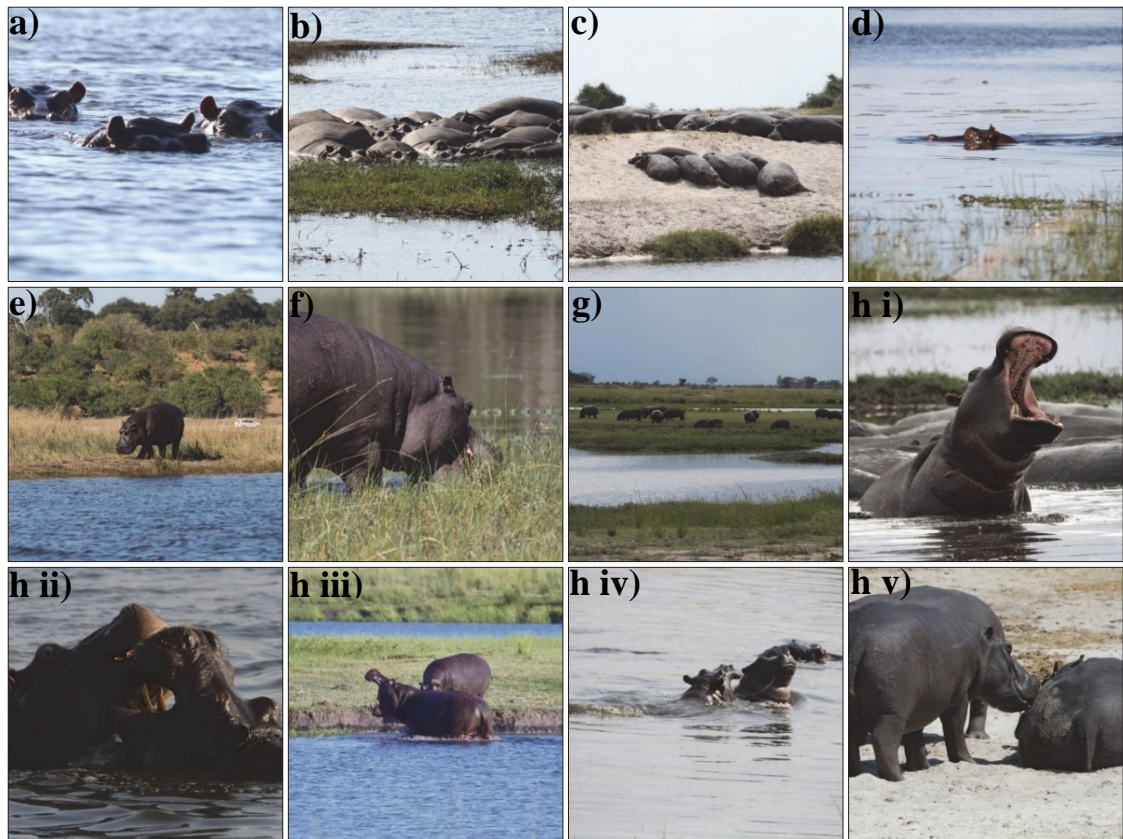
Figure 6.2. Photo examples of a) resting deep aquatic, b) resting shallow aquatic, c) resting terrestrial, d) moving aquatic, e) moving terrestrial, f) feeding aquatic, g) feeding terrestrial, and h) social: i) yawning ii) fighting, iii) aggression, iv) playing, v) grooming.

For every area and for every season, data were collected for three diurnal sessions and three nocturnal sessions. Areas were not sampled on consecutive days unless observations were incomplete due to an inability to find or follow hippos for a full observation period. This occurred mostly during nocturnal observations. During each observation session, the number of boats and cars within 200 m of any visible hippo was recorded. Only data from full day sessions (i.e. more than 8.5 hours' continuous recording) were analysed for best approximation of total daily vehicle (land and water) traffic.

6.2.2.2 Pod differentiation

It was sometimes difficult to differentiate adjacent hippo pods. This was particularly true in the Chobe River given the continuous aquatic habitat (a river). What appeared to be one pod (a group of hippos occurring within proximity to one another) would often change, as hippos joined or left the group throughout the day, often to move to a neighbouring group of hippos. In the Okavango Delta, hippos tend to live in discrete lagoons and movement between lagoons did not readily occur during the day, so a group of hippos within a lagoon was likely to be one pod. Given the difficulty in delineating pods, the activities of all hippos visible to the observer were recorded, even if there was significant separation between the hippo groups. In this way, the behavioural data are less likely to represent individual pods and more the behaviour of hippos within an area.

6.2.2.3 Analysis

While data were normally collected in diurnal and nocturnal sessions, each scan was assigned as diurnal or nocturnal based on the exact time of the scan and if it occurred before or after sunrise/sunset for that area and date (sunriset function from maptools package, Bivand & Lewin-Koh, 2019). The moon phase (new, waxing, full, waning) was assigned to each nocturnal scan based on the date (lunar.phase function from lunar package, Lazaridis, 2014). For each scan, the records for hippos of all age classes and sex were combined (reasons discussed below). The scans referring to each activity were summed over the hour and the proportion of hippos doing each activity was calculated, where all activity proportions over the hour summed to one. Expressing the activities as an hourly proportion reduced the effects of temporal correlation and variation in the numbers of hippos observed in each scan. Although methods aimed to be consistent for diurnal and nocturnal sessions, given the differences in visibility and the difficulty of

observing hippos at night, which led to fewer observations on fewer hippos, diurnal and nocturnal observations were analysed separately.

We tested the effect of season, area, their interaction, moon phase (for nocturnal behaviours), and time of day on hippo behaviour by fitting a series of generalized linear models (binomial distribution), separately for each activity for diurnal and nocturnal observations (glm function of lme4 package, Bates et al., 2015). Hourly proportion was the response variable, and time of day (hour), moon phase, season, area, and their interaction were fixed effects. The total hourly count of hippos was included as a weight in each of the models. For each model, we applied data dredge statistics (dredge function of MuMIn package, Barton, 2018) to automatically generate models with all valid combinations of the fixed effects. We used the corrected Akaike information criterion (AICc; where the best fitting model has the lowest value), ΔAICc (difference of AICc value from the best fitting model), and AICc weights to select the best fitting models for each activity. With the final models, the significance of the fixed effects were tested using the Anova function (car package, Weisberg & Fox, 2011), and differences among the levels of the effects were tested using post hoc pairwise comparisons, based on estimated marginal means, using a Tukey adjustment with the emmeans package (Lenth, 2019). We used the simulateResiduals function (DHARMa package, Hartig, 2019) to examine plots of distributions of residuals against the predictors and Q–Q plots of the normal distribution to test the assumptions of homogeneity of variance and normality of data. These assumptions were met, requiring no transformations. All statistics were conducted using the R computing environment (version 3.5.2) (R Core Team, 2018).

Difficulties in assigning ages to hippos resulted in low numbers in each category. Further, adult females were difficult to differentiate from young males when submerged, resulting in a bias of recording adult females when they participated in activities with most of their body exposed (e.g. terrestrial activities, and resting shallow aquatic). Consequently, all adult records were combined, and no formal analysis was performed on age classes. Instead, we investigated differences in behaviour among age classes by plotting the data. We investigated how hippo aggregations varied based on activities and based on age classes/sexes (aggregations were not subject to the same bias as above) by visually examining the plotted data.

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6.3 Results

We made a total of 9,043 scans (6,003 diurnal, 3,040 nocturnal), resulting in 19,173 activity records, which equated to 919 hours available for analysis (Figure 6.3, Table 6.3). Seasonally, for each area, we averaged 500 diurnal scans (range 381–896; 48 hourly proportions (range 37–91)), and 276 nocturnal scans (range 135–417; 31 hourly proportions (range 17–45)). The difference between the number of diurnal and nocturnal scans was mainly due to the difficulty of following hippos at night, but also partly an effect of the earlier than predicted onset of the wet season in Abu, which prevented us collecting nocturnal data for the dry season (med-low flood). Abu2 could not be sampled during the dry seasons due to flooding, nor could Chobe3 during the dry season (high flood). Further, the dry season (med-low flood) was sampled twice (2017 and 2018) for the three Chobe areas.

Table 6.3. Number of scans (with number of equivalent hourly proportions in brackets) for each area for each season, for diurnal and nocturnal sessions.

Area	Diurnal sessions			Nocturnal sessions			Total
	Dry (med-low)	Wet (low flood)	Dry (high flood)	Dry (med-low)	Wet (low flood)	Dry (high flood)	
Chobe1	591 (62)	464 (42)	401 (38)	303 (34)	164 (19)	298 (32)	2221
Chobe2	896 (91)	474 (44)	393 (39)	246 (26)	257 (25)	322 (39)	2588
Chobe3	671 (63)	433 (39)	0 (0)	135 (17)	182 (24)	0 (0)	1421
Abu1	381 (37)	448 (43)	406 (40)	0 (0)	400 (45)	316 (36)	1951
Abu2	0 (0)	445 (42)	0 (0)	0 (0)	417 (42)	0 (0)	862
Total	2539	2264	1200	684	1420	936	
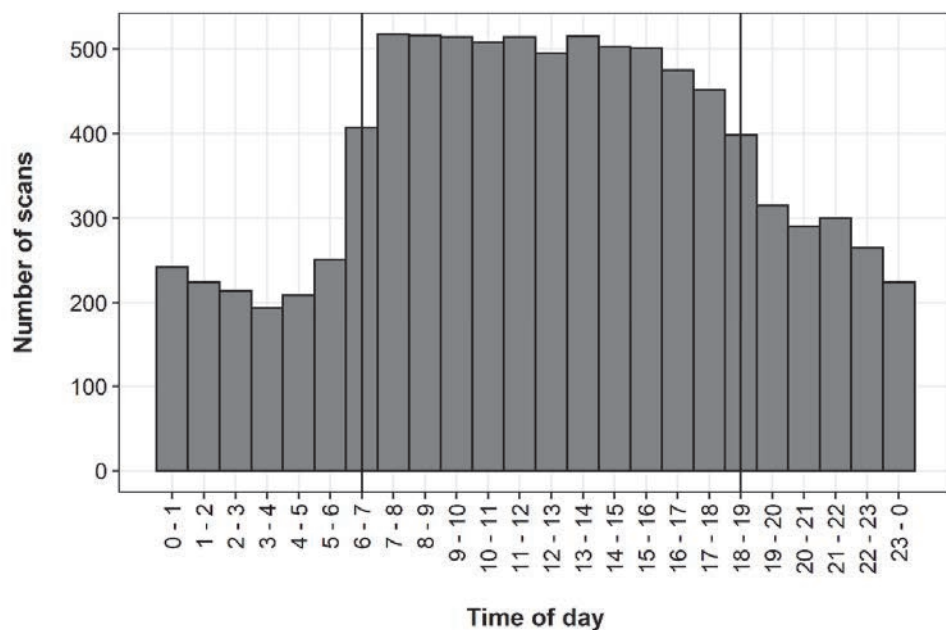
Figure 6.3. Histogram of number of scans at different times of day. Vertical black lines denote approximate sunrise and sunset times.

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The number of diurnal scans was relatively constant through the day, reducing slightly at sunset (Figure 6.3). However, due to difficulties in observing hippos at night, the number of nocturnal scans was lower overall and fluctuated hourly. Lower numbers of nocturnal scans were related to the lack of Abu data, mentioned above. The mean number of animals seen per diurnal scan was 13 (range 1–110), and for nocturnal was five (range 1–41).

The study areas had varying levels of visitation by cars and boats, and therefore hippos in the areas were subject to different levels of human disturbance (Table 6.4). Chobe2 had the greatest visitation, and Chobe3 and Abu2 had on average no car or boat traffic (Table 6.4). The number of cars and boats in areas differed with season. There was effectively no traffic in any area at night.

Table 6.4. Average number of cars and boats within 200 m of any visible hippo for each area, each season during the day.

Area	Dry season (med-low flood)		Wet season (low flood)		Dry season (high flood)	
	Cars	Boats	Cars	Boats	Cars	Boats
Chobe1	38	2	2	5	11	2
Chobe2	82	0	31	1	3	35
Chobe3	0	0	0	0		
Abu1	12	0	13	0	46	0
Abu2			0	0		

6.3.1 Daily activity budget

Combining all data, the average 24-hour activity budget of hippos (Figure 6.4) was 67.5% resting (38.9% resting deep aquatic (RDA); 23.7% resting shallow aquatic (RSA); 4.9% resting terrestrial (RT)), 18.4% moving (17.0% moving aquatic (MA); 1.4% moving terrestrial (MT)), 11.5% feeding (10.1% feeding terrestrial (FT); 1.4% feeding aquatic (FA)), and 2.6% social activity. Analysing diurnal/nocturnal observations separately (Figure 6.4), hippos rested during the majority of the day (74.5%: 40.6% RDA, 30.5% RSA, 3.4% RT), with 18.3% moving (17.8% MA, 0.5% MT), 4.6% feeding (4.2% FT, 0.4% FA), and 2.5% social activity. The majority (89.3%) of these activities occurred in the water, with 8.1% occurring on land (social activity not included). Resting was also the leading activity (55.5%) at night (36.0% RDA, 12.1% RSA, 7.4% RT), but feeding was the second most common activity (23.3%: 20.1% FT, 3.2% FA), followed by moving (18.5%: 15.7% MA, 2.8% MT) and 2.7% social activity. Even at night, hippos were mostly in the water (67.0%), with 30.3% of the time on land.

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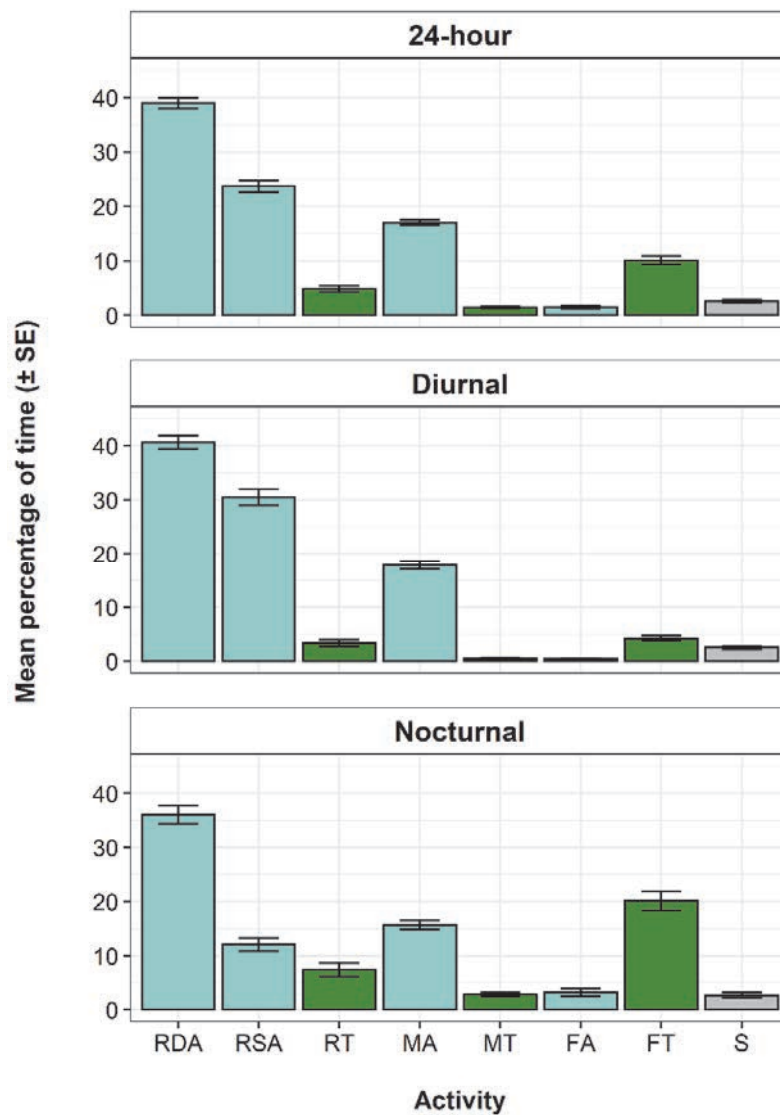
Figure 6.4. 24-hour, diurnal, and nocturnal activity budgets of hippos based on hourly proportions, combined from all seasons and areas. Colours indicate location (blue, aquatic; green, terrestrial; grey, unspecified).

6.3.2 Effect of time of day, moon phase, season, and area on hippo behaviour

The models that best described (i.e. had the lowest AICc values) all diurnal and nocturnal activities (except nocturnal moving terrestrial) included time of day, moon phase, season, area, and their interaction (Supplementary Table S6.1). All other models had ΔAICc greater than 10, indicating little support for them (Anderson & Burnham, 2004). The effect of time of day, moon phase, season, area, and their interaction, were highly significant for all models (all $p < 0.001$, except diurnal feeding aquatic which had $p = 0.008$ for area) (Supplementary Table S6.2). An exception was diurnal social activity, which had no significant effect of season ($p = 0.135$) (Supplementary Table S6.2). For nocturnal moving terrestrial, the model that best described the data included time of day,

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moon phase, season, and area, but not their interaction. However, the next best model included the season-area interaction and effectively had an equivalent AICc (ΔAICc = 0.33) (Supplementary Table S6.1) and therefore, to maintain consistency with the models used for the other behaviours, has been considered from hereon. Hour ($p < 0.001$), season ($p = 0.004$), area ($p < 0.001$), and moon phase ($p = 0.004$) were all highly significant, with the season-area interaction close to, but not below, the 0.05 significance level ($p = 0.062$) (Supplementary Table S6.2).

To enable a more general understanding of hippo behaviour we will initially discuss the effect of season on hippo activity, without differentiating between the study areas (Figure 6.5). Diurnally, hippos rested similar amounts in the dry season (med-low flood) (76.7%) and wet season (low flood) (75.4%), which was more than in the dry season (high flood) (67.9%). In both the dry season (high flood) and wet season (low flood), most of this was resting deep aquatic (44.9% and 44.3%, respectively), with less time resting shallow aquatic (22.0% and 30.8%) and only rarely resting terrestrial (1.0% and 0.3%). In contrast, in the dry season (med-low flood) hippos rested deep and shallow aquatic similar amounts of time (35.6% and 34.1%), with resting terrestrial 7.0% of the day. In the dry season (high flood) hippos spent 28.1% of their day moving (28.0% MA, 0.1% MT) compared to only 15.6% in the dry season (med-low flood) (14.7% MA; 0.9% MT) and 16.2% in the wet season (low flood) (15.9% MA, 0.3% MT). Hippos fed least (2.3%) during the day in the dry season (high flood) compared to the dry season (med-low flood) (5.0%) and wet season (low flood) (5.6%). Of this 2.3% in the dry season (high flood), the majority was feeding aquatic (1.6%) compared to feeding terrestrial (0.7%). In the dry season (med-low flood) and wet season (low flood), feeding terrestrial (4.8% and 5.5%, respectively) was more common than feeding aquatic (0.2% and 0.1%). Social activity was lowest during the dry season (high flood) (1.7%), but similar in the dry season (med-low flood) (2.7%) and wet season (low flood) (2.8%).

Nocturnally, hippos rested for similar amounts of time over all seasons: 58.7% dry season (high flood), 56.3% dry season (med-low flood), and 53.1% wet season (low flood), although the location of resting differed. In the dry season (high flood) and wet season (low flood), hippos rested deep aquatic more (37.4% and 38.0%), with less time resting shallow aquatic (15.9% and 14.8%) and resting terrestrial (5.4% and 0.3%). This contrasts

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to the dry season (med-low flood), where hippos rested deep aquatic (30.2%) for similar amounts of time to the other seasons, but rarely rested shallow aquatic (1.5%), instead spending 24.6% of the night resting terrestrial. Hippos moved more (23.4%) in the dry season (high flood) than in the dry season (med-low flood) (15.6%) and wet season (low flood) (16.6%). A minimal amount of this was moving terrestrial: 1.9% dry season (high flood); 3.0% dry season (med-low flood); 3.4% wet season (low flood). Hippos fed for similar amounts of time in the dry season (med-low flood) (26.1%) and wet season (low flood) (26.4%), but less in the dry season (high flood) (16.7%). During the dry season (med-low flood) and wet season (low flood), feeding aquatic at night was rare ($< 0.05\%$ and 0.2%), but in the dry season (high flood) hippos fed aquatic (9.7%), more than fed terrestrial (7.0%). Social activity at night increased from the dry season (high flood) (1.3%) to dry season (med-low flood) (2.0%) to wet season (low flood) (4.0%).
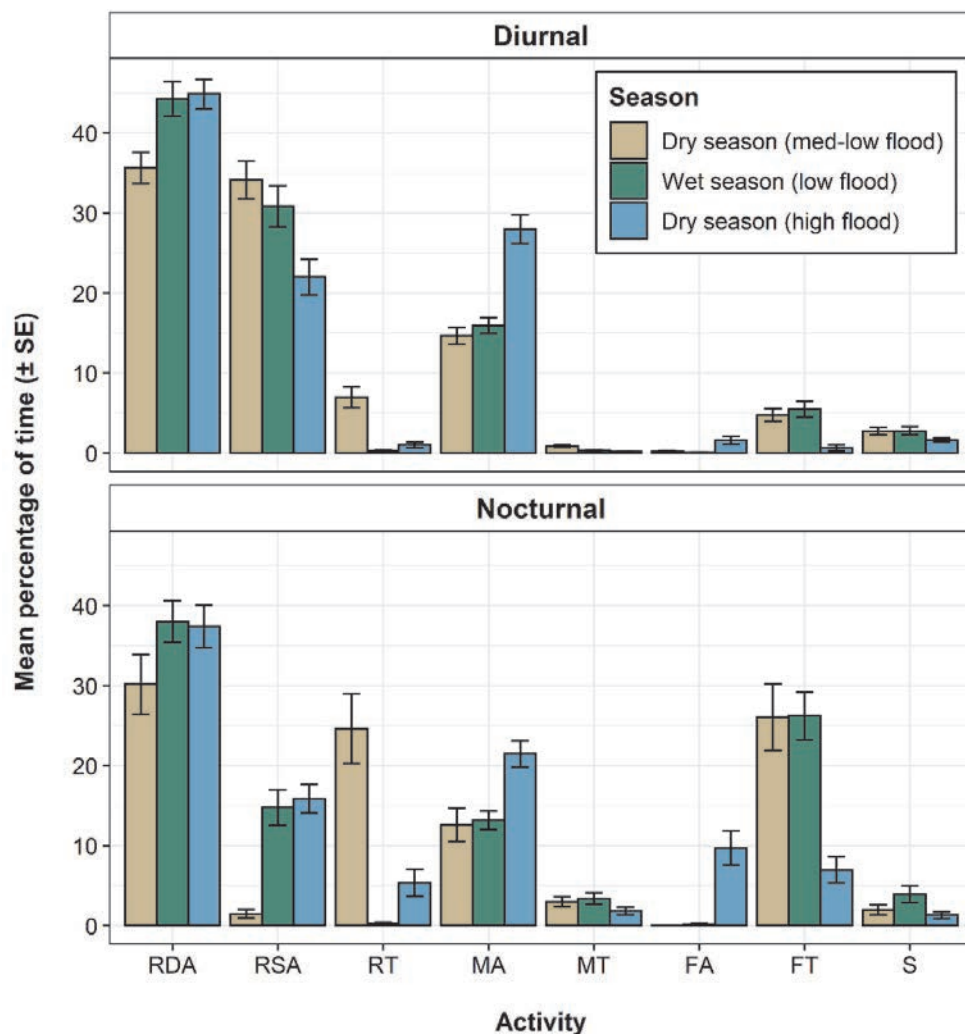
Figure 6.5. Seasonal variation in diurnal and nocturnal hippo activity budgets. Note there was a significant interaction between season and area (see Figure 6.6).

Examining differences in hippo behaviour between the study areas and how this varied with season (Figure 6.6), it can be seen that nocturnally, resting deep aquatic was a more common behaviour than resting shallow aquatic across all seasons and areas, except for Abu1 in the wet season (low flood) where it was approximately equal. Higher rates of resting deep aquatic also occurred diurnally, except in Chobe1 in the wet season (low flood), and Chobe2 and Abu1 in the dry season (med-low flood), where resting shallow aquatic was greater than resting deep aquatic. Further, for hippos in Chobe3 and Abu2, both diurnally and nocturnally over all measured seasons, the pattern was amplified, and they rested deep aquatic more, and rested shallow aquatic less, than average, as did hippos in Chobe1 in the dry season (med-low flood). Nocturnally in the wet season (low flood), hippos in Abu1 rested deep aquatic less than average. Diurnally in the dry season (med-low flood), hippos in Chobe1 rested terrestrial more than average, whereas hippos in Chobe2 rarely rested terrestrial. For Chobe2, nocturnally this switched, and the hippos rested terrestrial more than average. Also, in this season, hippos in Chobe3 rarely rested terrestrial nocturnally compared to average. Diurnally, in the dry season (med-low flood) and the wet season (low flood), hippos in Chobe2 fed terrestrial more than average. The reverse occurred at night, and in all seasons, hippos in Chobe2 fed terrestrial less than average. Hippos in Chobe1 also fed terrestrial diurnally more than the remaining areas in the wet season (low flood). Hippos in all other areas rarely fed terrestrial during the day. Nocturnally, in the dry season (med-low flood) hippos in Chobe3 fed terrestrial more than average, as did hippos in Abu1 in the wet season (low flood), though hippos in Abu2 fed terrestrial less than average in this season. In the dry season (high flood), hippos in Abu1 spent approximately 27.2% of the night feeding aquatic. Other than this, feeding aquatic was never a common activity. In terms of social activity, diurnally in the dry season (med-low flood) and diurnally and nocturnally in the wet season (low flood), hippos in Abu1 spent longer on social activity than other areas. In contrast, nocturnally in the wet season (low flood), hippos in Chobe3 and Abu2 spent little time on social activity.

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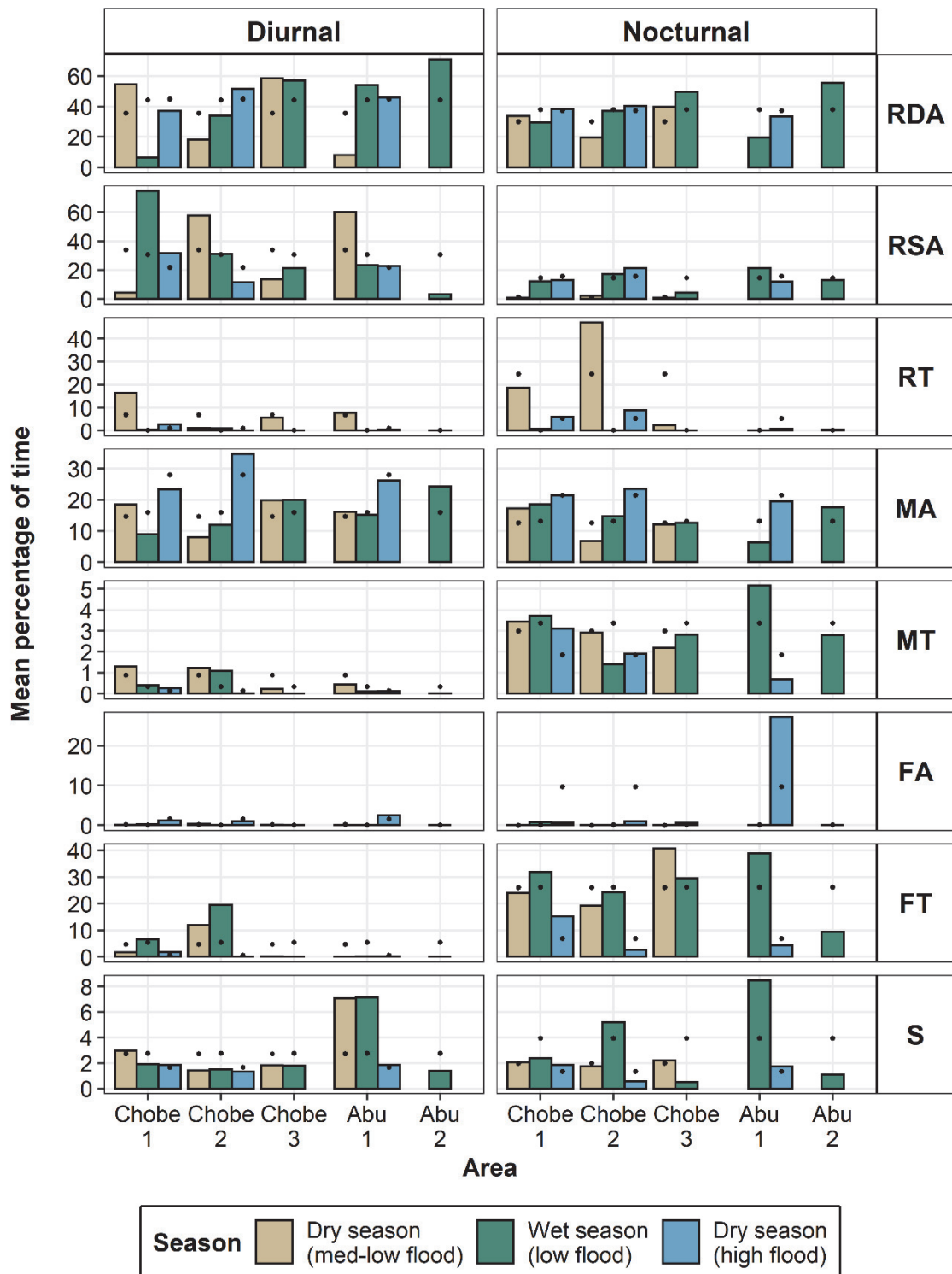
Figure 6.6. Seasonal and area variations in diurnal and nocturnal hippo activity budgets. Note the y axis scale varies between activities. Black dots indicate seasonal average value for that activity.

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The effect of time of day (hour) was significant (all $p < 0.001$) in all analyses, indicating hippo behaviour possessed a circadian rhythm (Figure 6.7). Peaks and dips in proportions of most activities centred on sunrise, sunset, the middle of the day and the middle of the night, with moving and feeding terrestrial peaking slightly after sunset and before sunrise, and feeding terrestrial also in the mid to late afternoon. Whilst behaviour did fluctuate, resting deep aquatic always remained above 20%. There was a one hour-period in which one activity occurred more than resting, and that was during the 8–9pm period, where hippos fed 42.7% of the time (37.4% FT; 5.3% FA) compared to 39.9% resting. There was no time period where hippos were on land more than in water, although between 8–10pm the values were approximately equal.
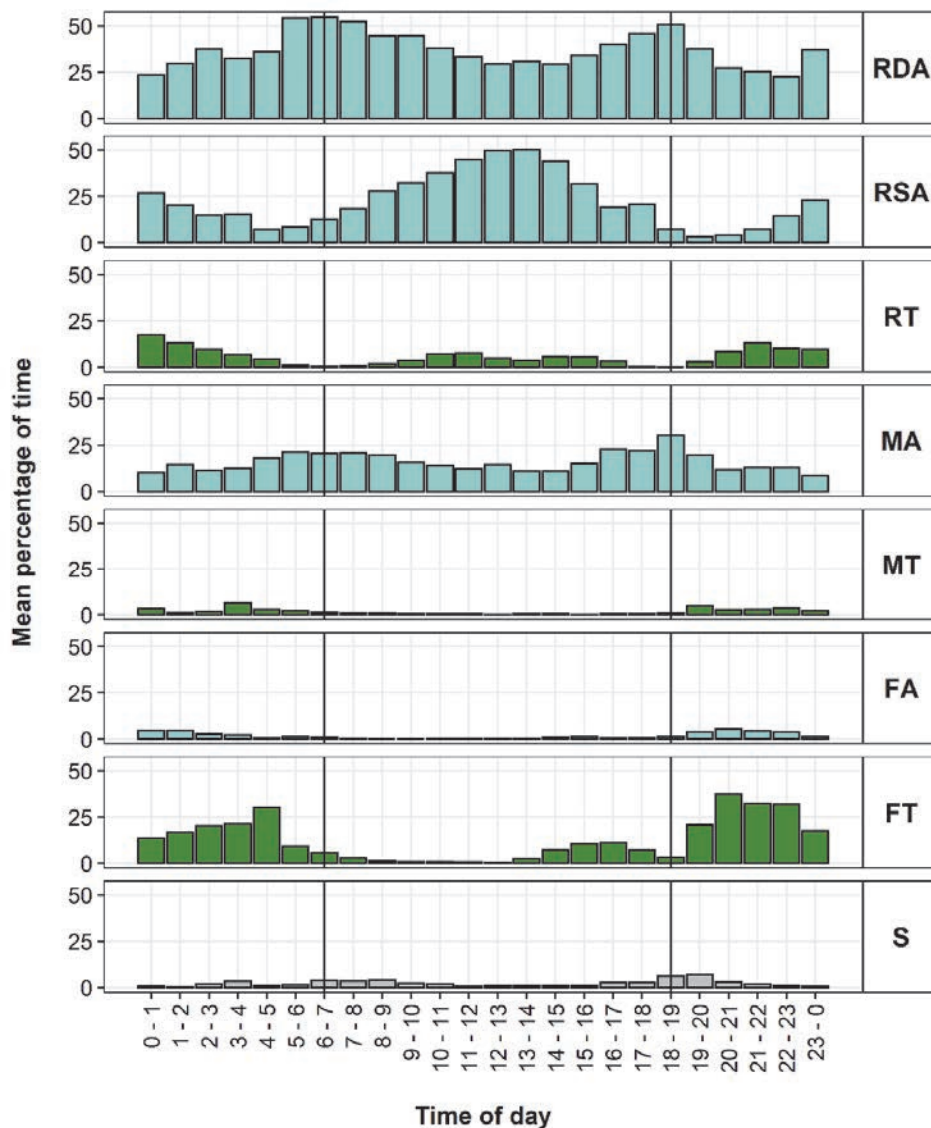
Figure 6.7. Hourly variations in hippo behaviour based on hourly proportions, combined from all seasons and areas. Colours indicate location (blue, aquatic; green, terrestrial; grey, unspecified). Vertical black lines denote approximate sunrise and sunset times.

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Moon phase significantly affected nocturnal hippo behaviour (Figure 6.8), though not always consistently with the pattern of illumination (i.e. new < waxing ≈ waning < full). Hippos rested deep aquatic similar amounts on nights with waxing and waning moons, substantially more than nights with full or new moons. Changes in rates of resting shallow aquatic followed the moon cycle, being highest on nights with a new moon and decreasing as the moon waxed, became full, and waned. Hippos rested terrestrial most during nights with full moons, also sometimes resting on land on moonless and nights with waning moons. Nights with full moons were characterised by higher rates of feeding aquatic.
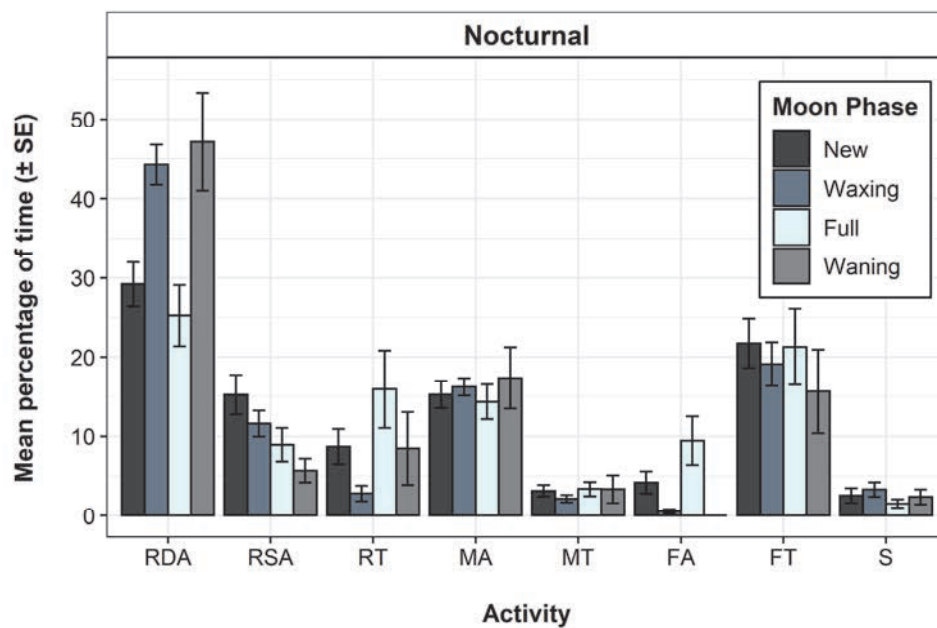
Figure 6.8 Variations in nocturnal hippo activity budgets based on moon phase.

6.3.3 Variations in behaviour among age classes

Diurnal and nocturnal hippo behaviour varied based on age (Figure 6.9). Diurnally, juvenile hippos rested least (63.8%), followed by subadults (67.5%) and then adults (76.5%). Juveniles, subadults, and adults rested deep aquatic similar amounts of time (36.8%, 34.4%, and 39.0%), but juveniles rested shallow aquatic (22.4%) less than subadults (30.3%) and adults (35.4%), and rested terrestrial more (4.6%; 2.8% subadults; 2.1% adults). Juveniles moved (25.3%) more than subadults (19.8%) and adults (15.3%), and subadults fed more (8.6%) than juveniles (6.9%) and adults (5.7%). Juveniles and subadults had similar amounts of social activity (3.9% and 4.1%), more than adults (2.4%). Nocturnally, subadults rested the least (49.2%), followed by juveniles (55.6%) and then adults (58.8%). Subadults and adults mainly rested deep aquatic (31.1% and

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34.6%), followed by resting shallow aquatic (14.8% and 21.5%), then resting terrestrial (3.3% and 2.7%). Juveniles also mainly rested deep aquatic (42.2%) but allocated similar time to resting shallow aquatic (5.9%) and resting terrestrial (7.5%). At night, subadults moved the most (22.3%), followed by juveniles (20.8%), and adults (14.4%). Juveniles fed less (17.4%) than subadults (20.9%) and adults (24.1%). Nocturnally, juveniles (6.1%) and subadults (7.5%) participated in similar amounts of social activity, which was more than adults (2.7%).
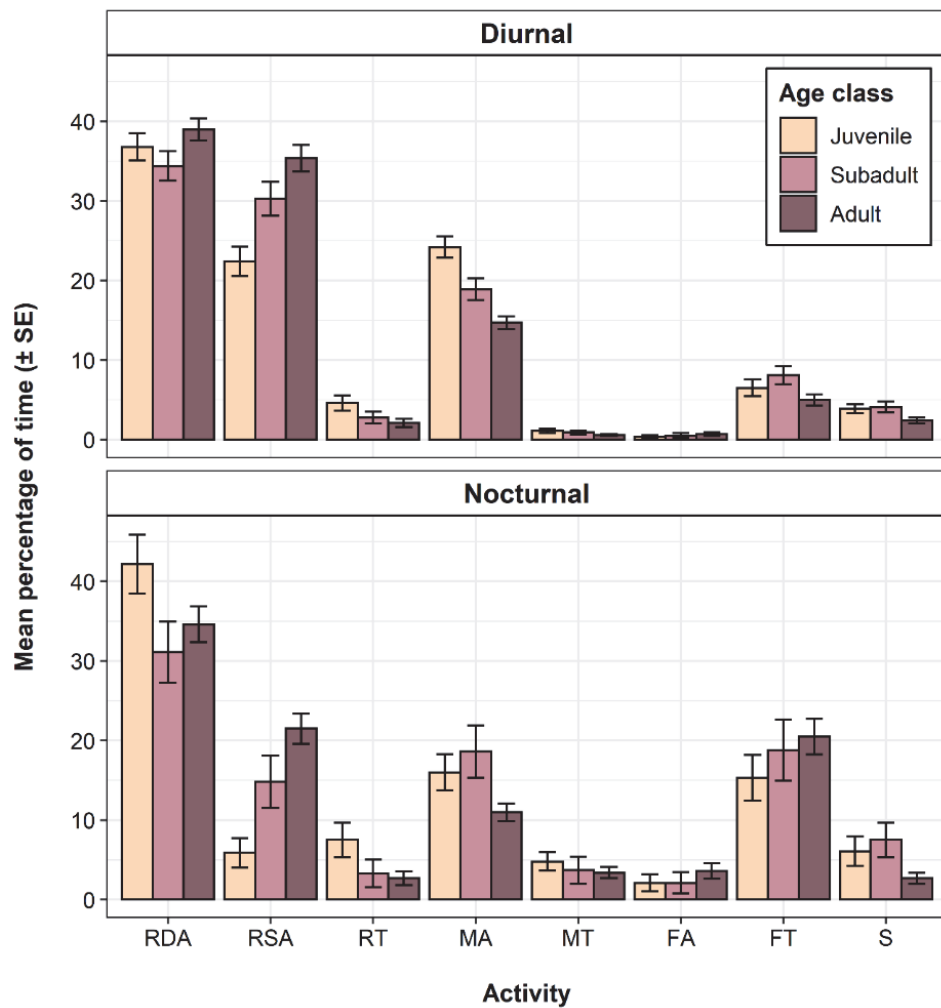
Figure 6.9. Variations in diurnal and nocturnal hippo activity budgets based on age.

6.3.4 Hippo social groupings

The number of hippo groups varied throughout the day. There were fewer groups at night and during the middle of the day, and more around sunrise and sunset (Figure 6.10). The number of hippos within each group (Figure 6.10) was lowest at night, increasing during sunrise, and peaking in the middle of the day, before decreasing in the afternoon and

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evening. The greatest number of separate groups seen during one scan was 40 and the greatest number of hippos seen in one group was 38 (both at Chobe2). The number of hippos in each group varied based on activity: on average hippos were in larger groups when they were resting, particularly when they were resting shallow aquatic (Figure 6.11). The number of hippos in a group varied based on age class and sex, with adult females being in larger groups, followed by juveniles and subadults, and adult males in smaller groups (Figure 6.11).
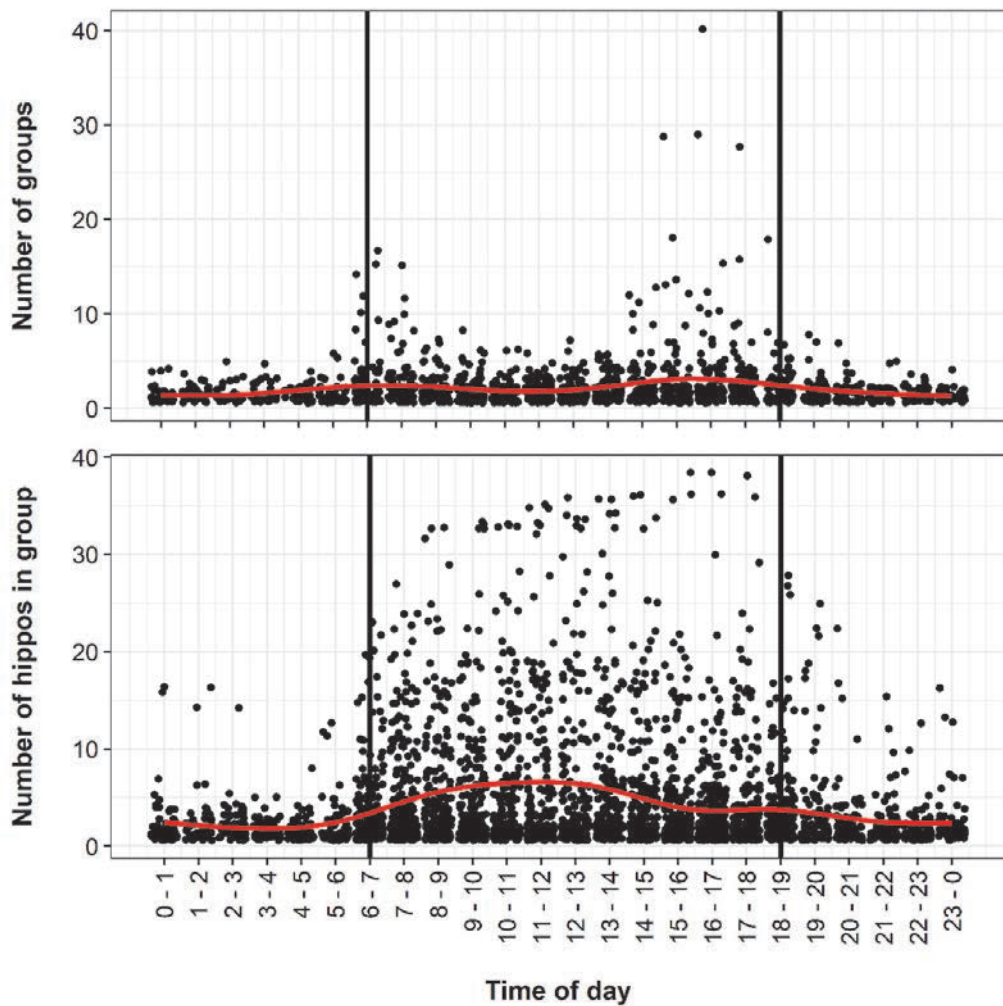
Figure 6.10. Number of groups and group size by time of day. Hippos < 3 lengths from other hippos were classed in the same group. Vertical black lines denote approximate sunrise and sunset times.
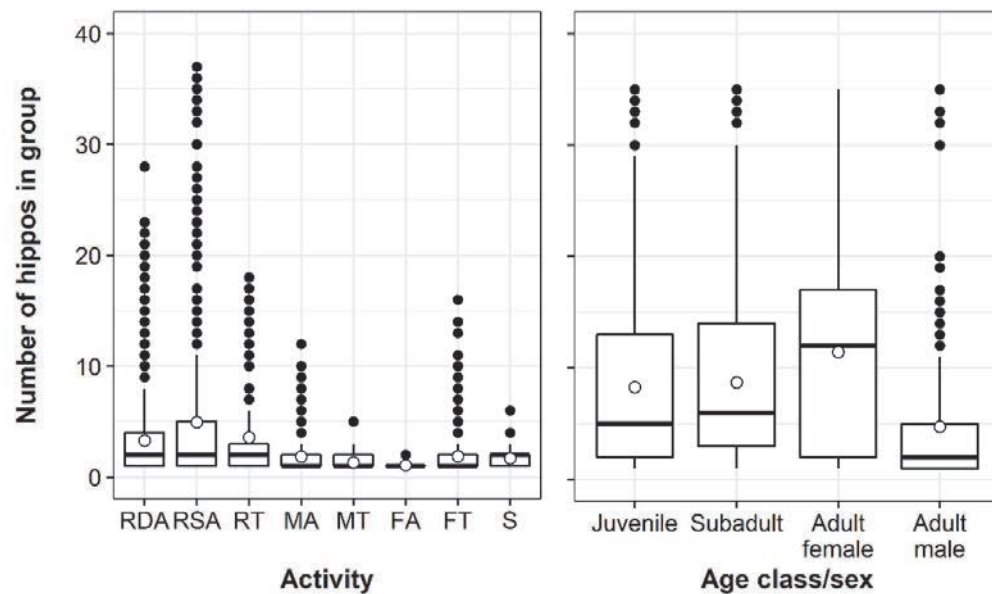
Figure 6.11. Boxplots (mean, circle) of number of hippos in each group based on activity and age class/sex.

6.4 Discussion

6.4.1 Daily activity budget

The 24-hour activity budget of hippos reveals a relatively sedentary existence: they rest two-thirds of their time, the remaining time being spent moving and feeding, with little time spent on social activity. The diurnal values for each activity are within range of the activity budgets recorded elsewhere (Table 6.5), although they are not consistently comparable to any one study.

Table 6.5. Comparison of diurnal and 24-hour activity budget of hippos from this study with four other studies. Activity codes were adapted for consistency.

Time	Source	Country	Activity			
			Resting	**Moving**	**Feeding**	**Social**
Diurnal	This study	Botswana	74.5%	18.3%	4.6%	2.5%
	Mekonen (2016)	Ethiopia	42.5%	34.2%	19.6%	3.7%
	Timbuka (2012)	Tanzania	53.3%	18.1%	19.3%	8.9%
	Prinsloo (2016)	South Africa	79.4%	10.4%	2.2%	7.9%
			Aquatic	**Resting land**	**Feeding land**	**Moving land**
24-hour	This study	Botswana	81.0%	4.9%	10.1%	1.4%
	Nuñez (2017)	Kenya	60.7%	9.0%	20.6%	9.7%

Hippos in South Africa (Prinsloo 2016) rested a similar amount to hippos in this study, whilst those in Ethiopia (Mekonen & Hailemariam 2016) and Tanzania (Timbuka 2012)

rested substantially less. Overall, hippos in this study and those in Tanzania (Timbuka 2012) spent similar amounts of time moving. This was less than hippos in Ethiopia (Mekonen & Hailemariam 2016) and more than hippos in South Africa (Prinsloo 2016), although we did observe similarly high/low rates of moving in some areas in the dry season (high flood) and the lower flood seasons, respectively. Diurnally, hippos in Botswana fed a similar amount as those in South Africa (Prinsloo 2016), much less than hippos in Tanzania (Timbuka 2012) and Ethiopia (Mekonen & Hailemariam 2016). Again, hippos in some areas (Chobe2 in the wet season (low flood)) had similarly high rates but overall feeding was much lower in this study. Feeding hippos were easily visible during the day, so the low rates recorded in this study are likely to be relatively accurate representations of their true behaviour. Hippos in Botswana appeared to be less social than in other countries. Whilst hippos in Abu1 had high levels of social activity compared to other areas, their rates were never as high as hippos in South Africa (Prinsloo 2016) and Tanzania (Timbuka, 2012). The 24-hour behaviour derived from GPS tag movement data (Nuñez, 2017) showed hippos spending around twice as much time resting terrestrial and feeding terrestrial, and almost seven times as much time moving terrestrial, as hippos in Botswana. The studies likely differ due to variations in climate, landscape, day length, and resource availability based on location (Prinsloo, 2016), season of data collection, and data collection intensity and sampling methods. For example, hippos in Kenya spent twice as much time on land (Nuñez, 2017) as hippos in this study, potentially a consequence of different environmental conditions. Alternatively, this difference may be due to the lack of an observer (data were collected from GPS tags) and therefore less disturbance to the hippos. Our results are arguably most similar to those from South Africa (Prinsloo, 2016), which has a similar climate to Botswana. Direct comparisons between our results and the other studies are difficult due to northern Botswana's unique environment, where peak flooding occurs during the dry season rather than in the wet season. In other countries the wet season offers an abundance of water and grass , whereas the wet season in northern Botswana is when water level is lowest.

Our results refute the commonly held belief that hippos rest in water all day and graze on land all night, and only at night (Clough, 1967; Field, 1970; Hoven, 1978; Owen-Smith, 1988; Eltringham, 1993b, 1999; Barklow, 1997; Klingel, 2013). On average, hippos in this study spent 75% of the day resting, meaning a quarter of their day was dedicated to

other activities. Specifically, hippos in Chobe2 spent as little as 63% of the day resting in the dry season (high flood), and as much as 20% feeding in the wet season (low flood), which, along with resting and moving terrestrial, equated to 21.5% of the day on land. On average, hippos fed a quarter of the night, half of the time that was spent resting; hippos in Chobe2 fed as little as 2.7% and rested as much as 70.4% of the night in the dry season (high flood). Further challenging the idea that hippos restrict themselves to land at night, in this study there was only a two-hour period (8–10pm) where hippos were as likely to be on land as in the water. Reports of hippos feeding and resting on land during the day, resting at night, and feeding in relatively short bouts at night do occur (Luck & Wright, 1964; Ansell, 1965a; Olivier & Laurie, 1974b; Viljoen & Biggs, 1998; Timbuka, 2012), however they are rarely referenced. Instead the simple "diurnal aquatic resting/nocturnal terrestrial feeding" dichotomy is repeated, which contrasts observations from this study where hippo behaviour was found to be less rigid. The low amount of time dedicated to feeding supports hippos having lower energetic demands and therefore needing lower quantities of food compared to similar sized mammals (Van Hoven 1982 in Lewison & Carter, 2004; Eltringham, 1993b, 1999; Klingel, 2013). Prinsloo (2016) suggested the higher levels of diurnal feeding observed in hippos in Tanzania (Timbuka 2012) could be because Tanzania has shorter nights than South Africa, forcing hippos to feed during the day to meet their food requirements. From our observations, hippos never fed the whole night, suggesting that night-time hours are unlikely to be a limiting factor. At night, it was easier to record feeding hippos due to their movement and the sound of their feeding. However, when disturbed, hippos sometimes stopped feeding and returned to the water, which may have led to nocturnal feeding being underrepresented. Upon saying this, there were nights when hippos did not appear to be disturbed by our presence and yet fed for a similar amount of time as the average results. In this study, terrestrial movement was a low percentage of hippos' activity budgets, as moving on land was almost always accompanied by feeding (Lewison & Carter, 2004). In contrast, moving aquatic was common, indicating hippos' preference to move between areas in deep water, either in channels or within the river, also seen in captive hippos (Blowers et al., 2012). The generally low proportion of social activity could be due to northern Botswana having sufficient water and lower hippo densities. This reduces male competition and therefore aggressive behaviours (Olivier & Laurie, 1974b; Karstad & Hudson, 1986; Bouché, 2004a; Blowers et al., 2010; Timbuka, 2012; Klingel, 2013).

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6.4.2 Effect of season on hippo behaviour

Hippo behaviour in this study was strongly affected by season, similar to other studies (Timbuka, 2012; Mekonen & Hailemariam, 2016). Diurnally, hippos rested less (particularly in shallow water) and moved aquatic more during the dry season (high flood) than the lower-flood seasons. This is likely related to the depth of water in this season; there may have been limited areas of shallow water to rest in, and when hippos rest in water above their height, they instinctively raise their heads to breathe, perhaps leading us to incorrectly to classify this activity as moving instead of resting. In addition, resting hippos were more difficult to observe in deep water because less of their body was visible. Further, there were higher levels of boat traffic during this season, and several times we noted resting hippos to be disturbed by boats and move away in the water, after which they remained agitated. Hippos rarely rested terrestrial during this season as the usual floodplain and sandbanks were flooded, and the only available land was frequented by cars; Nuñez (2017) showed that hippos display high site selectivity when resting on land. In the wet season (low flood), hippos rested in shallow water more than during the dry season (high flood) but still preferred to rest in deep water and almost never rested on land, despite the low water levels meaning that land was available. Hippos may have avoided resting in shallow water and on land as it would leave them exposed to biting insects, which were abundant in this season. In the wet season, we observed numerous hippos with skin covered with bumps, and Baker (1969 in Eltringham 1999) noted hippos suffer from insect bites. Timbuka (2012) also suggested hippos may adapt their behaviour due to insects. Alternatively, hippos may have been avoiding the rain downpours (Klingel, 2013). Without these issues, in the dry season (med-low flood), with water levels similar, if not deeper, than during the wet season, diurnally hippos rested in shallow water as much as in deep water, and often rested on land. Although there were large variations in resting locations among the seasons, the total amount of time spent was relatively consistent: diurnally there was a maximum of 8.8% difference and nocturnally only 5.6%. These variations were even lower than the maximum monthly variation (13.2%) noted by Timbuka (2012).

The amount of time spent feeding was lowest during the dry season (high flood), due to a lack of terrestrial grasses when the high water-level submerged the floodplains. Also, it was difficult to observe terrestrially feeding hippos at night in this season as they were

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forced to feed in the woodland where our observation distance was limited and we often had to move our car, which disturbed the hippos. In contrast, feeding aquatic was highest in this season as the water level encouraged aquatic vegetation growth. Timbuka (2012) also recorded less feeding in the dry season, but others suggest hippos fed for longer at night, and continued to feed in the day, in drier seasons (Mugangu & Hunter, 1992; Klingel, 2013). When food is scarce, low in quality, or far away, animals must resolve spending more time (and energy) attempting to meet intake requirements, or prioritising conservation of energy by minimising time spent foraging (Scotcher et al., 1978; Dasilva, 1992; Timbuka, 2012). During the lower-flood seasons, hippos fed more, and preferred terrestrial grasses over aquatic vegetation, as the relative abundances of each changed. During the wet season (low flood), rain promoted grass growth and hippos fed more; an increase in feeding in the wet season was also noted in Tanzania (Timbuka, 2012). There was almost equal feeding in the wet season (low flood) as in the dry season (med-low flood), even though there was no rain in the latter, likely due to grass growth in areas where the flood had receded (Bonyongo, 2009). Timbuka (2012) and Luck & Wright (1964) suggest hippos feed more in colder temperatures. However, in this study, hippos in Chobe fed more during the two hotter seasons than the cooler dry season (high flood). Further, hippos in this study fed mainly in the mid-afternoon, also seen by Mugangu & Hunter (1992), often the hottest part of the day.

Hippo social behaviours often occur under water (Barklow, 1997, 2004; Prinsloo, 2016), so the lower amount of social activity observed during the high flood season may be a result of reduced visibility at high water, rather than actual seasonal differences. Alternatively, the already low levels of aggressive social activity shown by hippos in this study may have reduced further during the high flood season with increased water availability (Olivier & Laurie, 1974b; Karstad, 1984; Karstad & Hudson, 1986; Timbuka, 2012; Mekonen & Hailemariam, 2016; Prinsloo, 2016).

6.4.3 Effect of area on hippo behaviour

Variations in hippo activity budgets between areas seen in this study were also noted in Tanzania (Timbuka, 2012), and are due to a combination of factors: water and graze availability, habitat availability, and habituation. Chobe1 and Chobe2 are within eight km of each other, occur along the same river within the same national park, and are subject

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to regular human presence. However, there are small-scale habitat differences between the areas, which have resulted in markedly different behaviour. In contrast to all other areas, hippos in Chobe1 almost never rested deep aquatic during the wet season (low flood), instead resting shallow aquatic more than double the average. Chobe1 was located in a relatively shallow area approximately 150 m from the main Chobe River channel and became a disconnected lagoon during lower flood seasons. Perhaps there was insufficient space for all hippos to rest deep aquatic during the day. Diurnally in the dry season (med-low flood), hippos in Chobe1 rested terrestrial twice as much as the other areas, as they had access to a large sandbank adjacent to the lagoon that was inaccessible to vehicles and therefore not subject to disturbance (Figure 6.12). We observed that hippos appear to prefer to sleep on sand, also reported elsewhere (Ansell, 1965a; Klingel, 1991b; Barklow, 1997; Onyeanusi, 2004). In contrast, in the same season, hippos in Chobe2 rarely rested terrestrial diurnally, yet nocturnally rested terrestrial almost twice as much as average. This was possibly because the available sandy areas were on/near the road, where resting hippos were subject to human disturbance during the day, but not at night. Diurnally, at times of low flooding, hippos in Chobe2 spent more time feeding terrestrial (up to 20% in the wet season) than the other areas. In these seasons, there was a vast area of exposed floodplain that was inaccessible to vehicles, encouraging diurnal grazing (Timbuka, 2012; Prinsloo, 2016). This was balanced by lower rates of feeding at night than the other areas. Chobe1 also had access to a (smaller) grazing area that was not subject to human disturbance, and diurnally hippos in this area fed more than those in Chobe3, Abu1, and Abu2.

Sharing even more similarities than the previous two areas, Abu1 and Abu2 were both lagoons surrounded by floodplains and close to one another (< four km). Here, differences in behaviour may be due to varying levels of habituation, with Abu1 occurring in a highly visited area. Hippos in Abu2 were skittish and less likely to settle and expose themselves (in shallow water or on land), instead retreating to deep water. Hippos in Abu1 spent more time on social activity than all other areas during the dry season (med-low flood) and wet season (low flood); this was mainly due to the presence of two bulls in the lagoon, who would mock-fight for long periods.

Like Abu2, Chobe3 also had low levels of visitation, and this may be reflected in the similar behaviour of hippos in these two areas. Hippos were less likely to rest shallow aquatic and more likely to be resting and moving in deep water with lower levels of social activity. In addition, diurnally, hippos in both areas fed terrestrial less than average. These patterns could be due to hippos minimising activities in which they feel vulnerable. However, nocturnally, whilst hippos in Abu2 fed less than half the average time, hippos in Chobe3 had higher than average rates of feeding. Hippos in Chobe3 also rested terrestrial close to the observer during the day. An alternative explanation as to why hippos in Chobe3 displayed behaviour more like those from Abu2 than the other areas (but were not hesitant to feed nocturnally or rest terrestrial diurnally), is unrelated to habituation, but possibly due to their location in a deeper, faster-flowing section of the Chobe River, where they would have fewer opportunities to rest shallow, and the deep water could have made social activity more difficult to observe (Maust-Mohl et al., 2015). Although I recorded low levels of visitation to Chobe3 during this study, prior to recent fencing the area had been accessible to the community.

Timbuka (2012) noted one pod had no seasonal differences in behaviour, attributed to that site having minimal variation in water throughout the year. In this study, Chobe3 had the least change in resources between the seasons and the hippos there had the most consistent behaviour (although only two seasons were compared owing to the area's inaccessibility in the dry season (high flood)), supporting seasonal changes as adaptations to resource availability.

6.4.4 Effect of moon phase on hippo behaviour

The nocturnal behaviour of species can vary with the phase of the moon, with the direction of the change (i.e. increased or decreased activity with moonlight) affected by the species primary sensory system (e.g. visual vs olfactory), its taxonomy, and the habitat type (Prugh & Golden, 2014). One strategy is for animals to increase activity during moonlit nights and/or supress activity on dark nights given a greater ability to detect, and therefore avoid, predators (e.g. Joubert & Eloff, 1971; Fernandez-Duque, 2003). Alternatively, some species increase foraging activity on dark nights (e.g. new moons), relying on predators having limited ability to detect them (Navarro-Castilla & Barja, 2014). In this study, hippos rested terrestrial (an activity in which they are arguable most

vulnerable) most on nights with a full moon, indicating they may utilise the former strategy of optimising detection of predators. Predators such as lions have been shown to have lower hunting success on moonlit nights (van Orsdol, 1984). However, hippos also rested and fed on land on nights with a new moon (e.g. dark nights). This may indicate they are utilising both strategies, or perhaps simply undertaking activities needed to meet energy requirements. In the field, we did not consider moon phase when planning the data collection schedule and therefore the interpretation of the results may be limited given unequal sample sizes and confounding factors. Further, the different moon phases and their corresponding illumination may have impacted our ability to detect hippos conducting certain behaviours, impacting the results.

6.4.5 Effect of age/sex on hippo behaviour and social groupings

Variations in behaviour based on age were also observed. Diurnally, juvenile hippos in this study rested least and moved most, also noted by Bouché (2004a) and Timbuka (2012), followed by subadults and then adults. When resting, juveniles were less likely than subadults and adults to rest shallow aquatic and more likely to rest terrestrially. A lack of resting in shallow water is likely due to them being physically unable to stand in the same area as adults and remain above the surface (Klingel, 2013), whilst younger hippos may bask more than adults due to their small size and associated high rate of heat loss, especially when the water is cold (Taylor in Klingel, 2013). At night, more resting terrestrially and less feeding compared to adults (also recorded by Timbuka, 2012) arises when juveniles accompany their mothers onto land, but do not always graze, instead resting close while the mother feeds. This behaviour has been observed in other studies (Bruton, 1978; Timbuka, 2012; Klingel, 2013). Over a full day and night, subadults and adults spent equivalent amounts of time feeding, which was more than juveniles. Juveniles are likely still to be suckling (a behaviour categorised as 'other': see Section 6.6.1.3), although even young juveniles grazed (Verheyen, 1954 in Clough, 1967; Laws et al., 1966; Young, 1966). Juveniles and subadults consistently spent more time on social activity than adults, also noted by Timbuka (2012) and Bouché (2004a), often chasing and play-fighting. Had we divided social activity into aggressive and non-aggressive, we would probably have seen higher levels of aggressive behaviours from adults (particularly males) and less from juveniles (Karstad, 1984; Karstad & Hudson, 1986).

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Hippos of different age and sex occurred in different sized social groups. Adult males were more likely to occur individually or in smaller groups, as they seek out bachelor groups or claim a territory without other conspecifics (Klingel, 2013), though they did still occur in large groups, as their presence will be tolerated by the dominant male if they act submissively (Klingel, 2013). In contrast, adult females were likely to occur along with their juvenile and subadult offspring in larger nursery groups (Klingel, 2013).

6.4.6 Effect of time of day on hippo behaviour and social groupings

Our results showed that hippos exhibit a strong circadian rhythm, with time allocated to each activity and their social groupings varying throughout the day. Around sunrise, hippos generally moved individually or in small groups from land into deep water, although some hippos continued to feed on land in the hours after sunrise. Several hours were spent moving and being social or resting in deep water in small groups distributed throughout the environment. From mid-morning to mid-afternoon, hippos settled in groups and most rested in shallow water, some in deep water or on land. In the mid to late afternoon hippos began to move into the deeper water, with some feeding for several hours on land, but returning to the water before sunset. In the hours before sunset, hippos broke into smaller groups and became active and social in the water, moving in the waterways to their preferred feeding location. Aspects of these diurnal rhythms have been noted in other studies (Luck & Wright, 1964; Karstad, 1984; Eltringham, 1993b; Barklow, 1997, 2004; Timbuka, 2012; Klingel, 2013; Mekonen & Hailemariam, 2016; Nuñez, 2017). After sunset, hippos moved onto land to feed for several hours, normally in smaller groups, although some remained in the water to feed on aquatic vegetation or rest. This observation differed from previous studies that reported that hippos graze independently, or in mother-offspring pairs only (Owen-Smith, 1988; Kayanja, 1989; Klingel, 1991b; Eltringham, 1999; Timbuka, 2012; Prinsloo, 2016). We often saw hippos grazing as a group, once up to sixteen hippos, though hippos were generally in smaller groups when feeding than resting. During the middle of the night resting (both aquatic and terrestrial) peaked, with hippos often reconsolidating into larger groups. This increase in nocturnal resting was also noted by Klingel (2013) and Nuñez (2017). The low number of groups observed at night was due to the limited range of vision using the spotlight and night scope, but this should not have affected the number of hippos seen per group; by definition, hippos in one group would have been close together and we should have been

able to see them all. For several hours before sunset, there was another period of feeding before the hippos returned to the water. The two feeding peaks (after sunset and before sunrise), also noted by Nuñez (2017), may be the basis of the idea that hippos spend all night grazing (Luck & Wright, 1964; Field, 1970; Hoven, 1977; Eltringham, 1993b; Barklow, 1997; Eltringham, 1999; Klingel, 2013), with people extrapolating their behaviour between these two periods, but our data showed that hippos only spend around 25% of the night feeding, taking long breaks in the night. Prinsloo (2016) did not find time of day to affect hippo behaviour, attributing this to the minimal temperature changes throughout the days of data collection. However, later they note that hippos were less visible in the late afternoon due to increased underwater social activity and moving, suggesting their behaviour was affected by time of day.

6.4.7 Feeding aquatic

Hippos are often reported as feeding solely on terrestrial grasses (Luck & Wright, 1964; Clough, 1967; Eltringham, 1993b) and that hippo "do not eat aquatic vegetation to any extent" (Eltringham, 1993b, 1999). However, our results suggest that aquatic vegetation can be a significant food source for hippos. Whilst aquatic feeding was generally uncommon, we observed it in most areas, and during the dry season (high flood), hippos in Abu1 spent 27.2% of their night on this activity (with 4% feeding terrestrial). Hippos were observed feeding on several species of aquatic vegetation, primarily grass species, but also on blue water lily (*Nymphaea nouchali*) and the stem of papyrus (*Cyperus papyrus*). Feeding on aquatic vegetation may be more common in Abu than Chobe, as the Okavango Delta is a swamp, with generally shallow, slow moving water, with abundant aquatic vegetation. Further, more grazing areas in Abu were submerged during the high flood season, whereas in Chobe there were always areas available. We were unable to access the other Abu study area (Abu2) during this season and therefore could not confirm if hippos there exhibited similar behaviour. Hippos have been recorded feeding on various species of aquatic vegetation (bulrush, Nile cabbage, water lilies, submerged macrophytes, aquatic grasses, sedges, and reeds), sometimes in large quantities (Taylor, 1975; Hoven, 1978; Mugangu & Hunter, 1992; Harrison et al., 2008; Klingel, 2013; Mekonen & Hailemariam, 2016; Prinsloo, 2016), but despite this are still referred to as exclusively terrestrial consumers. Feeding on aquatic vegetation could be a response to a scarcity, or lack of quality, of terrestrial grass (Mugangu & Hunter, 1992; Harrison et al.,

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2008; Klingel, 2013; Prinsloo, 2016), with terrestrial grasses having lower crude protein levels than aquatic vegetation, particularly during the dry season (Mugangu & Hunter, 1992). Alternatively, it could simply be a response to an abundance of palatable aquatic vegetation due to high flood levels that is not always available in hippo pools (Harrison et al., 2008; Klingel, 2013). Unlike their terrestrial feeding style, where grasses are plucked with their lips and their snout faces the ground, when hippos fed aquatic they took the plant in their mouth and chewed to break the stems, throwing their head back to swallow the vegetation. Particularly when eating papyrus and water lilies, this method was slow, taking the hippos longer to consume each mouthful, so they possibly consumed less than during terrestrial feeding. This inefficient feeding style may be the reason that hippos do not always feed on aquatic vegetation (Mugangu & Hunter, 1992). Studies show that hippo diet varies depending on the plants available to them (Taylor, 1975), even feeding on overhanging terrestrial plants (Mugangu & Hunter, 1992), suggesting a high level of flexibility in their diet.

6.4.8 Hippo diurnal use of water and their skin

Our study showed that hippos spend substantial amounts of time on land feeding and resting, even on hot days, disputing the belief that hippos rely on water during the day, and feed nocturnally, due to their skin physiology. Luck & Wright (1964) concluded that hippo skin had excessively high rates of evaporative water loss (EWL) when exposed to air, suggesting they lacked heat loss control at the skin surface and effectively could not thermoregulate, hence their reliance on water during the day. However, the EWL was deemed high compared to only two animals, humans and cattle. It has since been incorrectly referenced as the highest rate of EWL observed for *any* other mammal (Jablonski, 2004), which in turn has been referenced (e.g. Timbuka, 2012). Luck & Wright's (1964) conclusions were interpreted to mean that hippo skin is overly sensitive, that a hippo on land in hot weather risked rapid dehydration, and that hippo skin will desiccate and crack if exposed to air (Field, 1970; Estes, 1991; Eltringham, 1993b, 1999; Jablonski, 2004; Blowers, 2008; Mazza, 2015; Mpemba, 2015; Stommel et al., 2016; Prinsloo, 2016; Lewison & Pluháček, 2017), although Luck & Wright (1964) did not report desiccation or cracking. We did not observe hippo skin cracking and found only two examples where cracking of skin had been directly observed: a hippo kept out of water for six days (Arman & Field, 1973) and a juvenile zoo animal (Young, 1966). A

subsequent study showed that a hippo denied access to water on a hot day was able to effectively thermoregulate through controlled EWL, with no obvious consequences (no adverse skin effects) and no apparent discomfort (it remained placid throughout the nine hours) (Wright, 1975, 1987).

While resting in water and grazing at night undoubtedly aids in thermoregulation and lowers energy expenditure, our results indicate that hippos are not as physiologically reliant on water as has been suggested in other studies. Hippos grazing during the day may be seeking to meet daily food requirements (Mugangu & Hunter, 1992; Timbuka, 2012; Klingel, 2013), justifying their appearance out of the water, but we also saw hippos on land resting. Further, this study found that hippos were more likely to rest on land diurnally during the hottest dry season, and during the middle of the day, which has also been noted in other studies (Luck & Wright, 1964; Ansell, 1965a; Clough, 1967; Klingel, 2013). Noirard et al. (2008) found a positive effect of air temperatures on sun exposure, with hippos resting exposed at temperatures up to 50°C (his definition of "exposed" was > 50% of the body out of the water). We observed hippos resting on cloudless days, on sandbanks devoid of shade, in the middle of the day with temperatures reaching up to 35°C, for several hours (see Section 6.6.1.1); hippos in Chobe1 spent up to 16% of their day resting like this. Hippos basking in the sun for hours has been noted before (Olivier & Laurie, 1974b; Klingel, 1991b; Viljoen & Biggs, 1998), yet the significance of this behaviour is rarely pointed out, and the idea that hippos must exist in water is perpetuated. Timbuka (2012) had an activity code dedicated just to standing on land, which was 9% of the diurnal activity budget (feeding terrestrial was an additional 20% of the day). Remarkably, he mentions that, in the dry season, in the absence of water, hippos sought refuge under the shade of trees, suggesting that hippos were occurring in a habitat devoid of water. Our results, and references in the literature, suggest that hippo skin is unlikely to be as sensitive to desiccation as has been theorised.

We propose that in addition to thermoregulatory advantages, hippos use water as a refuge from disturbance, both predation and human harassment (Field, 1970; Martin, 2005). Their propensity to return to deep water, often running and triggering a mass return, at even the slightest disturbance (see Section 6.6.1.2 and Clarke 1953; Pooley, 1967; Klingel, 1991a; Eltringham, 1999; Onyeanusi, 2004) further supports this idea. During

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boat surveys, hippos lying on sandbanks rushed into the water upon seeing the observers (Ansell 1965), hippos preferring to bask in areas where human disturbance is minimal (Clarke, 1953; Klingel, 1991a, 2013; Onyeanusi, 2004), and hippos leaving the water at night for feeding often avoid people (Onyeanusi, 2004; Prinsloo, 2016). Hippos that had previously rested on land stopped this activity following a period of strong disturbance (e.g. hunting, persecution) (Ansell, 1965a; Klingel, 1991a; Bouché, 2004a). Preferentially resting terrestrial close to water (personal observation; Eltringham, 1999; Nuñez, 2017) has been explained as allowing a quick return in case of overheating (Eltringham 1999), but could also represent attempts to remain close to water for safety. We observed hippos preferentially moving to grazing areas using waterways, also noted by Klingel (2013) and Karstad (1984), even at night, supporting the idea of water as a refuge. Hippos undoubtedly feel vulnerable on land (Eltringham, 1999; Bouché, 2004a; Onyeanusi, 2004). Alternatively, hippos may also prefer resting and moving in water to reduce energy expenditure with the water supporting their heavy body (Field, 1970; Wright, 1973; Eltringham, 1999).

6.5 Conclusions

Our study reveals previously unknown details about hippo behaviour. Despite their importance to the African ecosystem (e.g. McCarthy et al., 1998; Stears et al., 2018) and status as a charismatic megafauna, this is the first observational study on the nocturnal activity budget of hippos, and the first diurnal activity budget to investigate specific habitat use by hippos. The results suggest an ideal hippo habitat would include a mixture of shallow and deep water for resting, deep water for moving and social activities, sandy areas for basking in the sun which (Olivier & Laurie, 1974; Karstad, 1984), along with grazing grounds, are inaccessible to human disturbance. Large variations in activity budgets between different areas indicate hippos adapt their behaviours to their environment, taking advantage of available resources (e.g. sandbanks for resting, and aquatic plants when terrestrial grasses are scarce), but emphasising the sensitive nature of hippos to human disturbance. This should be considered in tourist developments, where the constant presence of humans may be impacting natural hippo behaviour (Prinsloo, 2016).

6.6 Appendix

6.6.1 Notable field observations

<u>6.6.1.1 Resting terrestrial</u>

The longest continuous bout of resting terrestrial was by three hippos at Chobe2 for six hours (21:30–03:30, September 2017). Another notable occurrence occurred in October 2017, where 24 hippos rested terrestrial as a group for 3.5 hours (22:35–02:05, Chobe1). Diurnally, the longest uninterrupted bout was by one juvenile, who rested terrestrial for almost three hours from 09:15 to 12:25 (May 2018, Chobe1). In September 2018, two hippos rested terrestrial for almost 2.5 hours (14:10–16:30, Chobe3) with an average temperature during this time of 35.5°C. In addition, there were multiple occurrences of most hippos in Chobe1 (up to 28 hippos) hauling out from the water and resting terrestrial on the sandbank for around 2.5 hours in the middle of the day (Figure 6.12). These values are the minima; there were often hippos resting terrestrial before/after the given times, but we could rarely identify individual hippos.

Figure 6.12. Chobe1 hippo pod resting terrestrial on the sandbank adjacent to their lagoon.

<u>6.6.1.2 Interactions with predators, other animals, and humans</u>

We observed several interactions between hippos and predators, but never a successful attack or injuring. In August 2017, hippos at Chobe1 were resting terrestrial as a group when three lionesses approached and one pounced on a juvenile. Before the attack, the hippos were not vigilant, appearing not to notice the approaching lions although they were

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moving through an open area. Upon attack, all the hippos (including the juvenile) ran into the water and watched the lions move past the lagoon (Figure 6.13). The juvenile did not appear to be injured. After approximately 30 minutes, the hippos begun to move back onto land, although several times they became disturbed by unknown sources and ran back into the water, before again moving out. Towards the middle of the day the hippos settled and rested terrestrial without interruption. On another occasion, a lion walked past hippos resting aquatic, but the hippos did not appear to be disturbed. Another interaction occurred when a lone adult bull hippo at Abu1 left the water at sunset and begun feeding when a leopard ran towards the hippo from behind. The hippo turned to face the leopard without any other apparent aggressive display, and the leopard retreated. Several times, leopards and wild dogs were seen drinking from the water where hippos were resting, and the hippos remained vigilant but did not react in any other way. Hippos rarely seemed disturbed by hyena or jackal. We often observed hippos close to large crocodiles both in the water and on land, without any apparent changes in behaviour (though see Section 6.6.2). Hippos were often disturbed by elephants moving through the water, normally reacting passively by vocalising, yawning and moving away, although on several occasions we observed hippos acting aggressively, by moving towards the elephants and blocking their path, but retreating when the elephants charged. Hippos that were resting on land were sometimes disturbed by elephants walking nearby and would retreat into the water. No physical contact was ever observed between the two species. Clarke (1953) also noted that hippos were disturbed by elephants.

Figure 6.13. Hippos at Chobe1 watching a lion move past after an attempted attack on a juvenile.

The hippos were often vigilant towards, and disturbed by, the presence of humans, particularly when on land. Hippos acted aggressively towards me twice, one instance is mentioned in Section 6.6.2, and the other occurred after the above-mentioned leopard incident, where the hippo charged my car, stopping after a short distance. Disturbances were often accompanied by group vocalisations and almost always with all hippos retreating to the water. A single hippo entering the water would often result in all other hippos rushing back to the water, even if there appeared to be no obvious catalyst.

6.6.1.3 Social and other activities

Mating was observed seven times and in all three seasons; once on 18 January 2018 (Chobe3, diurnal), twice on 21 May 2018 (Chobe1, diurnal), once on 29 May 2018 (Chobe1, nocturnal), and three times on 8 September 2018 (Chobe2, diurnal). Consistent with other studies, we observed hippos mating more than once in a day (Krueger, 1997; Klingel, 2013; Mekonen & Hailemariam, 2016), but we could not confirm if it was the same bull and female mating. We only observed mating occurring in water, consistent with other studies (Laws et al., 1966; Scotcher, 1973; Klingel, 1991b, 2013; Eltringham, 1999; but see Onyeanusi, 2004), with the female almost entirely submerged, raising her nostrils to breathe every several minutes. Other hippos, particularly juveniles and subadults, would often remain close, diving around the mating pair, confirmed by Ansell (1965). We never observed the copulating pair displaying aggressive behaviour, which has been seen elsewhere (Scotcher, 1973; Krueger, 1997).

Grooming (licking) of conspecifics was a rare occurrence, recorded three times. Dung paddling occurred often, only ever by adult males, normally immediately when a hippo left or entered the water, but also when hippos were on land, sometimes far from the water. At Abu1, we observed two bulls leave the water and walk together, both stopping several times to dung paddle on the same spots one directly after the other. Despite the known territoriality of hippos, we only observed fighting between bulls three times (once, September 2017; twice, January 2018), though non-serious sparring was a common occurrence, especially by two bulls in Abu1.

The activity category 'other' was discarded prior to analysis due to the low number of times recorded (approximately 0.04% of the scans). Behaviours that were recorded as

'other' included rolling in the water, geophagia of sand (once, September 2017), blowing bubbles (differed from bubbles produced during communication), drinking (twice, September 2017 and February 2018), nursing (once, January 2018), and scratching snout on the sand. Nursing occurs predominately in water, with the female lying on her side and the juvenile submerging to suckle (Laws & Clough, 1966), which may be why it was so rarely observed.

6.6.2 Observations on the response of a pod of hippos to a dead juvenile hippo

The below field note detailing observations of hippos at Chobe1 reacting to a dead juvenile conspecific was published in the African Journal of Ecology. The data from this day was not included in the analysis for this chapter.

6.6.2.1 Introduction

Hippos are gregarious animals, generally occurring as pods comprising females and their young, a dominant male, and subordinate males (Klingel, 2013). The most stable relationship in a pod is between a mother and her young (Klingel, 2013). Within a pod, the dominant male has exclusive mating rights and has been known to commit infanticide, which is thought to reduce the interbirthing interval of the female (Lewison, 1998). Given their size and aggressive nature, adult hippos have few natural predators; however the smaller juveniles are more vulnerable (Klingel, 2013).

There is little published literature on the behaviour of hippos following the death of a conspecific. The available literature focuses on rare occurrences of hippos consuming the meat of a hippo carcass (Dorward, 2015). Records of mammals interacting with dead conspecifics in an epimeletic manner (maintaining physical contact, moving/carrying, and protecting carcasses), are increasing (e.g. Reggente et al., 2016; Bearzi et al., 2017). Species displaying these behaviours include giraffes (Bercovitch, 2013; Strauss & Muller, 2013), elephants (Douglas-Hamilton et al., 2006), non-human primates (Cronin et al., 2011; Fashing et al., 2011; Yang et al., 2016), and cetaceans (close relatives to hippos, Reggente et al., 2016), and reports commonly relate to a female interacting with the carcass of a juvenile. There are photographs/videos showing hippos interacting with hippo carcasses (Anon, 2006, 2008; Breen, 2010; Harris, 2014; ViralHog, 2016) and defending carcasses from other animals (Anon, 2008; Harris, 2014; Csaba, 2017);

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providing anecdotal evidence that hippos may also display epimeletic behaviour towards dead conspecifics.

This note documents detailed observations of an adult female hippo and pod interacting with a dead juvenile (< six months old) hippo within their aquatic habitat over the course of eleven hours.

6.6.2.2 Methods

As part of a project investigating hippo behaviour, the observer (Victoria Inman) regularly conducts full day observations on hippo pods. The observations reported here occurred from 06:45 to 17:30 on 14 September 2018 at a hippo pool (17.82823°S, 25.02928°E, 0.5 ha) in Chobe National Park, northern Botswana. The observations were made from a vehicle parked approximately 50 m from the edge of the pool, with the hippos between 50–160 m from the observer during the observation period. The behaviour, movements, and time of interactions were recorded as they occurred; opportunistic images and videos were also taken. Binoculars (8 x 42, FOV 426ft) were used to observe the hippos where necessary.

6.6.2.3 Results and discussion

The pool where the observations occurred was known to support a pod of 24–26 hippos (4 and 7 September 2018). At 6:45am on 14 September 2018, it was observed that there was only one adult female in the pool and a juvenile hippo carcass, for which the cause of death was unknown. We consider it likely that the adult female was the mother of the dead juvenile, as it was the only hippo that had remained with the carcass. Additionally, she was an adult female, and had enlarged mammary glands consistent with a lactating female (Laws & Clough, 1966). Other members of the pod were in the main channel approximately 110 m away from the pool.

From 6:45–12:30, the female alternated between moving around the pool, interacting with the carcass, attacking and chasing crocodiles feeding on the carcass, and for short periods of time resting in the water. The interactions involved the hippo pushing the carcass around the water with her muzzle (Figure 6.14), lifting the carcass out of the water with her head, and taking the carcass in her mouth and moving around the pool, diving and

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submerging (Figure 6.15). Several times the female shook the carcass quite forcefully. Twice, the female came to the edge of the pool, partially moved onto land, and displayed aggression by yawning at the vehicle. This behaviour was unexpected as these hippos are habituated to vehicles. The aggressive behaviour of the hippo towards the crocodiles is also uncommon; hippos and crocodiles generally share this pool without conflict (personal observation). Further evidence of uncommon behaviour was the amount of small bubbles the hippo created as it moved underwater. The majority of hippo communication occurs amphibiously (Barklow, 2004), and some sounds produce bubble streams (Maust-Mohl et al., 2018). Throughout the morning, the adult female vocalised three times, which garnered a response from hippos in the main channel.

Figure 6.14. Photograph of adult female hippo pushing juvenile carcass through water with her muzzle.

Figure 6.15. Photograph of adult female hippo moving with juvenile carcass in her mouth.

At around 12:30, seven hippos (two adult males, two adult females, one subadult, and two juveniles) moved as a group on land from the main channel to the pool where the original female was. Normally the hippos move from the main channel to the pool early in the morning; however, on this day they appeared to have delayed their arrival. Whilst the original female continued to interact with the carcass (Figure 6.16), as far as the observer could tell the other hippos did not.

Figure 6.16. Photograph of adult female hippo pushing juvenile carcass to the surface of the water with her body. Note adult male in background.

From 12:30–13:30, the original female continued interacting with the carcass, eventually pushing it to a shallow section of the pool, so that the carcass was half submerged. Immediately after this, at around 13:30, all the hippos, including the original female, moved as a group rapidly back towards the main channel (stopping on the sand bank adjacent to the channel).

Between 13:30–14:30, the group of hippos slowly and individually or in pairs walked back to the pool. Five additional hippos joined, making a total of thirteen hippos in the pool. This movement back and forth between the two areas was uncommon and possibly due to the presence of the carcass.

For the remainder of the observation period (14:45–17:30) all thirteen hippos stayed in the pool. Initially, the other hippos had limited interaction with the carcass, but this gradually increased as the day progressed. This ranged from touching the carcass, pushing it around the pool, and taking the carcass in their mouths and moving with it. At this time,

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it was impossible to distinguish the original observed adult female from the later arrivals and this individual behaviour was lost.

Cannibalism in hippos has been recorded (Dorward, 2015) and, whilst there were numerous times when different hippos had the carcass in their mouths, it was unclear if any consumption of the carcass occurred. In videos of hippos consuming meat, the hippos move their mouth up and down on the meat in a typical "chewing" motion and lift their head up to swallow. This head back swallowing motion has been seen numerous times by the observer when hippos eat aquatic vegetation. No hippo on this day was observed to be doing this action, however the possibility of cannibalism cannot be disregarded. Upon conclusion of the observation period, the carcass was significantly damaged, which can probably be attributed to crocodile scavenging.

This paper provides support for another mammal species exhibiting apparent epimeletic behaviours towards a dead conspecific. The interactions that occurred, particularly the adult female defending the carcass from crocodiles, lifting the carcass out of the water, and moving the carcass to a shallow section of water before leaving it, are consistent with other observations in highly social animals (King, 2013).

Chapter 7: General discussion

7.1 Summary of findings

The nature of hippos as a dangerous animal with a nocturnal, amphibious lifestyle has impeded researchers' ability to study them (Karstad, 1984; Krueger, 1997; Lewison, 2002). Our understanding of their biology and ecology is limited, particularly for hippos occurring in wetlands, yet management and conservation relies on understanding a species' distribution and size, habitat use, and response to environmental changes (Ríos-Saldaña et al., 2018; Stears et al., 2019). Without baseline information, our ability to assess the health of a population, its future trajectory and to predict how threats will impact them is hindered, and management efforts may be misplaced and ineffective (Sanderson et al., 2002; Ríos-Saldaña et al., 2018; Hawke et al., 2019). Knowing their importance to the ecosystem, researchers have urged for studies on hippos in the Okavango Delta for decades (Eltringham, 1993b; McCarthy et al., 1998b; Alonso & Nordin, 2003), yet my work is the first to be undertaken. In this thesis, I have collated and analysed information about hippos in the Okavango Delta over a broad range of topics and developed and provided new methods to aid future researchers in the continued study of this important species.

Studying a species at a population or landscape level is difficult, requiring both broad-scale data on that species, but also environmental datasets covering a large area, which are often difficult to obtain (Pidgeon et al., 2003; Murray et al., 2008; Shifley et al., 2008). This is even more likely in developing countries, where data are less likely to be available (Maeda & Torres, 2012; Nordling, 2019). Datasets that are available often do not cover the entire area of interest or are too broad scale (e.g. 1 km spatial resolution). This was true for the Delta, where previously developed flood maps were out of date, at coarse resolution, and not publicly available. Therefore, a necessary first step to examine the Delta's hippo population was to develop these resources. In Chapter 2, I adapted an existing classification method to produce flood maps of the Delta, using higher-resolution imagery than previously used and automating it for ease of use and adaptation to the dates I required. These maps had high accuracy, which ensured their validity for use in other chapters. The results of this work further emphasised the dynamic nature of water in the Delta, which throughout this thesis were shown to be a significant influence on hippos.

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In Chapter 3, I examined hippo spatial and temporal patterns in the Delta using aerial survey data collected by the Department of Wildlife and National Parks (DWNP) and Elephants Without Borders (EWB). I used rainfall and inflow data, as well as flood and surface water extent (both at the time of surveys and long-term patterns), and a vegetation classification, to investigate what drove variations in spatial and temporal abundances of hippos. Between 1996 and 2018, the Delta's hippo population has grown substantially. The increase most likely represents a recovery of the population after a period of extremely low rainfall/flooding prior to surveys, with population size increasing with long-term increases in rainfall and inflow within the region. Hippo distribution in the Delta was influenced by long-term flooding patterns and current surface water presence, with the seasonal swamps being the highest utilised areas, while hippos avoided the permanent swamps and main channels. At a fine-scale, hippos preferred areas with access to large areas of open water (e.g. large lagoons) for diurnal resting sites. Examining hippo population trends and the environmental factors driving them, and determining how hippos use the landscape, allows us to understand the relative importance of resources for hippos, and therefore to anticipate how future changes in the availability of these resources will impact the population.

In Chapter 4, I developed methods to monitor hippos at a finer scale using a drone, taking measurements from the drone images to assign ages to hippos. I determined that flying the drone at a low height, at a time of day when hippos are resting as a group with the majority of their body exposed, allows easy counting and ageing, that was as/more accurate than assessments from the ground. A weakness of the drone method was the inability to get full body length measurements for many hippos as they were not fully exposed (particularly young hippos). To overcome this, I collected several other body measurements and divided body length into head, neck, and back lengths, imputing missing values, and hence reducing the requirement to have a full body length measurement. This substantially increased the number of hippos I could age and increased the counts of juveniles and subadults. I also attempted to distinguish the sex of individual adults using this method with some success, although further development is required (see Section 7.2).

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I used these methods in Chapter 5 to investigate seasonal variations in hippo pod sizes, densities, demographic composition, and distributions. Hippo pods in the Delta were dynamic, varying with changing water throughout the seasons. When water was abundant, hippos spread out in the study area, whereas they aggregated together during the low flood season. In addition to responding to changes in water, the pods had a generally high baseline level of change, with hippos constantly moving between lagoons. This suggests hippos within the Delta do not form stable groupings, instead individually selecting habitats with suitable resources. Hippos generally preferred larger lagoons and these were particularly important in the low flood season when many other lagoons were drying, although some small lagoons were heavily occupied by hippos, suggesting hippo habitat selection is more complex than this study could account for. Compared to other populations, pods in the Delta were moderate in density and size and there were a high percentage of solitary hippos, indicating hippos in the Delta are not subject to overcrowding. The results obtained in this study on hippo reproduction (that hippo births peak in the wet season) were similar to other reported studies, emphasising the likely importance of high quality graze for lactating females (Laws & Clough, 1966; Clough, 1967; Marshall & Sayer, 1976; Smuts & Whyte, 1981).

Although more accurate at counting hippos, small multirotor drones like the one used in this study are not suitable to replace large scale aerial surveys owing to their limited battery life and range. They are however valuable as an alternative to small-scale ground surveys, being as accurate as other methods, minimising disturbance to wildlife, protecting researchers, and allowing access to remote or inaccessible areas (Francis et al., 2020). For example, in the Delta during the high flood season, vast tracts of floodplain were inundated, reducing my access by vehicle, with only six lagoons able to be (partially) surveyed from the ground. However, with the remote access of the drone, I was able to survey the entirety of 15–18 lagoons. Difficulties accessing hippo pods has restricted studies previously, including the behavioural chapter of this thesis, with researchers often choosing study areas based on accessibility (Scotcher, 1978; Timbuka, 2012; Prinsloo, 2016). Further, drones can collect data that would otherwise be problematic or impossible to obtain from the ground. For example, regarding the construction of age frequency tables of hippos, Eltringham (1999) states "this is difficult, if not impossible, with living animals as their ages cannot be determined in the wild". Yet

in this thesis, I was able to use measurements from drone images to collect and develop this information. I foresee the methods outlined in this thesis being used and adapted by other researchers to continue collecting count and demography data on hippo, removing a previous obstacle to hippo research.

In Chapter 6, I investigated hippo behaviour and established their 24-hour activity budgets, again examining how hippos were affected by seasonal variations in resources, at an even smaller scale. I extended this work to another site (Chobe River) to determine if behaviour varied between regions and habitat types. Hippo activity budgets were influenced by season, but also varied between pods within the same region. This is likely due to very fine-scale differences in resource availability for the different pods, with hippos adapting their behaviours to their environment, but also differing levels of habituation. In this chapter I noted a clear circadian rhythm for hippo behaviour, with peaks in activity at dawn and dusk; this is most likely the reason why hippos were thought to be active all night. I examined the commonness of behaviours and the habitats they used, finding many assumptions about hippos to be unsupported by my data. This study revealed previously unknown details about hippo behaviour, being the first observational study on the nocturnal behaviour of hippos, and the first diurnal behaviour study to investigate specific habitat use. Using these results, I outlined the minimum habitats requirements of hippos.

Although I collected data using different methods at different scales, results among chapters were consistent, corroborating the interpretations I made. For example, rapid population growth (Chapter 3), early reproductive maturity (Chapter 4), and small pod sizes (Chapter 5) indicate a population well below carrying capacity of the habitat, with little overcrowding, and unlikely to be experiencing suppression (Attwell, 1963; Laws & Clough, 1966; Clough, 1967; Laws, 1968b; Sayer & Rakha, 1974; Marshall & Sayer, 1976; Scotcher, 1978). The behaviour chapter was particularly valuable in explaining other results, demonstrating the value in collecting small scale data. In Chapter 4, I determined the middle of the day was the best time to count hippos with the drone, and the reason for this is apparent when looking at the behaviour data, with hippos tending to rest as one large group, often in shallow water, during the middle of the day. Further, it was more difficult to get body measurements for juveniles and subadults with the drone.

This was explained by the behaviour results, where juveniles and subadults spent less time resting in shallow water than adults and more time moving, restricting opportunities to take body measurements. I noted an increase in hippos feeding terrestrial in the lower-medium flood seasons and attributed it to higher grass availability. It may also be influenced by the presence of heavily pregnant/lactating females in these seasons (Chapter 5) which consume larger amounts of grass (Laws & Clough, 1966).

7.2 Limitations and future research suggestions

A field study must consider logistics, safety, practicality, and efficient use of time, and this can prevent continuous, complete data being collected. For example, in Chapter 5 I monitored hippo pods for a year, however I did not capture the entire period regularly, and instead took breaks between seasons. Constant regular monitoring throughout the year would have allowed me to capture the transitional periods between the seasons, where change was predicted to be the most dramatic. It would have also allowed me to determine the threshold of water at which hippos change lagoons. This schedule was not logistically viable in this study but would be of interest/consideration in future studies.

Hippos are typically surveyed alongside other species using standard strip-transect sampling (Chase et al., 2015, 2018). However, the clumped distribution of hippos, occurring diurnally in select waterbodies, means transects can significantly undercount hippos as large pods that occur between transects are missed. Therefore, in Chapter 5, I used existing data (location and size of lagoons) as an effective way to concentrate survey effort, surveying areas of open water (e.g. lagoons) only and restricting surveys to lagoons over a certain size (0.001 km^2). It is possible that hippos could have occurred in other areas, or in smaller lagoons, and would not be counted using this method; however, the survey effort had to be restricted to reduce flight times and ensure efficient use of battery life. I considered the likelihood of many hippos occurring outside of lagoons to be low. This conclusion was supported by no hippos being observed outside the surveyed lagoons during the aerial survey (Chapter 4) or when flying between lagoons during drone surveys. The smallest lagoon occupied by a hippo (and only one solitary hippo once) was 0.0016 km^2 and this was just above my threshold for surveying lagoons. The next smallest occupied lagoon was three times the threshold, providing support for the decision to restrict our survey effort to lagoons over a set size. It is more likely that hippos could be

adjacent to lagoons (e.g. resting on land, feeding in adjacent floodplains). The addition of a buffer around lagoons would increase confidence that all hippos were counted, and I recommended this for future drone surveys.

A limiting factor of the drone surveys was differentiating individual hippos, as well as males from females. I relied on spatial relationships to assign sexes (e.g. solitary hippos as male) and from this demonstrated scope to recognize large males, but not to differentiate smaller males from females. Future work collecting and analysing data on more hippos, as well as assigning sexes through visual assessment (though difficult in itself), could reveal subtle differences between the sexes. Improvements in sexing hippos from the drone, as well as identifying individuals, would allow detailed demographic and habitat selection studies, and the life history and movements of individuals could be tracked. Much of the current life history information on hippos (e.g. age-based mortalities) is taken from culled hippos, which are known to inaccurately represent younger animals (Laws & Clough, 1966; Pienaar et al., 1966; Laws, 1968a; Sayer & Rakha, 1974). Identifying individuals would be possible, though difficult, with drones. By flying lower or using a higher-quality camera with zoom, distinct features (e.g. scarring) or temporary markings applied through non-invasive techniques (e.g. paint, Klingel, 1991b) could be identified. Difficulties in identifying the sex of individual hippos also limited my ability to determine differences in behaviour between male and female hippos.

Despite their reputation, I observed hippos to be easily disturbed by humans, which limited my collection of behavioural data, particularly in less habituated pods. This disturbance may be observed in my data, where some pods did not partake in particular activities (e.g. resting terrestrial during the day) when access to this habitat included human presence. Nonetheless, the data I collected improves on our very-limited understanding of hippo behaviour. I noticed hippos were disturbed by boat traffic that occurred in Chobe National Park in the high flood season. Hippos are known to be sensitive to this (van der Sluis et al., 2017), with reports of large numbers of hippos relocating from an area due to increased boat traffic (Roodt, 1998 in Mbaiwa, 2003). The impact of human presence on hippo behaviour should be afforded more research and the results used to advise best practices to reduce wildlife disturbance in tourist locations.

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As mentioned in Chapter 6, an alternative to observational studies to collect behavioural data is GPS tracking devices, typically with accelerometers, where data are assigned to activities based on movement signatures (Handcock et al., 2009; Löttker et al., 2009; de Weerd et al., 2015; Nuñez, 2017). This method removes the requirement of a constant observer, saving considerable time for researchers and reducing disturbance to the animal (Löttker et al., 2009). However, fitting tracking devices to hippos is notoriously difficult; neck collars are not viable as the similar size of a hippo's head and neck allows it to slip off (Eltringham, 1999). Further, immobilising hippos is difficult due to a high drowning risk (even if darted on land hippos will attempt to return to water when disturbed) (Klingel, 1991a; Eltringham, 1999), with typically administered drugs causing high rates of apnea (Stoskopf & Bishop, 1978; Ramsay et al., 1998). New drug combinations alleviate some of these issues, although they risk spontaneous wake-up (Burroughs et al., 2006). Recently, GPS tags were attached to hippo skin with barbs using a crossbow (removing the need for immobilisation) and used to analyse hippo movements and behaviour (Nuñez, 2017). This method restricted assigned behaviours to broad classes (e.g. moving, feeding, resting) and tags were generally only attached for a few days (Nuñez, 2017). GPS ankle collars have also now been successfully fitted to hippos, though these required immobilisations (Stears et al., 2019). Future research should aim to dispense more of these GPS devices, fitting more hippos of broader age and sex range, as an alternative source for behaviour data and to investigate differences in behaviour between demographic groups. For example, I predict that female adult hippos would feed more than adult males due to increased energy requirements for pregnancy and lactation. Behavioural data derived from GPS devices also removes human-disturbance bias, particularly for nocturnal behaviours when hippos were most influenced by human presence. I hypothesise that hippos tagged with GPS devices would spend more time on land compared to when they are being observed, due to reduced human disturbance. However, a major disadvantage of GPS devices is that no data can be obtained when hippos are submerged in water and therefore behaviour cannot be assessed for a large portion of the day. Tracking could be complemented with aquatic observations to obtain a full view of behaviour. Alternatively, new devices could be developed, particularly those not requiring immobilisation, which can be attached to a hippo's head or neck so that even when resting in the water data can still be obtained. Potential devices could

include ear or nose tags, which have previously been dismissed (Eltringham, 1999), but may now be viable owing to technical advances and reductions in weight.

The multiple ways in which hippos act as ecosystem engineers have not been equally researched. The impact of hippos on grasslands (and consequently other herbivores) has been considered in depth (e.g. Field & Laws, 1970; Lock, 1972; Eltringham, 1974; McCauley et al., 2018) and, more recently, their role as vectors of nutrient transfer has been examined in several ecosystems (Dawson et al., 2016; Dutton et al., 2018; Stears et al., 2018). However, the impact of hippo movements on wetland ecosystems (specifically the Delta) although described in a seminal paper in 1998 (McCarthy et al., 1998b) and since widely referenced (e.g. Graham et al., 2002; Milzow et al., 2009a; Subalusky et al., 2015), has yet to be quantified. This is likely because, until recently, information on hippo movement was anecdotal or measured indirectly (e.g. measuring hippo trails) (Field & Laws, 1970; Lock, 1972; Harrison et al., 2008). GPS tracking devices now allow hippo movement to be directly quantified, though continue to have limitations (e.g. battery life can be limited if using short logging intervals). The two studies mentioned above (Nuñez, 2017; Stears et al., 2019) have already substantially improved our understanding of hippo movement, and subsequently their habitat use, home ranges, and their impacts on the ecosystem through nutrient transfer. Both studies were conducted in riverine ecosystems in east Africa (Tanzania and Kenya), and therefore may have limited relevance to the Delta wetland and therefore could be replicated in this ecosystem . Further, the detailed level of movement data available from GPS trackers would be invaluable to quantify the patterns and extent of the paths that hippos create throughout the landscape, which in the Okavango Delta are thought to maintain the floodplains that comprise it. Quantifying the impact of hippo movement on long-term changes in the Delta (e.g. the transition of hippo paths into main channels) would be difficult due to the timescale over which these changes occur. Nonetheless, examining the role of their movements over shorter time-periods in discrete areas would help to understand the mechanism of these changes. Based on descriptions in McCarthy et al. (1998b), I hypothesize that in the Delta:

- when hippos move through a new area they will create a path (an area with less vegetation than before)
- a highly used hippo path will be deeper, wider, retain water longer, and take longer to grow over with vegetation than a less-used hippo path

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- a path that hippos stop using will grow over with vegetation
- at the arrival of the flood, a hippo path will flood before the surrounding floodplains
- hippo paths will have higher rates of water flow than surrounding floodplains (only relevant at the proximal end of the Delta where water flow is higher)

To investigate this, path use by hippos could be quantified using GPS devices that maximise readings even when hippos are in water (so placed either on the head or neck of the hippos) and camera traps established along paths. Vegetation encroachment and path width could be measured from high-resolution orthomosaics developed from drone images or potentially from high commercial high-resolution satellite imagery (e.g. WorldView-3 imagery at 31 cm resolution). These could be supplemented by ground assessments of paths (e.g. depth, flow) where safe and logistically possible. Clarifying the role of hippos will improve our understanding of the functioning of this valuable wetland, also emphasising the importance of maintaining healthy hippo populations.

Ultimately, conservation relies on regular, accurate estimates of populations, so that reductions in number of individuals can be detected, factors triggering them can be mitigated, and the success of management assessed (Bennun, 2001; Kingsford & Porter, 2009; Robinson et al., 2018). Long-term survey data are invaluable for understanding the trajectory of a species, but also can be used for non-target research, such as examining habitat use as demonstrated in this thesis. Botswana's hippo population should continue to be monitored regularly using high quality survey techniques, such as EWB's use of cameras and surveying at a higher sampling intensity over smaller strata. Regular surveys provide a baseline, and therefore context, for changes in a population. For example, if a survey is conducted within the next few years, EWB's 2018 wildlife survey can act a baseline to assess the impact of the 2019 drought on hippos. Further, monitoring and research efforts are urgently needed for hippo populations occurring in west and central Africa; populations which are small, have little known about them, and which may comprise a different subspecies (Eltringham, 1999; Okello et al., 2005; Stoffel et al., 2015). For example, a recently published population estimate for Nigeria (using a combination of recent and older surveys) was only 220 hippos (Baker et al., 2020), with estimates from other countries based on data collected decades prior (Lewison & Oliver, 2008; Lewison & Pluháček, 2017). Small populations are more vulnerable to local

extinction and risks due to low genetic diversity (Ellstrand & Elam, 1993; Ginsberg et al., 1995; Matthies et al., 2004; Cremona et al., 2017) and therefore protection should be prioritised to maintain maximum genetic diversity (Stoffel et al., 2015). High quality surveys (restricted to potential hippo habitat and informed by local knowledge) would give a snapshot of the size, distribution, and density of these smaller hippo populations, from which informed conservation actions could be based.

7.3 The future for hippos in Botswana

It is clear that Botswana's hippo population (the majority which occur in the Delta) should no longer be dismissed as insignificant. Comparing populations estimates from recent surveys (Chase et al., 2018) to values provided by the IUCN (Lewison & Pluháček, 2017), suggests Botswana has the third largest population in Africa, and must therefore be recognised as an important stronghold population and prioritised in future research efforts. In contrast to many other countries where hippo populations are decreasing, sometimes substantially (Lewison & Pluháček, 2017), the hippo population of Botswana is increasing. The large size of the hippo population is probably at least partially explained by the protection they are afforded, being subject to minimal direct human impacts (e.g. poaching, hunting). In Botswana, poachers have not generally targeted hippos, concentrating their efforts for meat on smaller ungulates (e.g. impala) and for ivory on the large elephant population (Central Statistics Office, 2005; Statistics Botswana, 2015, 2017; Schlossberg et al., 2019). In 2018, hunting was re-opened, though historically hippos have not been hunted in Botswana (Barnett & Patterson, 2006). Hippo-human conflict is relatively minimal in Botswana, representing 0.5% and 2% of problem animal incidents between 1999–2003 and 2010–2014, respectively, which led to eight hippos killed between 1999–2003 (no data available for the latter dates) (Central Statistics Office, 2005; Statistics Botswana, 2017). This is owing to hippos being generally constrained to protected areas or wildlife management areas where agriculture is minimal (the Delta panhandle is an exception). Expansion of agricultural areas into hippo habitat could lead to increases in hippo-human conflict and subsequent increases in hippo mortalities, as seen elsewhere (Dunham et al., 2010; Kendall, 2011; Kanga et al., 2012). A potential threat to hippos in Botswana is their close proximity to international boundaries (e.g. the Delta panhandle with Namibia) making them vulnerable to differing management in those countries (Martin, 2005). If the current high standard of wildlife

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management and protection is maintained, and wildlife areas are preserved, the hippo population in Botswana is unlikely to be significantly negatively affected by direct human impacts.

However, the protection granted to hippos will not prevent them being negatively affected by anthropogenic changes to the environment and climate. The Delta is particularly vulnerable as its water sources occur over multiple international boundaries, making water management more challenging (Mosepele et al., 2019). Proposed water abstractions, damming, and increased use of water for agriculture in Namibia and Angola will reduce the amount and quality of water entering Botswana (Murray-Hudson et al., 2006; Milzow et al., 2010; Bamutaze et al., 2019). Further, climate change may exacerbate this issue, with decreased rainfall coupled with increased temperatures and evaporation further reducing water, as well as impacting on vegetation productivity (Andersson et al., 2006; Wolski & Murray-Hudson, 2008; Moses & Hambira, 2018). As a grazer relying on water for diurnal refuge, these changes will disproportionately affect hippos, particularly with reductions in the availability of aquatic/riparian habitat (Murray-Hudson et al., 2006; Wolski & Murray-Hudson, 2008; Milzow et al., 2010; Tsheboeng et al., 2017; Stears et al., 2019). The 2019 flood event was the lowest on record, with devastating impacts on wildlife, particularly hippos (Anon, 2019; Tebele, 2019; Thalefang, 2019a). Although the event was most likely due to natural cycles, it provides insight into how the hippo population would be impacted by environmental variability in the future. Even if the direct impacts of human disturbance alone are not severe, when coupled with these environmental changes, substantial declines in hippo populations are likely (Lewison 2007). In this situation, Botswana's current level of wildlife protection may no longer be enough to ensure the continued success of its hippo population.

7.4 Conclusions

Information on a species that originates from a select few populations can give the unfounded impression of a thorough understanding of that species, yet there is little evidence that this knowledge is transferable to a population in another habitat subject to different environment pressures. In this thesis, the first dedicated study on hippos in Botswana, I have reduced this knowledge gap, revealing previously unknown information about hippo distribution, habitat selection, pod dynamics and behaviour in the Delta

wetland. My work describes how hippos use their environment, and the dramatic impact that resource availability has on them at various levels. This information can be used to predict how they will be impacted by future changes to their ecosystem and incorporated into management for protecting them and their habitat. While the hippo population in Botswana has previously thrived, this should not make conservation and land managers complacent. Hippos are sensitive to environmental changes and responses in their population could be rapid, with the reductions of this species resulting in a significant loss to the ecosystem.

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Supplementary information

Chapter 1

<u>Text S1.1. Calculating number of publications on threatened African species</u>

I extracted all citations between 1950 to 2019 from Google Scholar about the African bush elephant, common hippo, giraffe, and lion using the Publish or Perish software. The aim of the search was not to find every article available, but to act as a rudimentary scale of the difference in research between animals in Africa. To increase the specificity of results, I used search criteria (Table S1.1) that aimed to filter out publications that mentioned the species but were not explicitly about the species. To do this, I searched the title section for the common name of the species and the main text for the scientific name (given publications often do not include scientific name in the title). Also, to ensure that publications on Asian elephants, African forest elephants, pygmy hippos, and Asiatic lions were not included, those words were deselected in the title search. Unfortunately, this meant that publications covering both species of animals would not be selected; for example, a publication about both pygmy hippos and common hippos would be removed from the search. Further, the search criteria meant publications without the common name in the title were not selected. Exact duplicates were removed, however subtle differences in spellings prevented all duplicates from being detected.

Table S1.1. Search criteria used to extract citations from Google Scholar.

	Search criteria	
Species	**Title**	**Keyword**
African bush elephant	elephant -asian -forest	"Loxodonta africana"
Common hippopotamus	hippo -pygmy	"Hippopotamus amphibius"
Giraffe	giraffe	"Giraffa camelopardalis"
African lion	lion -asiatic	"Panthera leo"

Chapter 2

Data S2.1. Inundation maps and Google Earth Engine code

Individual inundation maps (1990–2019), sum of all inundation maps, and variance of all inundation maps are available online at https://www.mdpi.com/2072-4292/12/8/1348/s1. Further, the Google Earth Engine code and inundation rasters are available on Github (https://github.com/VictoriaInman/OkavangoDelta_flooding) and Google Earth Engine (https://code.earthengine.google.com/?accept_repo=users/victoriainman/OkavangoDelta _TechnicalNote), and are archived on Zenodo (DOI: 10.5281/zenodo.3693153).
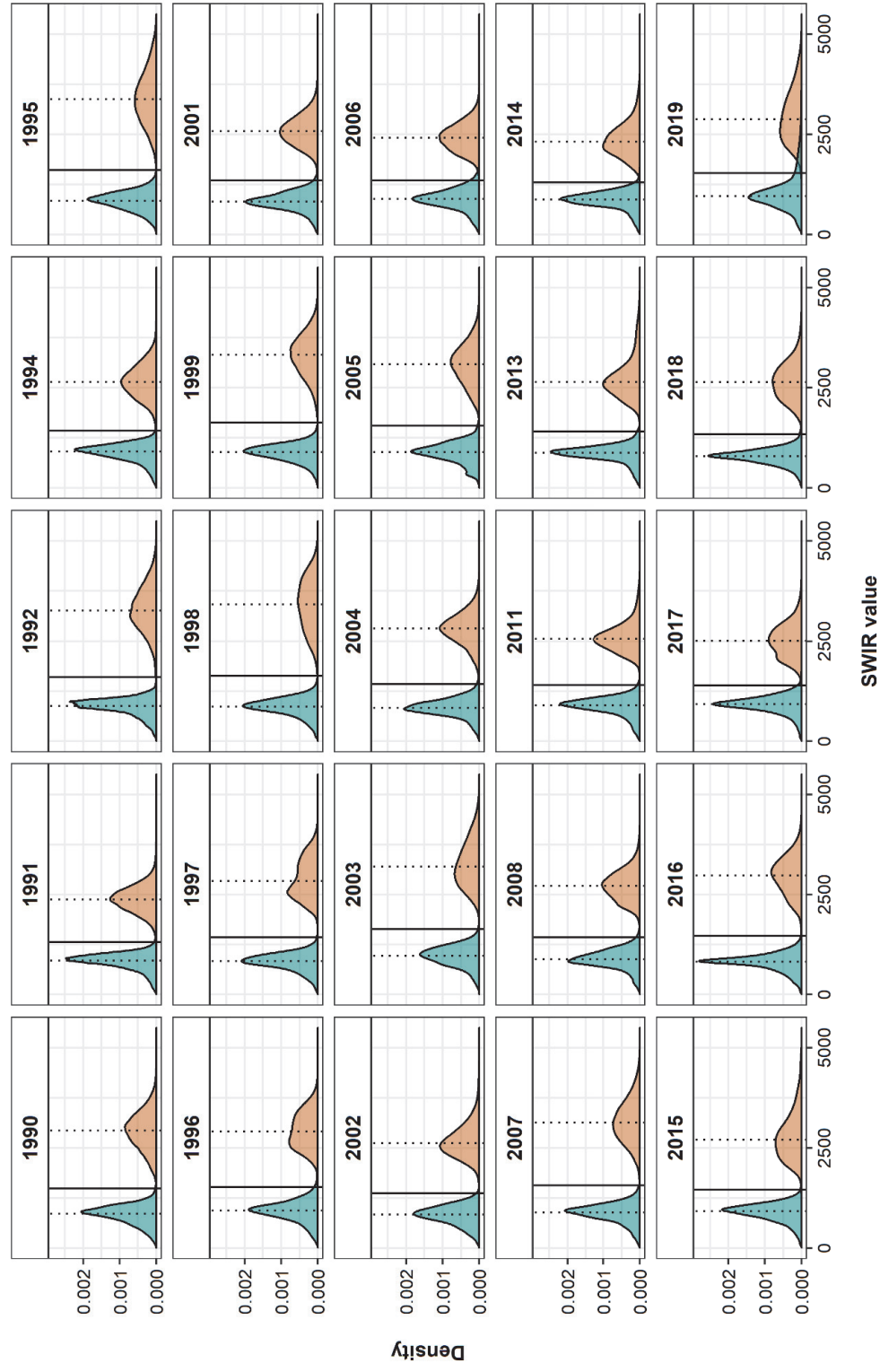
Figure S2.1. Density of SWIR values for permanent water and dry areas, with median values (dashed line) and threshold value (solid line) for each year.

Table S2.1. Error matrices and overall accuracy of inundation maps using image-based accuracy assessment (Landsat and high-resolution imagery) using alternative values of f in the threshold equation $SWIR_{threshold} = SWIR_{wet} + f * (SWIR_{dry} - SWIR_{wet})$

		Landsat		Hi-res visual interp.	
		Dry	Wet	Dry	Wet
Map	**Dry**	527	16	83	5
f = 0.25	**Wet**	2	146	1	34
Overall accuracy		97.4% (673/691)		95.1% (117/123)	
Map	**Dry**	522	7	82	3
f = 0.35	**Wet**	7	155	2	36
Overall accuracy		98.0% (677/691)		95.9% (118/123)	
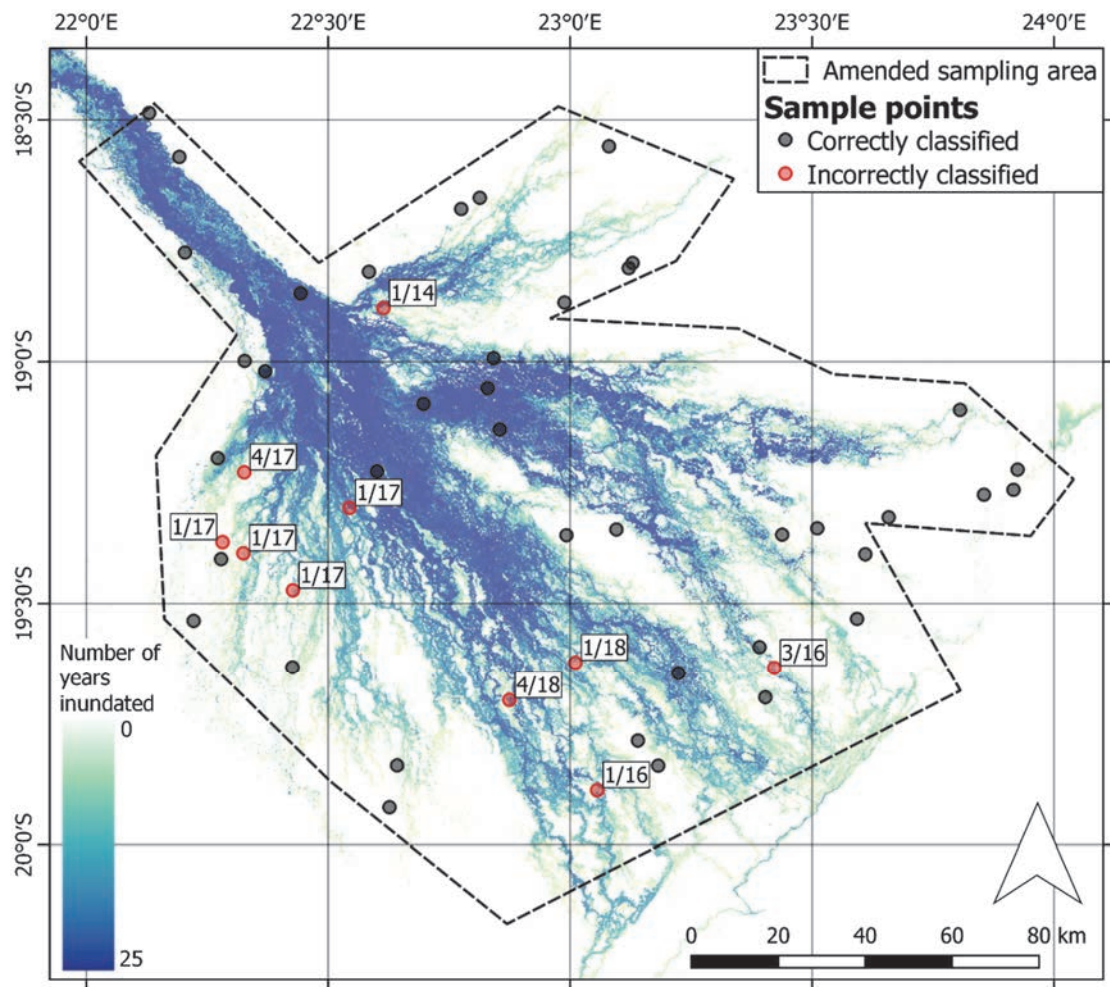
Figure S2.2. Location of validation points for image-based accuracy assessment. Black points were always correctly classified, red points were incorrectly classified at least once (label displays the number of times incorrectly classified out of total times classified). Dashed line represents amended area for point sampling and background map is the summed annual inundation map.

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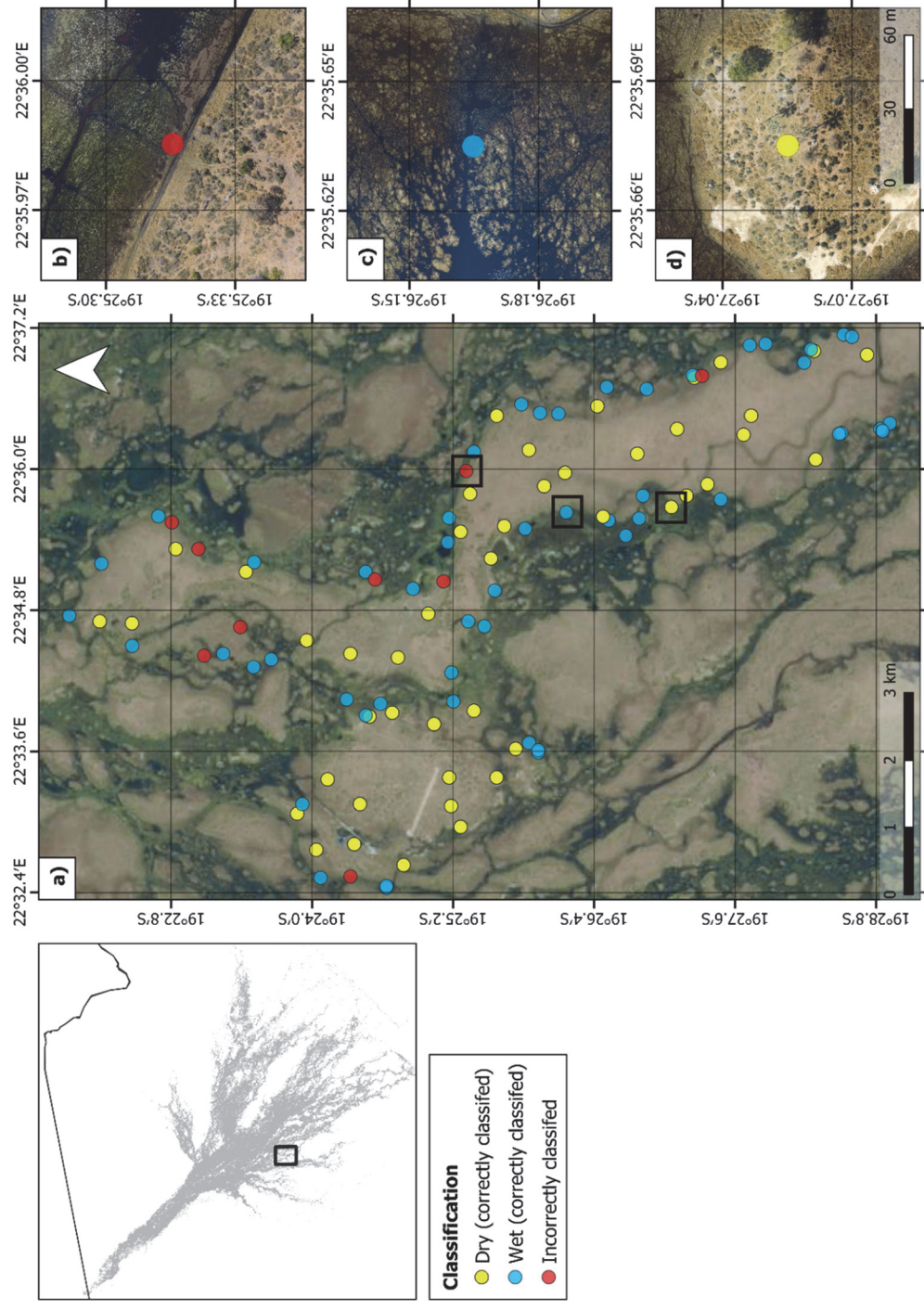
Figure S2.3. In situ accuracy assessment of a single inundation map (25 July 2018) showing (a) all sampling points and their classifications and examples of; (b) an incorrectly classified point that was classed as uncertain in the field; (c) a correctly classified inundated point; and (d) a correctly classified dry point. Overview map shows average inundation extent.

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Chapter 3

Table S3.1. Dates, primary organisation (Elephants Without Borders, EWB and Department of Wildlife and National Parks, DWNP), sampling intensity (average ± SD with range in different strata in brackets), and hippo estimates from aerial surveys.

Year	Survey dates	Organisation	Average sampling intensity (%)[a]	Hippo estimate[a]
1996	17 Sept – 6 Nov	DWNP	4.53 ± 1.73 (3.01–6.03)	1,243
1999	10 Aug – 6 Oct	DWNP	4.40 ± 1.58 (2.84–5.96)	1,747
2001	30 July – 10 Oct	DWNP	5.01 ± 1.85 (3.38–7.01)	1,705
2002	29 July – 6 Oct	DWNP	4.90 ± 1.79 (3.27–6.48)	2,532
2003	29 July – 24 Sept	DWNP	5.88 ± 2.17 (4.01–8.08)	1,247
2004	6 Aug – 17 Oct	DWNP	5.92 ± 2.45 (3.77–8.18)	2,808
2005	8 Aug – 6 Oct	DWNP	4.52 ± 1.80 (2.55–6.36)	2,187
2006	3 Sept – 26 Sept	DWNP	4.69 ± 1.81 (3.04–6.27)	2,473
2010	30 June – 13 Dec	EWB[b]	20.65 ± 8.82 (7.72–40.87)	5,212
2012	6 Aug – 17 Nov	DWNP	4.68 ± 1.79 (3.04–6.27)	2,691
2013	15 Nov – 10 Dec	DWNP	4.68 ± 1.79 (3.04–6.27)	4,730
2014	29 July – 22 Oct	EWB[b]	17.06 ± 4.29 (6.50–20.61)	6,698
2018	3 July – 3 Oct	EWB[b]	16.87 ± 3.69 (7.61–19.86)	9,665

[a] Values were calculated using study area shown in Figure 3.1, which represents the area intersected by all surveys. For true Delta-wide hippo estimates, consult relevant reports.
[b] EWB's aerial surveys include a DWNP observer.

<u>Text S3.1. Additional information on creation of predictor variable rasters</u>

All image acquisition, processing, and analysis was conducted in Google Earth Engine (Gorelick et al., 2017). Once created, rasters were exported at native resolution for further processing (see Methods).

<u>Flood extent</u>

All flood rasters (flood extent, flood mean, flood variance) were created using Landsat (Landsat 5 TM, Landsat 7 ETM+, Landsat 8 OLI) scenes, with 30 m spatial resolution (developer.google.com/earth-engine/datasets/catalog/landsat).

Eleven rasters (one for each survey year) showing the extent of flooding at the time of each aerial survey were made using a short wave infrared threshold technique as detailed in Inman & Lyons (2020). The method was amended to use Landsat scenes from one month before to one month after the dates of the aerial surveys (Table S3.1), rather than scenes from the annual high flood period.

Subsequently, we developed rasters showing long-term flood extent patterns. All Landsat scenes covering the study area between 1989 and 2019 were used to create bimonthly (January/February, March/April, May/June, July/August, September/October, and November/December) flood maps. Bimonthly flood maps were chosen as Landsat had insufficient temporal resolution to consistently produce monthly flood maps over the 30-year period. The resultant 160 bimonthly flood maps were reduced to a 'flood mean' and a 'flood variance' raster by calculating the mean value and the variance for every pixel.

<u>Surface water extent</u>

Eleven rasters showing the extent of the surface water at the time of each aerial survey were created from the European Commission's Joint Research Center (JRC) Global Surface Water Mapping MonthlyWater History v1.1 image collection (Pekel et al., 2016), containing monthly (1984–2018) surface water maps (at 30 m spatial resolution), where pixels were assigned values of 0 (no data), 1 (not water), or 2 (water). A composite was made for each aerial survey year by obtaining all water maps for one month before to one month after the dates of the aerial surveys (Table S3.1), masking 'no data' pixels, filling these masked pixels using a source raster, and obtaining the mean pixel value over all

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images for that year. The gap-filling source rasters were created individually for each year, by obtaining all water maps for the relevant months, for the year before to the year after, masking 'no data' pixels, and obtaining the mean pixel value over all images.

A raster of the long term occurrence of surface water was taken from the 'water occurrence' map of the JRC Global Surface Water Mapping project (Pekel et al., 2016), which showed the frequency of surface water occurrence between 1984–2018, with pixel values representing the percentage of time that water occurred (e.g. values of 100 indicate water occurred 100% of the time for that pixel and 0 indicates there was never water occurrence). The raster was created by selecting the occurrence band (band 0) from the JRC Global Surface Water Mapping layer.

Vegetation class

This raster was created using Level-1C imagery from the Sentinel-2 MultiSpectral Instrument, with 20 m spatial resolution (developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2). To account for the high level of inter and intra-annual variation in the phenological state of vegetation in the Delta, we utilised a multi-temporal image stack, comprised of composites for the three major seasons of northern Botswana (wet season, dry season at high flood, and dry season at low flood). The seasonal image composites were generated by acquiring all images over the study area, captured during 2016–2018, masking clouds (developers.google.com/earth-engine/datasets/catalog/COPERNICUS_S2), and calculating the median value of all images for that season.

For each seasonal composite, the visible (B2, B3, B4), red edge (B5, B6, B7, B8A), near infrared (B8), and short-wave infrared (B11, B12) bands were retained and used for classification. Further, four indices (normalized difference vegetation index, normalized difference water index, enhanced vegetation index, and soil adjusted vegetation index) and texture (standard deviation) at three scales (2, 10, and 100-pixel radiuses) were added as additional bands. All bands for the three seasonal composites were stacked to create one image to classify.

To classify the image into a vegetation map, a supervised machine learning random forest (500 trees) image classifier was implemented. To train and test the classifier, we utilised field-collected vegetation class samples. In total, 796 samples were collected from seven vegetation classes in the Delta's southeast in 2010 (Bennitt et al., 2014), then resampled into five classes (floodplain, grassland, riparian woodland, mixed shrubland, and low woodland). Samples outside the study area (129 points) were filtered out. All bands of the image to classify were sampled at native resolution for the 667 sample points. These data were randomly split into training data (70%), used to train the classifier, and testing data (30%), used to evaluate performance. The classifier had an overall accuracy of 81.4% (Table S3.2). The classifier was then retrained with all sample data and used to classify the image and create the vegetation map.

Table S3.2. Error matrix and accuracy for the vegetation classification in five classes. Note: Rows represent ground-data and columns are classified image.

	Floodplain	Low woodland	Grassland	Mixed shrubland	Riparian woodland
Floodplain	39	0	3	0	3
Low woodland	0	13	4	0	2
Grassland	2	0	31	1	1
Mixed shrubland	0	0	3	7	0
Riparian woodland	1	1	3	0	15

Overall accuracy = 81.4%

Model S3.1. Global model used to explain variation in Delta hippo population estimates in relation to rainfall and inflow and the two organisations which flew the surveys (Elephants Without Borders and Department of Wildlife and National Parks). Lagged and averaged (one to five years prior) rainfall and inflow variables also included.

```
Model1 <- lm(Estimate_logged ~
 Organisation + Year +
 Flow + Flow1YearLag + Flow2YearLag + Flow3YearLag + Flow4YearLag + Flow5YearLag+
 Flow2YearAvg + Flow3YearAvg + Flow4YearAvg + Flow5YearAvg + Flow6YearAvg +
 Rain + Rain1YearLag + Rain2YearLag + Rain3YearLag + Rain4YearLag + Rain5YearLag +
 Rain2YearAvg + Rain3YearAvg + Rain4YearAvg + Rain5YearAvg + Rain6YearAvg)
```

Model S3.2. Global model used to explain variation in hippo spatial counts in relation to organisation, year, flood (flood extent, flood mean, flood variance), water (water extent, water history) and vegetation class at three scales (≤ 3 km, ≤ 1 km, ≤ 175 m), including polynomial relationships for flood and water variables.

```
Model2 <- glmmTMB(Count~
 Organisation + Year +
 VegClass3km + VegClass1km + VegClass175m +
 sqrtWaterExtent3km + sqrtWaterExtent1km + sqrtWaterExtent175m +
 poly(sqrtWaterExtent3km,2) + poly(sqrtWaterExtent1km,2) + poly(sqrtWaterExtent175m,2)+
 sqrtWaterHistory3km + sqrtWaterHistory1km + sqrtWaterHistory175m +
 poly(sqrtWaterHistory3km,2) +poly(sqrtWaterHistory1km,2)+poly(sqrtWaterHistory175m,2)
 FloodExtent3km + FloodExtent1km + FloodExtent175m +
 poly(FloodExtent3km,2) + poly(FloodExtent1km,2) + poly(FloodExtent175m,2) +
 FloodVariance3km + FloodVariance1km + FloodVariance175m +
 poly(FloodVariance3km,2) + poly(FloodVariance1km,2) + poly(FloodVariance175m,2) +
 FloodMean3km + FloodMean1km + FloodMean175m +
 poly(FloodMean3km,2) + poly(FloodMean1km,2) + poly(FloodMean175m,2) +
 family = truncated_nbinom2(link = "log"))
```

Chapter 4

Table S4.1. Relationship between total length and age for male and female hippos (Martin 2005). Averaged lengths and demographic classes added.

Age (years)	Male length (cm)	Female length (cm)	Average (cm)	General age class
0	86	86	86	Juvenile
1	143	143	143	Juvenile
2	184	184	184	Subadult
3	212	212	212	Subadult
4	233	233	233	Adult
5	247	247	247	Adult
6	257	257	257	Adult
7	264	264	264	Adult
8	269	269	269	Adult
9	275	274	274.5	Adult
10	280	279	279.5	Adult
11	283	282	282.5	Adult
12	287	285	286	Adult
13	290	288	289	Adult
14	293	290	291.5	Adult
15	295	292	293.5	Adult
16	298	294	296	Adult
17	300	296	298	Adult
18	302	298	300	Adult
19	304	299	301.5	Adult
20	307	301	304	Adult
21	309	303	306	Adult
22	311	304	307.5	Adult
23	313	306	309.5	Adult
24	315	308	311.5	Adult
25	317	309	313	Adult
26	319	311	315	Adult
27	321	313	317	Adult
28	324	314	319	Adult
29	326	316	321	Adult
30	328	318	323	Adult
31	330	319	324.5	Adult
32	332	321	326.5	Adult
33	334	323	328.5	Adult
34	336	324	330	Adult
35	338	326	332	Adult
36	340	328	334	Adult
37	343	329	336	Adult
38	345	331	338	Adult
39	347	333	340	Adult
40	349	334	341.5	Adult
41	351	336	343.5	Adult
42	353	338	345.5	Adult
43	355	339	347	Adult
44	357	341	349	Adult
45	359	343	351	Adult

Table S4.2. Effect of survey height, time of day, their interaction, survey date, and inclusion of an AR(1) covariance structure on variations in total hippo count (model 1) using glmmTMB function (glmmTMBpackage), comparing full and reduced models with the anova function. Where models showed no significant interaction effect and no significant improvement with the inclusion of an AR(1) covariance structure, models were rerun removing these variables. Pairwise comparisons of effect of time of day and height were conducted using the emmeans function (emmeans package) (but are not provided here).

i) Effect of inclusion of AR(1) variable

Analysis of Variance Table using likelihood ratio tests
Mod.AR1=glmmTMB(total.count ~ height*time + (1|date) + ar1(times+0|group))
Mod   =glmmTMB(total.count ~ height*time + (1|date))

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Mod	18	467.64	516.58	-215.82	431.64		
Mod.AR1	20	468.10	522.47	-214.05	428.10	3.548	0.170

ii) Effect of interaction between time and height

Analysis of Variance Table using likelihood ratio tests
Full.mod.int = glmmTMB(total.count ~ height*time + (1|date))
Full.mod   = glmmTMB(total.count ~ height + time + (1|date))

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Full.mod	9	460.92	485.39	-221.46	442.92		
Full.mod.int	18	467.64	516.58	-215.82	431.64	11.276	0.257

iii) Effect of height

Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(total.count ~ height + time + (1|date))
Red.mod = glmmTMB(total.count ~ time + (1|date))

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	467.10	483.41	-227.55	455.10		
Full.mod	9	460.92	485.39	-221.46	442.92	12.180	0.007**

iv) Effect of time

Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(total.count ~ height + time + (1|date))
Red.mod = glmmTMB(total.count ~ height + (1|date))

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	493.30	509.61	-240.65	481.30		
Full.mod	9	460.92	485.39	-221.46	442.92	38.384	<0.001***

v) Effect of date (random effect)

Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(total.count ~ height + time + (1|date))
Red.mod = glmmTMB(total.count ~ height + time)

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	8	523.68	545.43	-253.84	507.68		
Full.mod	9	460.92	485.39	-221.46	442.92	64.757	<0.001***

Table S4.3. Effect of survey height, time of day, their interaction, survey date, and inclusion of an AR(1) covariance structure on variations in percentage of hippos assigned to age classes (number of juveniles, subadults, and adults divided by the total count for each drone/land survey; model 2). Analysis as above.

i) Effect of inclusion of AR(1) variable

```
Analysis of Variance Table using likelihood ratio tests
Mod.AR1 = glmmTMB(percentage ~ height*time + (1|date) + ar1(times+0|group),
          family=binomial, weights=total)
Mod     = glmmTMB(percentage ~ height*time + (1|date),
          family=binomial, weights=total)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Mod	17	463.07	509.29	-214.54	429.07		
Mod.AR1	19	448.31	499.97	-205.16	410.31	18.760	<0.001***

ii) Effect of interaction between time and height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod     = glmmTMB(percentage ~ height*time + (1|date) +
               ar1(times+0|group),family=binomial, weights=total)
Full.mod.add = glmmTMB(percentage ~ height + time + (1|date) +
               ar1(times+0|group), family=binomial, weights=total)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Full.mod.add	10	447.42	474.61	-213.71	427.42		
Full.mod	19	448.31	499.97	-205.16	410.31	17.100	0.047*

iii) Effect of date (random effect)

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(percentage ~ height*time + (1|date) + ar1(times+0|group),
           family=binomial, weights=total)
Red.mod  = glmmTMB(percentage ~ height*time + ar1(times+0|group),
           family=binomial, weights=total)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	18	446.32	495.25	-205.16	410.32		
Full.mod	19	448.31	499.97	-205.16	410.31	0.002	0.968

Table S4.4. Effect of survey height, time of day, their interaction and survey date on variations in counts of juveniles (model 3). Analysis as above.

i) Effect of interaction between time and height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod.int = glmmTMB(Juvenile ~ height * time + (1|date), ziformula=~1,
               family=poisson)
Full.mod     = glmmTMB(Juvenile ~ height + time + (1|date), ziformula=~1,
               family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Full.mod	9	139.80	164.26	-60.899	121.80		
Full.mod.int	18	149.80	198.74	-56.902	113.80	7.994	0.535

ii) Effect of height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Juvenile ~ height + time + (1|date), ziformula=~1,
           family=poisson)
Red.mod  = glmmTMB(Juvenile ~ time + (1|date), ziformula=~1,
           family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	152.97	169.28	-70.485	140.97		
Full.mod	9	139.80	164.26	-60.899	121.80	19.172	<0.001***

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iii) Effect of time

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Juvenile ~ height + time + (1|date), ziformula=~1,
             family=poisson)
Red.mod  = glmmTMB(Juvenile ~ height + (1|date), ziformula=~1,
             family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	136.96	153.27	-62.478	124.96		
Full.mod	9	139.80	164.26	-60.899	121.80	3.158	0.368

iv) Effect of date (random effect)

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Juvenile ~ height + time + (1|date), ziformula=~1,
             family=poisson)
Red.mod  = glmmTMB(Juvenile ~ height + time, ziformula=~1,
             family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	8	137.85	159.59	-60.923	121.85		
Full.mod	9	139.80	164.26	-60.899	121.80	0.048	0.826

Table S4.5. Effect of survey height, time of day, their interaction and survey date on variations in counts of subadult (model 4). Analysis as above.

i) Effect of interaction between time and height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod.int = glmmTMB(Subadult ~ height * time + (1|date), ziformula=~1,
                 family=poisson)
Full.mod     = glmmTMB(Subadult ~ height + time + (1|date), ziformula=~1,
                 family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Full.mod	9	152.44	176.90	-67.219	134.44		
Full.mod.int	18	157.80	206.73	-60.899	121.80	12.640	0.180

ii) Effect of height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Subadult ~ height + time + (1|date), ziformula=~1,
             family=poisson)
Red.mod  = glmmTMB(Subadult ~ time + (1|date), ziformula=~1,
             family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	170.59	186.90	-79.294	158.59		
Full.mod	9	152.44	176.90	-67.219	134.44	24.151	<0.001***

iii) Effect of time

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Subadult ~ height + time + (1|date), ziformula=~1,
             family=poisson)
Red.mod  = glmmTMB(Subadult ~ height + (1|date), ziformula=~1,
             family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	6	157.33	173.65	-72.667	145.33		
Full.mod	9	152.44	176.90	-67.219	134.44	10.896	0.012*

iv) Effect of date (random effect)

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Subadult ~ height + time + (1|date), ziformula=~1,
             family=poisson)
Red.mod  = glmmtTMB(Subadult ~ height + time, ziformula=~1,
             family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	8	150.94	172.69	-67.471	134.94		
Full.mod	9	152.44	176.90	-67.219	134.44	0.505	0.477

Table S4.6. Effect of survey height, time of day, their interaction, survey date, and inclusion of an AR(1) covariance structure on variations in counts of adult (model 5). Analysis as above.

i) Effect of inclusion of AR(1) variable

```
Analysis of Variance Table using likelihood ratio tests
Mod.AR1 = glmmTMB(Adult ~ height*time + (1|date) + ar1(times+0|group),
                ziformula=~1, family=poisson)
Mod     = glmmTMB(Adult ~ height*time + (1|date),
                ziformula=~1, family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Mod	18	456.49	505.42	-210.25	420.49		
Mod.AR1	20	454.26	508.63	-207.13	414.26	6.228	0.044*

ii) Effect of interaction between time and height

```
Analysis of Variance Table using likelihood ratio tests
Full.mod     = glmmTMB(Adult ~ height*time + (1|date) + ar1(times+0|group),
                ziformula=~1, family=poisson)
Full.mod.add = glmmTMB(Adult ~ height + time + (1|date) + ar1(times+0|group)
                ziformula=~1, family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Full.mod.add	11	461.12	491.02	-219.56	439.12		
Full.mod	20	454.26	508.63	-207.13	414.26	24.854	0.003**

iii)Effect of date (random effect)

```
Analysis of Variance Table using likelihood ratio tests
Full.mod = glmmTMB(Adult ~ height*time + (1|date) + ar1(times+0|group),
                ziformula=~1, family=poisson)
Red.mod  = glmmTMB(Adult ~ height*time + ar1(times+0|group),
                ziformula=~1, family=poisson)
```

	Df	AIC	BIC	logLik	Dev	Chisq	Pr(>Chisq)
Red.mod	19	452.26	503.92	-207.13	414.26		
Full.mod	20	454.26	508.63	-207.13	414.26	0	1.000

Table S4.7. Effect of survey method (drone and aerial) on hippo count using generalized linear model (family Negative Binomial) (manyglm function).

```
Analysis of Deviance Table
Model = manyglm(hippo.count ~ lagoon + survey.method,
                family = negative.binomial)
Multivariate test:
```

	Res.Df	Df.diff	Dev	Pr(>Dev)
(Intercept)	33			
lagoon	17	16	56.63	<2e-16***
survey.method	16	1	3.60	0.074

```
Arguments: P-value calculated using 9999 resampling iterations via PIT-trap
resampling (to account for correlation in testing).
```

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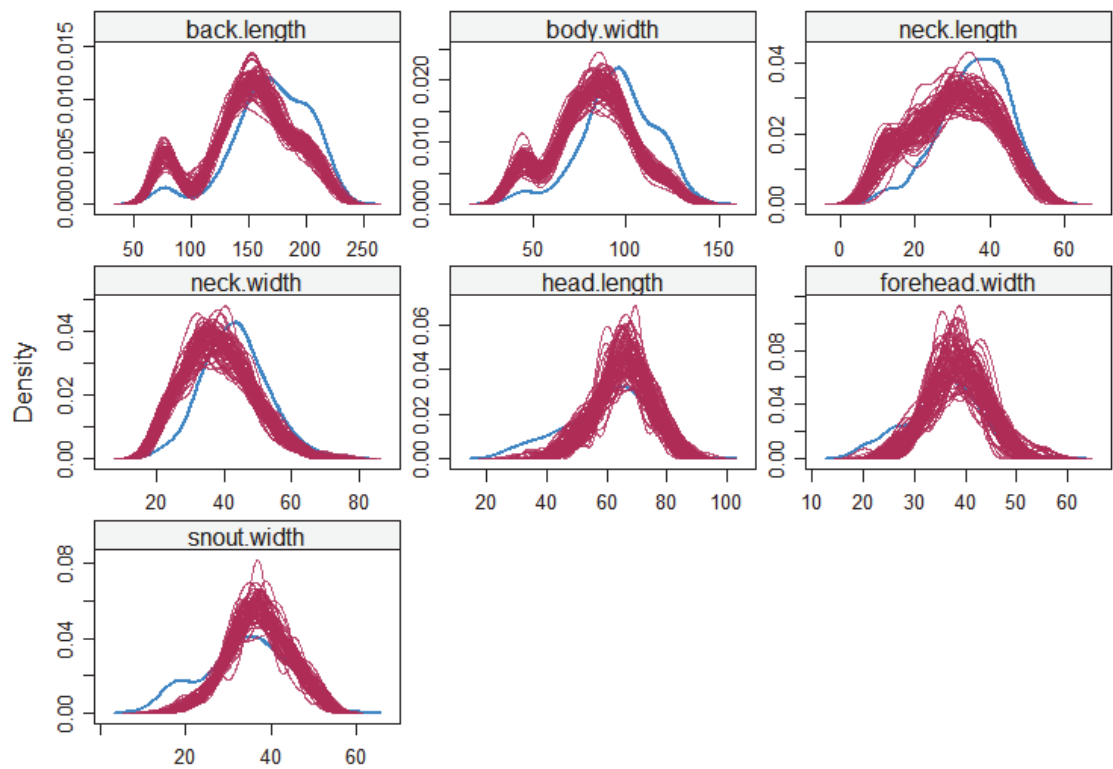
Figure S4.1. Density plots comparing measured data (blue) to multiple imputations (red).

Chapter 5

<u>Text S5.1. Mapping the study area</u>

To collect drone images, flight transects and photo points were automatically calculated for the study area by the DJI GS Pro app, run through a tablet, based on input altitude of 120 m, front overlap of 75%, side overlap of 50%, and gimbal pitch angle of -90° (facing directly downward). Flight speed was calculated automatically at 9.8 m/s (shutter interval 4.0 seconds). The drone flight and image capture were controlled using the app. For each orthomosaic, the collection of drone images spanned two consecutive days.

In addition to the drone's GPS, which automatically assigns coordinates to each image taken, I used ground control points (GCP) to improve the georeferencing accuracy of the orthomosaics and allow the time-series to be aligned. Eight GCPs were placed on the borders of the study area on islands which were accessible year-round. The GCPs were made of four 30 cm x 30 cm tiles painted blue with thick white tape placed diagonally on each tile so that when placed together they made a larger square with a visible white cross. To ensure consistent placement of the GCPs during each drone flight, a 1.8 m metal stake was hammered into the ground at the chosen locations and remained there for the duration of the study. Prior to surveying, the GCPs were placed at the base of these metal stakes, in the same position for every mapping event. Over time, three of the metal stakes were disturbed and their exact original location unable to be determined, therefore these GCPs were not used for the remaining study period. The locations of the GCPs were recorded using a using handheld Garmin GPSMAP® 64 GPS, with accuracy to three m. Given the loss of some GCPs in the field, an additional six "natural GCPs" that were visible and in a consistent location throughout the study (e.g. corners of roofs of buildings) were used.

The orthomosaics were created using Pix4DMapper (version 4.4.12), which uses a structure-from-motion processing technique to detect matching features (keypoints) in overlapping images and uses the camera position and orientation for every image to determine the 3D point coordinates of the keypoints. The resulting 3D point cloud is densified and textured with images and used to create a digital surface model and ultimately a georeferenced orthomosaic. The GCP co-ordinates were input during processing and the GCPs were used as manual tie points as in this tutorial: https://support.pix4d.com/hc/en-us/articles/204373409-How-to-align-projects.

Chapter 6

Table S6.1. Automatically generated (dredge function) models with all valid combinations of the fixed effects for all behaviours, diurnal and nocturnal.

i) Diurnal - Resting deep aquatic (RDA)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
0.842	+	+	+	+	24	-9622	19295	0	1
-0.318	+		+	+	12	-11169	22363	3068	0
0.955	+	+	+		19	-12851	25741	6446	0
0.015	+	+			17	-13735	27505	8210	0
-0.101	+		+		7	-14412	28838	9544	0
-0.868	+				5	-15171	30351	11056	0
0.601		+	+		15	-16733	33498	14203	0
-0.036		+			13	-17237	34500	15205	0
-0.242			+		3	-18010	36026	16732	0
-0.780					1	-18471	36943	17649	0

ii) Diurnal - Resting shallow aquatic (RSA)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-3.206	+	+	+	+	24	-12281	24611	0	1
-0.577	+		+	+	12	-16985	33994	9383	0
-3.139	+	+	+		19	-19748	39536	14924	0
-2.129	+	+			17	-20739	41514	16903	0
-2.785		+	+		15	-23118	46267	21656	0
-2.029		+			13	-23836	47698	23087	0
-0.954	+		+		7	-23886	47787	23175	0
-0.222	+				5	-24582	49173	24562	0
-0.838			+		3	-26620	53247	28636	0
-0.296					1	-27219	54440	29828	0

iii) Diurnal - Resting terrestrial (RT)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-4.562	+	+	+	+	24	-2959	5969	0	1
-4.627	+	+	+		19	-3234	6506	538	0
-3.256	+		+	+	12	-3780	7584	1615	0
-3.319	+		+		7	-4044	8102	2134	0
-3.511	+	+			17	-4524	9083	3114	0
-5.364		+	+		15	-4685	9400	3431	0
-1.892	+				5	-5334	10678	4710	0
-4.150			+		3	-5539	11084	5115	0
-5.079		+			13	-5883	11793	5824	0
-3.092					1	-6615	13233	7264	0

iv) Diurnal – Moving aquatic (MA)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAIC	weight
-0.796	+	+	+	+	24	-3776	7603	0	1
-0.432	+	+	+		19	-4022	8084	482	0
-1.650	+		+	+	12	-4513	9051	1448	0
-0.545		+	+		15	-4536	9103	1501	0
-1.462	+	+			17	-4717	9470	1867	0
-1.284	+		+		7	-4793	9600	1997	0
-1.500		+			13	-5150	10328	2725	0
-1.299			+		3	-5248	10503	2900	0
-2.106	+				5	-5377	10764	3162	0
-2.066					1	-5786	11574	3971	0

v) Diurnal - Moving terrestrial (MT)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-5.158	+	+	+	+	24	-613	1277	0	1
-5.413	+	+	+		19	-644	1327	51	0
-3.823	+	+			17	-678	1391	114	0
-6.322	+		+	+	12	-711	1446	169	0
-5.452		+	+		15	-713	1456	180	0
-6.528	+		+		7	-742	1499	223	0
-3.859		+			13	-750	1527	250	0
-4.945	+				5	-779	1568	291	0
-6.630			+		3	-815	1635	358	0
-5.019					1	-855	1712	435	0

vi) Diurnal – Feeding aquatic (FA)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-4.357	+	+	+	+	24	-412	874	0	1
-4.044	+	+	+		19	-438	915	41	0
-3.993		+	+		15	-445	920	47	0
-4.930	+		+	+	12	-474	973	100	0
-4.625	+		+		7	-499	1012	138	0
-4.490			+		3	-507	1021	147	0
-5.538	+	+			17	-523	1081	207	0
-5.788	+				5	-572	1155	281	0
-5.918		+			13	-571	1168	294	0
-6.014					1	-621	1244	371	0

vii) Diurnal – Feeding terrestrial (FT)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-4.009	+	+	+	+	24	-3534	7118	0	1
-5.724	+	+	+		19	-3649	7338	219	0
-2.895	+	+			17	-4807	9650	2532	0
-4.722		+	+		15	-6436	12904	5785	0
-4.493	+		+	+	12	-6819	13663	6545	0
-6.209	+		+		7	-6931	13876	6758	0
-1.731		+			13	-7456	14938	7820	0
-3.418	+				5	-8242	16493	9375	0
-5.240			+		3	-9988	19982	12863	0
-2.280					1	-11136	22274	15155	0

viii) Diurnal – Social (S)

Intercept	AREA	HOUR	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-3.106	+	+	+	+	24	-1441	2932	0	1
-3.181	+	+			17	-1465	2964	32	0
-3.317	+	+	+		19	-1463	2964	32	0
-3.159		+	+		15	-1545	3121	189	0
-3.412		+			13	-1550	3126	194	0
-4.149	+		+	+	12	-1669	3363	431	0
-4.276	+		+		7	-1693	3400	468	0
-4.022	+				5	-1699	3407	475	0
-4.166					1	-1776	3554	621	0
-4.069			+		3	-1775	3555	623	0

ix) Nocturnal – Resting deep aquatic (RDA)

Intercept	AREA	HOUR	MOON	SEASON	AREA:SEASON	df	logLik	AICc	ΔAICc	weight
-1.583	+	+	+	+	+	26	-2252	4560	0	1
-1.556	+	+	+	+		22	-2337	4722	162	0
-1.717	+	+	+			20	-2392	4828	268	0
-1.495		+	+	+		18	-2479	4996	436	0
-1.279	+	+		+	+	23	-2499	5047	488	0

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Intercept	AREA	HOUR	MOON	SEASON	AREA:SEASON	df	logLik	AICc	ΔAIC	weight
-1.206	+	+		+		19	-2538	5117	557	0
-1.342		+	+			16	-2590	5214	655	0
-0.795	+		+	+	+	14	-2664	5358	798	0
-1.621	+	+				17	-2686	5408	848	0
-0.799	+		+	+		10	-2743	5507	947	0
-1.112		+		+		15	-2745	5521	961	0
-1.117	+		+			8	-2795	5606	1046	0
-0.751			+	+		6	-2858	5729	1169	0
-0.847			+			4	-2932	5871	1311	0
-0.468	+			+	+	11	-2929	5880	1320	0
-0.498	+			+		7	-2960	5934	1374	0
-1.066		+				13	-3041	6110	1550	0
-0.993	+					5	-3081	6172	1612	0
-0.352				+		3	-3160	6327	1767	0
-0.435						1	-3393	6789	2229	0

x) Nocturnal – Resting shallow aquatic (RSA)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAIC	weight
-0.459	+	+	+	+	+	26	-1472	3000	0	1
-0.623	+	+	+	+		22	-1486	3020	20	0
-0.154		+	+	+		18	-1561	3161	161	0
-0.933	+	+		+	+	23	-1595	3239	238	0
-1.294	+	+		+		19	-1621	3282	282	0
-1.124	+		+	+	+	14	-1663	3355	355	0
-1.321	+		+	+		10	-1681	3383	383	0
-0.827		+		+		15	-1695	3422	422	0
-1.342	+	+	+			20	-1728	3500	499	0
-0.868			+	+		6	-1756	3524	524	0
-1.604	+			+	+	11	-1806	3636	635	0
-2.039	+			+		7	-1844	3703	703	0
-0.682		+	+			16	-1839	3712	712	0
-2.220	+	+				17	-1861	3758	758	0
-1.560				+		3	-1912	3830	830	0
-2.130	+		+			8	-1913	3843	842	0
-1.465			+			4	-2028	4063	1063	0
-1.537		+				13	-2044	4115	1114	0
-2.899	+					5	-2056	4122	1122	0
-2.178						1	-2213	4429	1429	0

xi) Nocturnal – Resting terrestrial (RT)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-1.741	+	+	+	+	+	26	-976	2008	0	1
-1.421	+	+	+	+		22	-1012	2072	63	0
0.022		+	+	+		18	-1350	2738	730	0
-1.931	+	+	+			20	-1540	3122	1114	0
-1.174	+	+		+	+	23	-1566	3181	1173	0
-0.937	+	+		+		19	-1583	3206	1197	0
-1.097		+		+		15	-1752	3535	1526	0
-3.786	+		+	+	+	14	-2077	4184	2176	0
-3.563	+		+	+		10	-2105	4231	2223	0
-0.679		+	+			16	-2407	4848	2840	0
-2.588			+	+		6	-2515	5043	3035	0
-2.459	+		+			8	-2572	5161	3153	0
0.517	+	+				17	-2604	5245	3236	0
-2.939	+			+	+	11	-2664	5351	3343	0
-2.370	+			+		7	-2689	5392	3383	0
-2.939				+		3	-2900	5806	3797	0
-1.984			+			4	-3314	6636	4627	0

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-0.480		+				13	-3365	6756	4748	0
-0.977	+					5	-3593	7196	5188	0
-1.944						1	-4398	8798	6790	0

xii) Nocturnal – Moving aquatic (MA)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-2.286	+	+	+	+	+	26	-977	2011	0	1
-2.269	+	+		+	+	23	-989	2028	18	0
-2.139	+	+	+	+		22	-992	2030	20	0
-2.060	+	+		+		19	-1002	2045	34	0
-2.229		+	+	+		18	-1017	2072	62	0
-2.133		+		+		15	-1038	2107	96	0
-2.584	+	+	+			20	-1060	2163	153	0
-2.500		+	+			16	-1085	2203	192	0
-2.660	+	+				17	-1102	2240	230	0
-2.467		+				13	-1141	2309	299	0
-1.478	+		+	+	+	14	-1154	2338	327	0
-1.344	+		+	+		10	-1174	2369	359	0
-1.457	+			+	+	11	-1180	2382	372	0
-1.456			+	+		6	-1191	2395	384	0
-1.320	+			+		7	-1195	2405	395	0
-1.356				+		3	-1231	2469	458	0
-1.838	+		+			8	-1241	2498	488	0
-1.829			+			4	-1252	2511	501	0
-1.945	+					5	-1288	2587	576	0
-1.721						1	-1325	2651	641	0

xiii) Nocturnal – Moving terrestrial (MT)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-4.953	+	+	+	+		22	-452	951	0.00	0.38
-4.955	+	+	+	+	+	26	-448	952	0.33	0.32
-4.661	+	+		+		19	-456	952	0.72	0.27
-4.472	+	+	+			20	-457	958	6.38	0.02
-4.670	+	+		+	+	23	-454	958	6.64	0.01
-4.026	+	+				17	-465	966	15	0
-5.424		+	+	+		18	-467	972	21	0
-5.022		+		+		15	-476	984	33	0
-4.838		+	+			16	-476	986	35	0
-3.924	+			+		7	-492	998	47	0
-4.091	+		+	+		10	-490	1000	48	0
-4.134	+		+	+	+	14	-485	1000	49	0
-4.002	+			+	+	11	-490	1002	51	0
-3.577	+		+			8	-496	1008	57	0
-3.331	+					5	-500	1009	58	0
-4.416		+				13	-492	1012	61	0
-4.586			+	+		6	-501	1015	64	0
-4.371				+		3	-509	1024	73	0
-4.017			+			4	-510	1029	78	0
-3.789						1	-522	1045	94	0

xiv) Nocturnal – Feeding aquatic (FA)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-3.695	+	+	+	+	+	26	-213	483	0	1
-4.131	+	+		+	+	23	-254	558	75	0
-2.622	+	+	+	+		22	-262	572	88	0
-4.296	+		+	+	+	14	-285	599	116	0

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Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-3.030	+	+		+		19	-293	627	143	0
-3.120	+		+	+		10	-329	680	196	0
-4.970	+			+	+	11	-329	681	198	0
-3.760	+			+		7	-363	740	257	0
-4.510	+	+	+			20	-355	753	270	0
-4.623	+	+				17	-390	816	333	0
-1.746		+	+	+		18	-394	826	343	0
-4.708	+		+			8	-414	844	361	0
-5.071	+					5	-442	893	410	0
-2.112			+	+		6	-452	915	432	0
-1.963		+		+		15	-496	1024	541	0
-2.499				+		3	-548	1103	620	0
-3.336		+	+			16	-692	1417	934	0
-3.510			+			4	-731	1470	987	0
-3.583		+				13	-788	1603	1120	0
-3.973						1	-810	1621	1138	0

xv) Nocturnal – Feeding terrestrial (FT)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-2.471	+	+	+	+	+	26	-2548	5153	0	1
-2.532	+	+		+	+	23	-2567	5183	30	0
-3.336	+	+	+	+		22	-2726	5499	346	0
-3.794	+	+		+		19	-2776	5592	439	0
-3.637		+	+	+		18	-2882	5801	648	0
-3.806		+		+		15	-2933	5898	745	0
-1.929	+	+	+			20	-2965	5973	820	0
-2.230	+	+				17	-2987	6009	856	0
-2.529		+	+			16	-3111	6255	1102	0
-1.613	+		+	+	+	14	-3175	6380	1227	0
-2.629		+				13	-3180	6387	1234	0
-1.638	+			+	+	11	-3210	6442	1289	0
-2.428	+		+	+		10	-3370	6760	1607	0
-2.658	+			+		7	-3431	6877	1724	0
-2.573			+	+		6	-3526	7065	1912	0
-2.698				+		3	-3595	7196	2043	0
-1.072	+		+			8	-3612	7240	2087	0
-1.300	+					5	-3636	7283	2130	0
-1.497			+			4	-3731	7470	2317	0
-1.665						1	-3785	7572	2419	0

xvi) Nocturnal – Social (S)

Intercept	AREA	HOUR	MOON	SEASON	AREA: SEASON	df	logLik	AICc	ΔAICc	weight
-5.631	+	+	+	+	+	26	-426	909	0	1
-5.943	+	+	+	+		22	-442	931	22	0
-5.515	+	+		+	+	23	-445	940	30	0
-5.654	+	+		+		19	-458	957	48	0
-5.902		+	+	+		18	-525	1088	179	0
-4.031	+		+	+	+	14	-539	1107	197	0
-5.644		+		+		15	-538	1108	199	0
-4.874	+	+	+			20	-535	1112	202	0
-4.470	+		+	+		10	-562	1144	235	0
-4.822	+	+				17	-563	1161	252	0
-3.761	+			+	+	11	-580	1182	273	0
-4.871		+	+			16	-578	1190	281	0
-4.206	+			+		7	-596	1207	298	0
-4.737		+				13	-610	1247	337	0
-3.700	+		+			8	-630	1276	366	0
-4.368			+	+		6	-664	1341	432	0

-3.620	+			5	-673	1356	447	0
-3.659		+		4	-689	1386	477	0
-4.079			+	3	-692	1389	480	0
-3.381				1	-734	1471	562	0

Table S6.2. ANOVA of top binomial models for all behaviours, diurnal and nocturnal, using Anova function (car package).

i) Diurnal – Resting deep aquatic (RDA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	3093.7	12	<0.001***
SEASON	1768.0	2	<0.001***
AREA	7765.4	4	<0.001***
SEASON: AREA	6457.0	5	<0.001***

ii) Diurnal – Resting shallow aquatic (RSA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	9408.3	12	<0.001***
SEASON	1982.7	2	<0.001***
AREA	6740.1	4	<0.001***
SEASON: AREA	14935.2	5	<0.001***

iii) Diurnal – Resting terrestrial (RT)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	1640.5	12	<0.001***
SEASON	2580.6	2	<0.001***
AREA	2902.2	4	<0.001***
SEASON: AREA	548.5	5	<0.001***

iv) Diurnal – Moving aquatic (MA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	1473.9	12	<0.001***
SEASON	1389.9	2	<0.001***
AREA	1027.5	4	<0.001***
SEASON: AREA	492.5	5	<0.001***

v) Diurnal – Moving terrestrial (MT)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	195.1	12	<0.001***
SEASON	67.7	2	<0.001***
AREA	137.7	4	<0.001***
SEASON: AREA	61.4	5	<0.001***

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vi) Diurnal – Feeding aquatic (FA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	125.2	12	<0.001***
SEASON	169.8	2	<0.001***
AREA	13.7	4	0.008**
SEASON:AREA	52.2	5	<0.001***

vii) Diurnal – Feeding terrestrial (FT)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	6570.6	12	<0.001***
SEASON	2316.5	2	<0.001***
AREA	5574.4	4	<0.001***
SEASON:AREA	230.1	5	<0.001***

viii) Diurnal – Social (S)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
HOUR	456.6	12	<0.001***
SEASON	4.0	2	0.135
AREA	165.2	4	<0.001***
SEASON:AREA	42.8	5	<0.001***

ix) Nocturnal – Resting deep aquatic (RDA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
MOON	494.6	3	
HOUR	824.8	12	<0.001***
SEASON	110.3	2	<0.001***
AREA	283.1	4	<0.001***
SEASON:AREA	171.3	4	<0.001***

x) Nocturnal – Resting shallow aquatic (RSA)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
MOON	245.4	3	<0.001***
HOUR	382.1	12	<0.001***
SEASON	484.3	2	<0.001***
AREA	150.1	4	<0.001***
SEASON:AREA	28.9	4	<0.001***

xi) Nocturnal – Resting terrestrial (RT)

Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)

	Chisq	Df	Pr(>Chisq)
MOON	1179.7	3	<0.001***
HOUR	2203.0	12	<0.001***

	Chisq	Df	Pr(>Chisq)
SEASON	1054.9	2	<0.001***
AREA	675.5	4	<0.001***
SEASON: AREA	72.8	4	<0.001***

xii) Nocturnal – Moving aquatic (MA)

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)
```

	Chisq	Df	Pr(>Chisq)
MOON	24.7	3	<0.001***
HOUR	354.3	12	<0.001***
SEASON	137.5	2	<0.001***
AREA	51.1	4	<0.001***
SEASON: AREA	29.1	4	<0.001***

xiii) Nocturnal – Moving terrestrial (MT)

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)
```

	Chisq	Df	Pr(>Chisq)
MOON	13.3	3	0.004**
HOUR	75.8	12	<0.001***
SEASON	10.9	2	0.004**
AREA	29.7	4	<0.001***
SEASON: AREA	9.0	4	0.062

xiv) Nocturnal – Feeding aquatic (FA)

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)
```

	Chisq	Df	Pr(>Chisq)
MOON	82.0	3	<0.001***
HOUR	143.2	12	<0.001***
SEASON	186.0	2	<0.001***
AREA	263.3	4	<0.001***
SEASON: AREA	97.6	4	<0.001***

xv) Nocturnal – Feeding terrestrial (FT)

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)
```

	Chisq	Df	Pr(>Chisq)
MOON	36.6	3	<0.001***
HOUR	1254.2	12	<0.001***
SEASON	478.9	2	<0.001***
AREA	311.4	4	<0.001***
SEASON: AREA	355.3	4	<0.001***

xvi) Nocturnal – Social (S)

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Model: glm(prop ~ HOUR + MOON + SEASON*AREA,
family = binomial, weights = hourly_total)
```

	Chisq	Df	Pr(>Chisq)
MOON	37.2	3	<0.001***
HOUR	224.6	12	<0.001***
SEASON	184.9	2	<0.001***
AREA	165.7	4	<0.001***
SEASON: AREA	31.4	4	<0.001***

Table S6.3. Diurnal and nocturnal hippo activity budgets for study areas over three seasons (mean ± SE).

Area	Season	Time	RDA	RSA	RT	MA	MT	FA	FT	S
Chobe1	Dry season (high flood)	Day	37.2 ± 3.1	31.9 ± 4.1	2.6 ± 1.0	23.2 ± 3.2	0.3 ± 0.2	1.2 ± 0.5	1.8 ± 1.1	1.8 ± 0.5
		Night	38.3 ± 5.3	13.3 ± 3.6	6.1 ± 4.0	21.4 ± 2.9	3.1 ± 1.2	0.6 ± 0.4	15.2 ± 4.5	1.9 ± 0.6
	Dry season (med-low flood)	Day	54.5 ± 3.9	4.5 ± 1.8	16.4 ± 3.9	18.5 ± 2.2	1.3 ± 0.3	0.2 ± 0.1	1.6 ± 0.7	3.0 ± 0.7
		Night	33.7 ± 5.8	1.0 ± 0.3	18.6 ± 6.0	17.2 ± 4.1	3.5 ± 1.1	0.0 ± 0.0	24.0 ± 6.2	2.0 ± 1.0
	Wet season (low flood)	Day	6.4 ± 1.9	74.8 ± 4.9	0.5 ± 0.2	9.0 ± 1.9	0.4 ± 0.1	0.3 ± 0.1	6.7 ± 1.9	1.9 ± 0.7
		Night	29.4 ± 7.5	12.3 ± 6.6	0.8 ± 0.5	18.6 ± 4.9	3.7 ± 1.9	0.8 ± 0.6	31.9 ± 9.6	2.3 ± 1.3
Chobe2	Dry season (high flood)	Day	51.4 ± 2.6	11.6 ± 2.6	0.0 ± 0.0	34.6 ± 3.2	0.0 ± 0.0	1.0 ± 0.4	0.0 ± 0.0	1.3 ± 0.3
		Night	40.2 ± 3.9	21.3 ± 3.0	8.9 ± 3.2	23.4 ± 2.3	1.9 ± 0.7	1.0 ± 0.9	2.7 ± 1.4	0.6 ± 0.3
	Dry season (med-low flood)	Day	18.3 ± 2.4	57.7 ± 3.5	1.0 ± 0.3	8.0 ± 0.9	1.2 ± 0.2	0.4 ± 0.1	12.0 ± 1.9	1.4 ± 0.3
		Night	19.5 ± 5.3	2.5 ± 1.6	47 ± 8.5	6.9 ± 2.0	2.9 ± 0.9	0.0 ± 0.0	19.3 ± 5.6	1.8 ± 0.5
	Wet season (low flood)	Day	34.0 ± 4.2	31.1 ± 5.4	0.9 ± 0.3	11.9 ± 1.5	1.1 ± 0.2	0.0 ± 0.0	19.5 ± 3.6	1.5 ± 0.3
		Night	37.1 ± 5.7	17.5 ± 6.6	0.0 ± 0.0	14.6 ± 2.0	1.4 ± 0.5	0.0 ± 0.0	24.2 ± 7.3	5.2 ± 1.8
Chobe3	Dry season (high flood)									
	Dry season (med-low flood)	Day	58.3 ± 2.4	13.7 ± 2.0	5.8 ± 2.2	19.8 ± 1.9	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	1.8 ± 0.5
		Night	39.6 ± 8.8	0.9 ± 0.6	2.3 ± 1.5	12.1 ± 3.2	2.2 ± 1.2	0.0 ± 0.0	40.7 ± 10.	2.2 ± 1.7
	Wet season (low flood)	Day	57.1 ± 3.1	21.2 ± 4.3	0.0 ± 0.0	19.9 ± 2.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 0.5
		Night	49.4 ± 7.1	4.5 ± 1.5	0.0 ± 0.0	12.6 ± 3.0	2.8 ± 1.8	0.6 ± 0.6	29.5 ± 8.6	0.5 ± 0.3
Abu1	Dry season (high flood)	Day	45.9 ± 3.4	22.7 ± 3.9	0.5 ± 0.4	26.1 ± 2.8	0.1 ± 0.1	2.5 ± 1.3	0.2 ± 0.1	1.9 ± 0.5
		Night	33.5 ± 4.8	12.2 ± 2.4	0.9 ± 0.4	19.5 ± 3.2	0.7 ± 0.3	27.2 ± 5.2	4.3 ± 1.8	1.7 ± 1.1
	Dry season (med-low flood)	Day	8.2 ± 2.2	60.3 ± 7.2	7.8 ± 4.1	16.1 ± 4.1	0.5 ± 0.3	0.0 ± 0.0	0.1 ± 0.1	7.1 ± 2.8
	Wet season (low flood)	Day	54.2 ± 4.6	23.3 ± 4.6	0.0 ± 0.0	15.1 ± 3.1	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.2	7.2 ± 2.3
		Night	19.6 ± 4.8	21.3 ± 5.2	0.2 ± 0.2	6.2 ± 2.1	5.2 ± 2.0	0.0 ± 0.0	39.0 ± 6.3	8.5 ± 3.3
Abu2	Dry season (high flood)									
	Dry season (med-low flood)									
	Wet season (low flood)	Day	70.9 ± 2.1	3.3 ± 0.6	0.1 ± 0.1	24.3 ± 1.8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.4 ± 0.5
		Night	55.7 ± 3.3	13.1 ± 3.0	0.4 ± 0.2	17.6 ± 1.7	2.8 ± 0.7	0.0 ± 0.0	9.3 ± 2.4	1.1 ± 0.5