Aspects of common hippopotamus (*Hippopotamus amphibius*) behavioural ecology and their consequences in managed systems in South Africa

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ABSTRACT

Following severe depletion in wildlife populations as a consequence of hunting in the last 200 years, the vast majority of large mammal species remaining in South Africa are restricted to fenced protected areas and game farms. By 2060, sub-Saharan Africa is projected to experience the largest increases in human population numbers of any other region globally. If these increases are realised, along with other negative direct and indirect effects of human expansion and climate change, the species in the region will incur the greatest increases in extinction risk of any other species in any other region in the world, of which large- and medium-sized mammals are the most susceptible.

The common hippopotamus (*Hippopotamus amphibius*) (hereafter: hippo) is one of Africa's most iconic mammal species. In addition to being iconic, hippos play an important and understudied role as ecosystem engineers in their environment. In particular, ecological and behavioural research on hippos is relatively scarce. Recent worldwide hippo population estimates suggest that numbers have declined by >20% over the past 10 years. Consequently, hippos are listed on CITES as a Schedule II species and have a Red Data classification of Vulnerable (VU A4cd), further outlining the need for additional research on the species.

The use of an unmanned aerial vehicle (UAVs) had not been documented for comprehensive population surveys of hippos. Therefore, using a low-cost, consumer-grade, DJI Phantom 3 Advanced multi-rotor UAV, 47 surveys were conducted of the hippo population at Ndumo Game Reserve (NGR), South Africa, between August 2016 and July 2017. In addition, comparisons were drawn between the results of and the logistical requirements and costs of the respective helicopter and UAV surveys conducted on the same day of the same hippo population. The use of a consumer-grade UAV permitted frequent, accurate, and comparatively low-cost

surveys to identify temporal changes in the number of hippos present in NGR and at different locations within NGR.

We investigated monthly changes in hippo abundance, density, and pod composition at the most used wading areas in NGR. Using a consumer-grade UAV, we conducted four subsequent day-long population censuses of hippos, every month, to determine their geographical locations and pod sizes in NGR. When the inundation area was above the mean, large nursery pods of up to 103 hippos disseminated into smaller pods where mean (± SD) pod size went from 15.6 ± 19.4 to 8.0 ± 9.7 hippos decreasing overall individual and pod density. Our findings suggest that aspects of hippo biology coincide with inundation-driven changes in population social structure, highlighting the importance of the amount and timing of environmental flows for populations of hippos in river-floodplain systems. Also, these changes in population structure may determine both the temporal and spatial scale at which hippos make ecological contributions in river-floodplain systems.

Comparisons between the NGR 2016-2017 hippo population estimates and historical aerial count data in NGR from the past 65 years were made to identify trends in hippo population dynamics. When compared with historical data, a significant decrease from > 400 to 250-300 hippo in the past 20 years was evident. Significant differences in hippo numbers and distribution through different locations in NGR were observed, with 85-95% of the population utilising the uSuthu and Phongolo Rivers and associated floodplains. Hippo population increases were attributed to increased wading area availability, particularly in the dry season after biannual releases from the Pongolopoort Dam upstream. Severe drought periods in 1980, 1990, and 2015 caused dramatic decreases in the population.

Land claim issues between EKZNW and neighbouring communities have instigated the removal of NGR's eastern boundary fence by community members in 2008 and again in 2011. Community encroachment issues have followed along with increased instances of illegal activity, including poaching and deforestation, which have dramatic effects on species in NGR. During the 1-year monthly survey of the hippo population at NGR, we opportunistically documented illegal activity in NGR and summarised these data. People were observed taking part in various activities in NGR during the study period, including hunting, poaching, fishing, livestock herding, farming, burning and clearing, and washing laundry. The most apparent and widespread human impacts in NGR were the clearing and burning of floodplain grasslands and peripheral forests and their subsequent transformation into agricultural plots.

To understand the drivers of individual hippo space use in a perennial river system, we captured and fitted GPS-GSM UHF transmitter collars on adult, male hippos (n = 4) in an impoundment system and in the Olifants River in Kruger National Park (KNP), South Africa, from 2019-2020. We used three different capture methodologies and compared capture success, cost, and effort. Active helicopter-based methods (A-H) were the cheapest, most time and effort efficient method attempted in this study; however, these methods also resulted in the most capture-related mortalities. Passive capture methods using a capture boma (P-B) are the most widely used and accessible method to conservation entities in Africa. Therefore, a guide, based on average cost values experienced in periods of this study, is presented to help determine what capture attempt rate is most appropriate when using P-B based capture once the project timeline is established.

Hippo space use data were interpreted using three home range estimation methods (MCP, KDE, *a*-LoCoH) to identify different patterns in overall and seasonal space use of hippos. We found that the mean home range size was ~6 km^2 using a-LoCOH methods, which was comparable

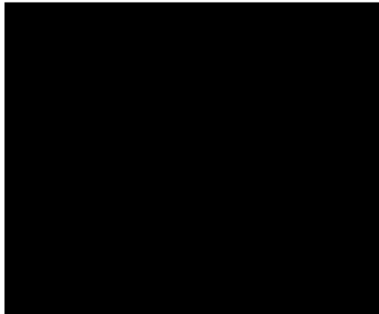
but slightly smaller than home ranges than those identified using similar home range estimation methods on the seasonal Ruaha River system, Tanzania. Our results highlighted how home range size and shape vary between individuals occupying different levels of social status, between individuals inhabiting different systems, and seasonally within the same individual.

Understanding the environmental requirements and drivers of space-use of hippos form the most fundamental understanding of their behaviour and will be pivotal in future conservation efforts. In addition, understanding the drivers of hippo population dynamics and trends are important factors when managing populations in protected areas. The results of our study offer new insights for the future management of hippos in South Africa and provide additional management and monitoring tools to conservation managers across Africa.

PREFACE

The data described in this thesis were collected in the Republic of South Africa from July 2016 to August 2020. Experimental work was conducted while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use was made of the work of others, it is duly acknowledged in the text.



Camille A.J. Fritsch

December 2020

I certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.

……………………………..

Professor Colleen T. Downs

Supervisor

December 2020

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DECLARATION 1 - PLAGIARISM

I, Camille J.A. Fritsch, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
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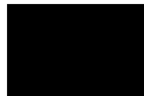

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis:

PUBLICATION 1

CJA Fritsch & CT Downs

Evaluation of low-cost consumer-grade UAVs for conducting comprehensive high frequency population censuses of hippopotamus populations

Author contributions:

CJAF conceived paper with CTD. CTD and CJAF sourced funding. CJAF collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 2

CJA Fritsch, M Plebani, CT Downs

Identifying seasonal changes in hippopotamus pod structure and population distribution in a river-floodplain system using a drone

Author contributions:

CJAF conceived paper with CTD. CTD and CJAF sourced funding. CJAF collected the data. CJAF analysed data with MP. CJAF wrote the paper. CTD and MP contributed valuable comments to the manuscript.

PUBLICATION 3

CJA Fritsch & CT Downs

Human and climatic drivers of hippopotamus population trends in Ndumo Game Reserve and its associated wading areas from 1951-2017

Author contributions:

CJAF conceived paper with CTD. CTD and CJAF sourced funding. CJAF collected and analysed data and wrote the paper. CTD contributed valuable comments to the manuscript.

PUBLICATION 4

CJA Fritsch & CT Downs

Home range size of the common hippopotamus in perennial river systems in the Kruger National Park, South Africa

Author contributions:

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PUBLICATION 5

CJA Fritsch, PE Buss & CT Downs

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Author contributions:

CJAF conceived paper with CTD. CTD and CJAF sourced funding. CJAF and PEB collected data. CJAF analysed data and wrote the paper. CTD and PEB contributed valuable comments to the manuscript.

PUBLICATION 6

CJA Fritsch & CT Downs

Various neighbouring community impacts on the Phongolo Floodplain at Ndumo Game Reserve, South Africa

Author contributions:

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Signed: ………………………………………………………

Camille Fritsch

December 2020

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"I used to think the top environmental problems were biodiversity loss, ecosystem collapse and climate change. I thought that with 30 years of good science we could address those problems. But I was wrong. The top environmental problems are selfishness, greed and apathy, and to deal with those we need a spiritual and cultural transformation – and we scientists don't know how to do that".

- Gus Speth

CHAPTER 1

Introduction

1.1 Threats to large herbivores in Africa, including hippopotamus

A variety of anthropogenic factors, including climate change, land-use change and habitat fragmentation, invasive species and pollution, and overhunting, threaten the future of conservation and management of large herbivores and large herbivore reserves in Africa (IPCC 2007, United Nations Population Fund 2007, Tilman et al. 2017). In addition to these more conventional, environmental and direct human-induced threats, conservation also depends on the financial and political situations within countries with target conservation areas (Tilman et al. 2017). Large herbivores, because of a combination of intrinsic characteristics and environmental factors, succumb easily to rapidly changing environments, especially ones driven by political and social instability (Cardillo et al. 2005). Therefore, the future of conservation of large herbivores will rely heavily on research focused on the close monitoring of target species to guide fundamental conservation initiatives and management goals so that scientific recommendations are addressed on environmental, social, and political fronts (Tilman et al. 2017).

Climatic variations have occurred naturally over short and long-term timescales; however, the current climatic pattern, e.g. the current rate of global warming, shaped by anthropogenic activity, is changing the planet more rapidly than ever before (Woodward et al. 2010). These effects are mostly inevitable and will play a significant role in the future alignment of conservation priorities (Tilman et al. 2017). The effects of climate change have put freshwater systems, especially at risk (Vörösmarty et al. 2000, Hutchins et al. 2018). In South Africa, 54% of rivers are listed as threatened (Driver et al. 2012). Rainfall in sub-Saharan Africa is predicted to decrease by 10% by 2050, leading to major water shortages and reducing river drainage by 30-50% (de Wit

& Stankiewicz 2006). Some dry regions at mid-latitudes and in dry tropics, like South Africa, are predicted to have decreases in water availability of up to 30% by 2050 (Milly et al. 2005). Southern Africa has particularly sensitive freshwater resources, and the aridification of the region will have a wide range of effects on ecological resources and processes like primary production (Magadza 1994, Fouchy et al. 2019). Studies on rainfall in South Africa in the past 100 years show increased extreme rainfall events yet decreased rainfall days and total rainfall (Mason et al. 1999, Easterling et al. 2000, MacKellar et al. 2014). In particular, the transition of sub-tropical regions to more xeric regions will dictate freshwater availability, impacting the distribution of species reliant on freshwater as a resource and for habitat (Kundzewicz et al. 2008, Woodward et al. 2010, Dallas & Rivers-Moore 2014).

Outside predicted climate change effects, the leading cause of species extinctions is habitat destruction and fragmentation (Pimm & Raven 2000). Human development is permanent and expanding, causing perpetual natural habitat loss in addition to facilitating the propagation of invasive species and expanding the effects of pollution (Fahrig 1997, Czech et al. 2000, Clavero & Garciaberthou 2005, Dabrowski & de Klerk 2013, Kyei & Hassan 2019). In 2017 the global human population was ~7.3 billion people (Tilman et al. 2017). By 2060 the global population is predicted to increase by 3.2 billion, with an expansion of 1.7 billion in sub-Saharan Africa alone (Tilman et al. 2017). As the human population expands, so does the amount of land area needed to sustain growing human populations. Land-use change brought about by human expansion threatens 80% of all terrestrial bird and mammal species, with agriculture and logging posing the most significant threats (Czech et al. 2000, Marzluff et al. 2001, McKinney 2002, Tilman et al. 2017). An additional 710 million ha of cropland will be required to sustain the predicted global human population increase by 2060, with 430 million ha of cropland expansion predicted to occur

in sub-Saharan Africa (Tilman et al. 2017). The inevitable expansion of human populations will have dramatic effects on the distribution and viability of natural ecosystems.

Additional pressures on wildlife increase as people gain access to more remote natural areas. According to the IUCN, a quarter of the world's species are threatened because of the effects of hunting (Nassar & Salamanca 2018). The poaching of mammals for valuable body parts like horn and ivory, as well as for subsistence purposes like bush meat, has led to catastrophic declines of sub-Saharan mammals (Tilman et al. 2017, Andersson & Gibson 2018). Relatively little research has been conducted on the impacts of poaching and the bushmeat trade on hippopotamus *Hippopotamus amphibius* (hereafter referred to as hippo) in Africa. Historically, hippos were targeted for their meat and ivory in South Africa. In the 1830's, hunting became a predominant source of income for Europeans in South Africa (McCracken 2008). In addition to being hunted, wild game competed with cattle for grazing and was susceptible to diseases carried by the livestock (McCracken 2008). By the 1860's most of the large-ranging herbivores in Zululand, South Africa, had been decimated, with the last remnant African elephants *Loxodonta africana* being shot in 1916 (McCracken 2008). Historically, hippos occupied the majority of the large rivers and water systems of Eastern, Western Central, and Southern Africa (McCracken 2008, Nassar & Salamanca 2018). In South Africa, the highest densities of hippos were concentrated along the rivers of modern-day St. Lucia and Richards Bay (McCracken 2008). Hunting in the early 1800's by European settlers had a drastic negative effect on the hippo populations. Following the end of the peak of hippo hunting in the early 1850's, only reclusive hippo populations remained. A reported minimum of 30,000 lbs of hippo ivory was exported out of Durban, South Africa, from 1860-1870, and larger quantities still in the 1850's (McCracken 2008). The first measures taken to protect the large game in Zululand were introduced in the 1890's (McCracken 2008). Today the impacts of

hunting by early Europeans are still apparent as numbers of wildlife have never been able to recover (McCracken 2008). Hunting in Africa remains a convoluted subject because of the economic value of the poaching, bush meat, and commercial hunting industries. However, poaching, the bushmeat trade, and the commercial hunting industry still impact the volume of wildlife present in and outside of nature reserves designed to protect wildlife (Lindsey et al. 2007, 2013, Ripple et al. 2016, Tilman et al. 2017).

Conservation is a widely accepted and pursued ideology in developed countries; however, this is not always the case in developing countries. Developing countries are especially important to consider as part of conservation initiatives as they have a large portion of the planets remaining natural ecosystems (Tilman et al. 2017). Besides being inhibited financially, developing countries lack the management, legislation, education and public awareness to effectively integrate and develop conservation initiatives (McKee et al. 2004, Ghazanfar 2008). These countries are also particularly susceptible to rapid human expansion, which puts the natural systems within them especially at risk (McKee et al. 2004). The largest diversities of large mammal species (≥10 kg) are found in South East Asia (155 spp.) and sub-Saharan Africa (125 spp.) (Tilman et al. 2017). These regions are almost exclusively comprised of developing countries and are experiencing some of the quickest and largest human population expansions on the planet (McKee et al. 2004, Tilman et al. 2017). Between 1960 and 2010, South East Asia experienced a population increase of 2 billion people, and today has more threatened vertebrates and large mammals than anywhere in the world (Tilman et al. 2017). Similarly, 46 of Africa’s 54 countries are considered developing countries (Jahan 2016). As previously seen in South East Asia, sub-Saharan Africa is experiencing rapid population growth and increasing income per capita, which correlate with increased threats to vertebrates and especially large mammal species (McKee et al. 2004, Tilman et al. 2017).

In addition, several sub-Saharan African countries have several further negative mitigating factors, including low agricultural and industrial productivity, a lack of foreign exchange, high indebtedness, a poor balance of payments position, political instability, chronic mismanagement of economic resources, and relatively high levels of corruption (McKee et al. 2004). To avoid repeating patterns from the past, quality and informative scientific research are required to ensure continued quality management of conservation areas for target conservation species in developing countries in Africa (McKee et al. 2004, Ghazanfar 2008).

1.2 Study species

1.2.1 Hippo species description

The hippo is Africa's third-largest megaherbivore. Hippos are diurnally aquatic and nocturnally terrestrial (Field 1970, Skinner & Chimimba 2005). Hippos lose water quickly through their skin, so they seek refuge in water during the day and forage for food almost exclusively at night (Field 1970). Although hippos spend the majority of their time in the water, they are not apt swimmers and rely more on their buoyancy when wading (Field 1970). Hippos generally prefer to wade in water about 1.5-2 m in depth. Gently graded banks allow hippos to wade further away from the water's edge providing more security (Field 1970, Blowers et al. 2012). Within river ecosystems, hippos will usually congregate around river bends and along sandbanks where the water is shallower (Chansa et al. 2011a).

Hippos are selective nocturnal grazers that consume an estimated 25-50 kg of grass/night (Field 1970, Lewison & Carter 2004, Skinner & Chimimba 2005, Chansa et al. 2011b). Hippos are close crop grazers that use the rough edges of their lips to pluck the tops off the grasses they feed on, leaving behind lawn-like short grass patches (Lock 1972, Chansa et al. 2011b, Zoeller &

Bond 2013, Kanga et al. 2013). Although hippo grazing depends on species availability, previous studies on grass species composition from hippo dung at Ndumo Game Reserve (NGR) showed that they predominantly fed on *Panicum maximum* (perennial tufted grass), *Urochloa mosambicensis* (perennial tufted grass), *Cynodon dactylon* (perennial rhizome grass), *Hermathria altissima* (perennial rhizome grass) and *Echinocloa pyramidalis* (perennial tufted grass) (Scotcher et al. 1978). Comparatively, around St. Lucia, South Africa, *Ischaemum arcuatum* (perennial rhizome grass) was the hippos' preferred species (Scotcher et al. 1978). In a study in Queen Elizabeth Park, Uganda, on the stomach contents of 90 hippos at varying times of the year, stomach contents showed their preference for *Bothriochloa* spp. (perennial tufted grass), *Brachiaria decumbens* (perennial tufted grass), *Chloris gayana* (perennial stolon grass), *Sporobulus pyramidalis* (perennial tufted grass), and *Themeda triandra* (perennial tufted grass). *Heteropogon contortus* (perennial tufted grass), *Hyparrhenia filipendula* (perennial tufted grass), *Sporobolus homblei* (perennial tufted grass), and dicotyledons were also present (Field 1970).

Estimates for grazing area required per hippo vary considerably as grazing area is predominantly influenced by resource availability and ecosystem type. Some estimates state that 5-7 ha of grazing area are required per hippo (Lewison & Carter 2004, Chansa et al. 2011b). Another study showed that 80 hippos could share 1 square mile (3.23 ha/hippo) of optimal foraging habitat, and 18 hippos would be able to share 1 square mile (14.39 ha/hippo) of less than optimal habitat (Field 1970). Hippo foraging distance is also widely disputed and also dependent predominantly on resource availability. However, it is estimated that hippos travel between ~2-7 km each night to find suitable grazing (Field 1970, Lewison & Carter 2004, Chansa et al. 2011b, Stears et al. 2019). Recent insights into hippo space use along the Mara River, Tanzania, showed that male hippo space use depended on their size and social status and changed temporally

depending on the season (Stears et al. 2019). There is no space use data for female hippos as yet (Supplementary Information Table S1.1). Relatively little previous research has been conducted on hippo's social behaviour and pod structure (Supplementary Information Table S1.1). Hippos are highly social animals and assemble in pods varying in number (Klingel 1979, Karstad & Hudson 1986, Blowers et al. 2010). Large congregations can occur in low water levels (Sayer & Rakha 1974, Smuts & Whyte 1981). Hippo pods are usually constructed of smaller family groups, with male hippo fighting for dominance over pods (Klingel 1979, Karstad & Hudson 1986).

1.2.2 Hippo habitat use and behaviour

Hippos require large land areas, especially in densely numbered populations where competition for resources is higher (Owen-Smith 2002). Hippo populations are less affected by predation and disease and are rather limited by the availability of suitable wading habitat and foraging (O'Connor & Campbell 1986). Distribution of hippos is generally first determined by the presence of suitable wading areas and second by the availability of grazing, especially in the dry season (Field 1970, Sayer & Rakha 1974, Harrison et al. 2008, Chansa et al. 2011a). When wading area is limited, hippo populations are forced to congregate in perennial wading areas (Viljoen 1995, Chansa et al. 2011a). The increase in the overall number of hippos within each pool often leads to overcrowding, increased aggressive behaviour and increased stress levels (Pienaar et al. 1966, Sayer & Rakha 1974, Smuts & Whyte 1981). These stressful wading conditions, in addition to limited food availability, cause hippos to show signs of degrading body condition, subsequently leading to declines in their physiological condition, and they are no longer able to breed or give birth (Chansa et al. 2011a).

When rainfall is considerable and grazing is readily available, the distance hippos are required to travel in search of quality grazing decreases, therefore decreasing the grazing area and overall area required for each hippo (Chansa et al. 2011b). For example, in the Luangwa Valley, Zambia, reduced rainfall reduced food availability, which in turn caused reduced hippo birth rates and caused an overall population decline (Sayer & Rakha 1974). In Liwonde National Park, Malawi, river flow was substantial, and wading areas were readily available; however, lack of rainfall created food limitations within the park for hippos. The hippos then turned to forage within the river during the day, a behaviour rarely recorded elsewhere, but this was interpreted as a response to food shortage and a population which exceed the carrying capacity (Mugangu & Hunter 1992, Harrison et al. 2008).

1.2.3 Hippos as ecosystem engineers

Hippos physically alter the environment they live in, creating feeding lawns, paths, and channels in swampland, and depositing valuable nutrients in aquatic environments (Moore 2006, Mosepele et al. 2009, Kanga et al. 2013, Subalusky et al. 2014, Dutton et al. 2018, Schoelynck et al. 2019). When hippos systematically graze, they generate functionally favourable feeding lawns used by other herbivores (Voysey et al. 2020). In areas where grass quality is lower, grazing by hippo may create nutritionally superior grazing lawns with larger leaf to stem ratios for other herbivores (Verweij et al. 2006). The uniformity of these lawns also facilitates the propagation of a diversity of palatable grass and shrub species (Field 1970). The array of palatable species available encourages the use of these lawns by various herbivore species, further facilitating overall diversity (Field 1970). The absence of hippos as pasture generators in ecosystems has shown the degeneration of feeding lawns and decreased overall herbivore biomass (Field 1970, Voysey et al.

2020). When moving to, from, and between feeding areas, hippos create vegetation-free pathways through reed beds and thick brush (pers. obs.). These vegetation-free paths are used by other species that can more easily move through the thick vegetation (pers. obs.). Hippos also create channels when moving in and out and between water bodies (McCarthy et al. 1998). These channels alter river flow and eventually change river characteristics (McCarthy et al. 1998). These alterations in river characteristics facilitate the distribution of fish and other aquatic species (McCarthy et al. 1998).

Hippos also play important roles as nutrient contributors in aquatic systems (Shurin et al. 2020, Dawson et al. 2020a, b). Animals that move between ecosystems form important linkages, especially when it comes to Carbon and other nutrient transport (Kitchell et al. 1979, Polis et al. 1997, Vanni 2002). Flooding in combination with soil, detritus from plants, and mammalian faeces are the primary sources of nutrients used by aquatic systems (Høberg et al. 2002, Mosepele et al. 2009, Taylor 2013). When nutrients flow into water systems, they can often support large blooms of phytoplankton and zooplankton (Høberg et al. 2002, Mosepele et al. 2009). These blooms then provide necessary nutrients for larval stage and juvenile fish (Mosepele et al. 2009). Previous research has shown that shallow bodies of water whose primary sources of nutrients are mammalian herbivore dung host substantial healthy fish populations (Fox 1976, McCauley et al. 2015). Not only do hippos and other mammals play an important role in transforming vegetation biomass into a form that aquatic species can readily use, but they also facilitate the spreading of nutrients through grazing, defecating on land, as well as other actions (Mosepele et al. 2009). In addition, hippos provide valuable nutrients to terrestrial systems and play a role in seed dispersal (Mosepele et al. 2009, McCauley et al. 2018, Muñoz-Concha et al. 2020, Hwang & Metcalfe 2020).

Larger, denser, and more ecologically influential hippo populations can also have dramatic negative impacts within an ecosystem (Mosepele et al. 2009). According to previous research, the total nutrient loading for one year by hippos in the Mara River, Tanzania was 3125 metric tons of dry matter, 1277 metric tons of C, 180 metric tons of N and 18 metric tons of P (Subalusky et al. 2015). This nutrient offload contributes greatly to aquatic ecosystem function and biogeochemical dynamics (Subalusky et al. 2015). Substantial nutrient offload in dung in combination with decreased water flow can cause eutrophication and the dying-off of most if not all aquatic species in that ecosystem (Mosepele et al. 2009, Stears et al. 2018, Stears & McCauley 2018). Hippo populations can also physically negatively alter their environment or contribute to overgrazing (Field 1970, Harrison et al. 2008, Mosepele et al. 2009, Dutton et al. 2018). This is typically seen in larger hippo populations that are exceeding carrying capacity (Harrison et al. 2008, Mosepele et al. 2009). In Liwonde National Park, Malawi, an excessive hippo population caused increases in erosion into the water bodies (Harrison et al. 2008). This has implications on streamflow as well as in the transportation and presence of nutrients in the water system (Mosepele et al. 2009).

1.2.4 Hippo conservation status in South Africa

Historically, hippos occupied many rivers and wetland habitats throughout continental Africa (Lewison & Pluhacek 2017). It was not until pressures induced by hunting and habitat loss caused dramatic declines in numbers and fragmented the remaining populations (McCracken 2008). Humans have also indirectly affected hippo as many riverine, and wetland habitats that historically hosted significant hippo populations have now been fragmented, disturbed, polluted, or otherwise destroyed (Grantham et al. 2019, Acosta et al. 2020). Recently the total hippo population in eastern, western, and southern Africa has been estimated at 125,000-148,000 hippo (Lewison & Pluhacek

2017). A total of 36 African countries have hippo populations, yet half have declining populations, and only one country (Zambia) has a growing population (Lewison & Pluhacek 2017). Currently, South Africa has one of the largest hippo populations in Africa. Within South Africa, the largest hippo populations occur in Kruger National Park (KNP; 3,500-5,000), iSimangaliso Wetland Park (iSWP; 800-1,000), and Ndumo Game Reserve (NGR; 200-300) (Taylor 2013, Eksteen et al. 2016, Lewison & Pluhacek 2017). According to KNP management staff, hippos are the most vulnerable species in KNP when the park is threatened by water scarcity induced food shortages (pers. comm. M. Hofmeyer 2016). KNP staff also reported that management had not had enough time or money to invest in hippo research because of the constant demand for conservation of other species (e.g. white rhino (*Ceratotherium simum*), black rhino (*Diceros bicornis*), and African elephant (pers. comm. M. Hofmeyer 2016).

1.3 Study areas

1.3.1 Ndumo Game Reserve

Ndumo Game Reserve (NGR) (32°18'48.85"E 26°54'32.48"S) is part of the Lubombo Ndumo-Tembe-Futi Transfrontier Conservation and Resource Area, created by the governments of South Africa, Mozambique and Swaziland. NGR is situated in Maputaland on the Mozambique border where the uSuthu River forms its northern boundary. The other major river system, the Phongolo River runs through the eastern side of the park. NGR is mostly flat and relatively small, spanning 10,117ha (103 km^2). Originally established as a hippo sanctuary (Calverley & Downs 2014), NGR currently hosts South Africa’s third-largest hippo population with ~300 hippos (pers. comm. C. Hanekom). Ndumo Game Reserve also hosts South Africa’s densest Nile crocodile (*Crocodylus niloticus*) population (Calverley & Downs 2014). However, NGR is perhaps best known for its

birdlife, with the highest bird count in South Africa of 430 species (Calverley & Downs 2014). In addition to the rivers that flow within and along the reserve, NGR also has numerous rain and floodwater fed pans. Nyamithi, a saltwater pan, is the most well-known and biodiverse of NGR's pans. NGR also has within it a varied selection of terrestrial habitats, including extensive wetland areas and reed beds, river floodplains, and riverine, acacia (*Vachellia* spp.), sand, and Matakini clay forests (Calverley & Downs 2014).

1.3.2 Human-wildlife conflict in South Africa and NGR

Human and wildlife conflict is a prevalent issue in South Africa. Historically, communities that neighboured protected areas were not allowed the economic and social benefits experienced by other people (Meer & Schnurr 2013). This was especially true for black South Africans who, during the apartheid era, were allowed only restricted access to protected areas (Beinart 1989, Carruthers 1995). Due to this discrimination, justifiably, rural black South Africans often held negative views towards protected areas (Meer & Schnurr 2013). Since the demise of the apartheid era, these negative views amongst black South Africans have changed, and there is a general consensus that the abolition of certain protected areas in South Africa would have negative socio-economic impacts (Picard 2003). Nevertheless, demands by the rural majority for land reform, poverty alleviation, and job creation have continued, and associations between protected areas and the apartheid era have not ceased to exist (Picard 2003). Many of these issues are because of a knowledge and communication gap between rural communities and protected area management authorities (Picard 2003). Generally, rural South Africans do not realise the global importance of conservation areas in South Africa (Picard 2003, Meer & Schnurr 2013). However, rural South Africans cannot justify the continued management of conservation for the benefit of the world

when they depend on them as a source of food, medicinal resources, and cultural and religious beliefs (Picard 2003, Meer & Schnurr 2013). The continued growth of South Africa's rural population, who receive relatively little government support and have little direct contact with people involved in the conservation of protected areas, will ensure that issues regarding the management of protected areas continue (Meer & Schnurr 2013).

Unfenced boundaries on the northern and eastern boundaries of NGR make NGR an open system, where people and fauna can come and go from the reserve (Meer & Schnurr 2013, Calverley & Downs 2014). Historically, during high flow, the uSuthu River created a temporary semipermeable boundary that was as wide as 60 m across. However, currently, all flow from the uSuthu River is directed to a tributary that runs through NGR, exposing the majority of the uSuthu River riverbed on the eastern half of the park. Additionally, the little flow in the uSuthu River during the dry season on the western half of the park is spread across a 50 m riverbed in shallow streams of 1-2 m in depth (Calverley & Downs 2014). Along the Mozambican border, the majority of the land opposite the uSuthu River from NGR is transformed with small rural farming communities (pers. obs.). Although more difficult in high flow, during low flow on the uSuthu, fauna, as well as people, can move in and out of NGR (Meer & Schnurr 2013, Calverley & Downs 2014).

Historically, the eastern boundary of NGR was fenced and was only forcefully removed in 2008 by neighbouring communities (Meer & Schnurr 2013). Community members from small farming communities along the eastern boundary forcefully collapsed the eastern boundary fence to gain access to farming and grazing land within the Phongolo floodplain. Ezemvelo KZN Wildlife has since become more involved with the communities along the eastern boundary to find a compromise that has allowed these communities access to 10% of the reserve (Meer & Schnurr

2013). Since this, communities have had impacts further inside the reserve and now occupy more than the allotted initial 10% (Meer & Schnurr 2013).

1.3.3 Kruger National Park and the Olifants River

Kruger National Park (KNP, 23°58'05.8"S, 31°33'48.0"E) is located in the Limpopo and Mpumalanga Provinces in South Africa and shares its eastern border with Mozambique. Managed by South African National Parks (SANParks), KNP is South Africa's largest conservation area, encompassing a total of 19,485 km^2 of low-lying savannah. At 65 km wide and 360 km long, the park is stretched longitudinally, with rainfall increasing from north to south and from east to west. Average annual rainfall experienced is 300-500 mm and 500-700 mm in the northern and southern regions, respectively, most of which falls in austral summer (November-April). With over 140 mammal species and over 500 bird species, KNP is one of Africa's most diverse conservation areas (South African National Parks 2011). Six major perennial river systems flow through KNP, including the Sabie and Olifants Rivers, the largest of which is the Olifants River. These two river systems host the largest hippo populations in KNP, with the Olifants River historically hosting the largest.

The Olifants River more or less forms the boundary between KNP's northern and southern sections. Within the boundaries of KNP, the Olifants River flows through the Mopane bioregion. It is predominantly characterised by Lowveld Rugged Mopaneveld and Mopane Basalt Shrubland, and the Lebombo uplands ecoregion that is characterised by Tshokwane-Hlane Basalt Lowveld and Northern Lebombo Bushveld (South African National Biodiversity Institute 2012). The Olifants River is widely regarded as one of the most polluted rivers in South Africa (Association of Water and Rural Development No Date, Verhaert et al. 2019, Kyei & Hassan 2019). Its socio-

economic importance outside of KNP's boundaries is evident with over 4.2 million people dependent on it (of which 70% live in rural areas) and an export market value of ~ZAR1 billion, most of which is rooted in industrial mining and agriculture (Association of Water and Rural Development No Date). The Olifants River also holds tremendous ecological and tourism value as many lodges and parks, including KNP, are situated along the river. The Olifants River is under increased threat because of the aforementioned anthropogenic impacts and recent accelerated climatic impacts that have accentuated the flood/drought cycle currently experienced along the system (Ferreira & Pienaar 2011, Woodborne et al. 2012, Verhaert et al. 2019, Kyei & Hassan 2019).

1.4 Drones in conservation

The cost-effectiveness and quality of data resulting from the implementation of Unmanned Aerial Systems (UAS) in conservation have resulted in the rapid expansion in the use and application of these systems. Implementation of UASs in field research have enabled researchers to overcome challenges in monitoring species with large geographic ranges, low population densities, inaccessible habitats, elusive behaviour, and sensitivity to disturbance (Gonzalez et al. 2016). UASs have already been used on a variety of research projects ranging from large marine mammals and reptiles to birds and large terrestrial mammals (Chabot & Bird 2012, Vermeulen et al. 2013, Hodgson et al. 2013, Ditmer et al. 2015, Fiori et al. 2017, Bevan et al. 2018). In addition to research on wildlife ecology, UASs are also being used to collect data from out-of-range radio collars, and as part of monitoring and anti-poaching programs (Dos Santos et al. 2014, Mulero-Pázmány et al. 2017). Although the benefits are evident, there are still some limitations of implementing UAS's as part of research and monitoring programs, including the processing of imagery, disturbance to

wildlife, and issues of limitations in battery life and reception (Ezat et al. 2018, Fritsch & Downs 2020).

1.5 Motivation and objectives of the study

Research on hippo behaviour and ecology is relatively limited and scarce (Eltringham 1999; Supplementary Information Table S1.1). However, their reliance on water bodies and grasslands has implications for their persistence, particularly with ongoing climate change impacts such as extended drought (low rainfall levels) in South Africa and other parts of Africa. In addition, the loss of this species may have detrimental cascading effects through already vulnerable wetland and riparian environments. Therefore, labelling the species as vulnerable may be an understatement of the immediate concern surrounding the loss of members of the species in NGR and KNP and across southern and continental Africa.

NGR was originally established as a hippo sanctuary and historically hosted healthy hippo populations. Up until recently, NGR had ~300 hippos, accounting for ~10% of the total South African hippo population (pers. comm. C. Hanekom). Relatively little ecological research had been conducted on hippo populations in South Africa (Scotcher 1974, 1978, Hancock 1978, Scotcher et al. 1978, Dawson et al. 2016, 2020a, b, Voysey et al. 2020). In particular, there remains a paucity of data detailing hippo behaviour to quantify their ecological effects better. Bush encroachment has been a continuing focal point for reserve managers at NGR as grasslands required by hippos, and other species, are shrinking every year (pers. obs.) In addition, current political complications have put NGR in a state of uncertainty. Bordering communities have moved into NGR, often poaching on various mammalian species and manipulating the important wetland areas (Meer & Schnurr 2013, pers. obs.). Due to the current political situations plaguing South Africa, including

poverty, mixing between cultural and political leadership, and recent and ongoing recovery from apartheid, politicians as well as conservationists are increasingly acknowledging the potential value of the resources inside NGR for the surrounding communities (Meer & Schnurr 2013). This has left NGR management with no choice but not to interfere as local communities move into the reserve (various pers. comm.). NGR's stable hippo population is becoming more valuable but also more vulnerable. It is hoped that the outcomes of this research will aid in ensuring that NGR remains a conservation area and hippo sanctuary.

Comparatively, KNP is a well-established conservation area in South Africa. However, dense hippo population numbers within fenced boundaries and accelerating human and climate impacts outside and along KNP's boundaries and rivers have created issues for management (Buss & Bengis 2012, Bengis et al. 2016). The Olifants River has a combination of anthropogenically introduced upstream stressors, which threaten the persistence of the Olifants River system (Ferreira & Pienaar 2011, Woodborne et al. 2012, Verhaert et al. 2019, Kyei & Hassan 2019). Hippos contribute significant amounts of allochthonous nutrients into the Olifants River, further contributing to the nutrient loads currently experienced in the system (Subalusky et al. 2014, Shurin et al. 2020, Dawson et al. 2020b). Therefore, it is important to understand how hippo behaviour, along with the nutrients introduced by hippos into the system, affect the resilience of the Olifants River socio-ecological system. These findings will provide additional context to the repercussions of excessive use of water resources in the Olifants River catchment, and the impact of this excessive use on water quality, quantity, habitat availability and biota characteristics.

Consequently, the goals of the present study were to detail aspects of hippo behaviour to help quantify their ecological impact on their environment in NGR and KNP and increase understanding for their conservation and management. The main objectives were to investigate the

factors that determine population size, distribution, and demographics within NGR as well as understand which environmental and anthropogenic constraints impact the population. Next, using telemetry and drone imagery, the goal was to highlight aspects of hippo behaviour that contribute to their ecology in aquatic and terrestrial systems in NGR and KNP. In addition, using the data collected in combination with historical data from NGR, drivers of population trends were assessed. The experimental implementation of novel telemetry, UAV census, and capture methods will contribute to future conservation and ecological understanding of hippos and their ecosystems. It was hoped that the overall results would provide conservation management with important data for ongoing management strategies and contribute to research and monitoring required to underpin sound conservation of hippo in and around NGR and KNP, and in the larger context of the conservation of hippo in continental Africa. Hence, it was hoped that this project would contribute to the body of knowledge to increase the overall understanding of this iconic but poorly known species and their role as ecosystem engineers.

According to the review of hippo literature I have conducted, I have found that, until recently, relatively little research had been conducted on hippo ecology and even fewer studies on hippo behaviour (Supplementary Information Table S1.1). In particular, relatively little is known about aspects of hippo behaviour like spatial ecology, social dynamics, and herd structure and how these drive hippo population dynamics and shape their ecological contributions in aquatic and terrestrial systems (Field 1970, Lewison & Carter 2004, Lewison 2007; Supplementary Information Table S1.1). In addition to answering questions about hippo behaviour and ecology, the value of UAVs as a method for estimating hippo populations, the utilisation of Global Positioning System (GPS) telemetry on hippos, as well as experimentation with capture methods will be assessed. Although previous studies have shown that UAV systems are valuable for

estimating, surveying, and managing populations of species, little research has been conducted on the implementation of UAV for population-level monitoring of hippos before the present study (Lhoest et al. 2015, Ezat et al. 2018, Linchant et al. 2018, Inman et al. 2019, Fritsch & Downs 2020). Only one recent study on male hippo spatial ecology was successful in East Africa; however, no studies have been conducted on perennial river systems nor in South Africa (Stears et al. 2019; Supplementary Information Table S1.1). Hippo capture methods are understudied, and at this point, are also costly, effort-intensive, dangerous and relatively ineffective (Pienaar 1963, 1967, Burroughs et al. 2012, Miller et al. 2014). Therefore, experimentation with various capture methods and quantification of budgetary and effort requirements will benefit future studies as well as conservation management of hippos. In addition, these methods are required for the implementation of GPS telemetry studies of hippos.

1.6 Thesis structure

This thesis comprises nine chapters; an introduction (includes a review of literature, aims, and justification) followed by seven data chapters, then a final chapter with conclusions and management recommendations. All data chapters were formatted for submission to international peer-reviewed journals. Therefore, some repetition was unavoidable. The hypotheses or predictions, and outcomes are presented in the respective chapters.

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1.8 Supplementary information

Supplementary Information Table S1.1 Summary of peer-reviewed publications on hippo ecology and behaviour, with a focus on non-captive studies.

Author	Year	Title	Subject	Country	Site
Verheyen	1954	Monographie éthologique de l'hippopotame:(*Hippopotamus amphibius* Linné)	Behaviour	Congo	Virunga National Park
Kain	1956	South Africa's hippo herds are on the march	Behaviour	South Africa	Various
Laws and Clough	1966	Observations on reproduction in the hippopotamus *Hippopotamus amphibius* Linn	Behaviour	Various	
Phillipson and Pomeroy	1972	Hippopotamus defending carcass	Behaviour	Unknown	
Physick	1972	Hippopotamus behaviour	Behaviour	Unknown	
Schutte	1973	Hippopotamus behaviour after shooting an adult female	Behaviour	South Africa	KwaZulu-Natal
Greasley	1973	Protective maternal behavior of hippopotamus	Behaviour	Zambia	Luangwa River
Scotcher	1973	Observations on the breeding behaviour of hippopotamus	Behaviour	South Africa	KwaZulu-Natal
Hill	1976	Non-aggressive tactile interactions of *Hippopotamus amphibius* Linn. with *Syncerus caffer* (Sparrman)	Behaviour	Uganda	Ruwenzori National Park
Scotcher	1978	Hippopotamus numbers and movements in Ndumu Game Reserve	Behaviour	South Africa	Ndumo Game Reserve
Klingel	1979	Social organization of *Hippopotamus amphibius*	Behaviour	Uganda	Queen Elizabeth National Park
Karstad and Hudson	1986	Social organization and communication of riverine hippopotami in southwestern Kenya	Behaviour	Kenya	Mara River
Barklow	1997	Some underwater sounds of the hippopotamus (*Hippopotamus amphibius*)	Behaviour	Tanzania	Ruaha National Park
Lewison	1998	Infanticide in the hippopotamus: evidence for polygynous ungulates	Behaviour	Tanzania	Katavi National Park

Barklow	2004	Amphibious communication with sound in hippos, *Hippopotamus amphibius*	Behaviour	Tanzania	Ruaha National Park
Barklow	2004	Low-frequency sounds and amphibious communication in *Hippopotamus amphibius*	Behaviour	Tanzania	Ruaha National Park
Noirad et al.	2008	Seasonal variation of thermoregulatory behaviour in the Hippopotamus (*Hippopotamus amphibius*)	Behaviour	Niger	River Niger
Blowers et al.	2010	Social behaviors within a group of captive female Hippopotamus amphibius	Behaviour	Captive	
Pluháček and Bartošová	2011	A case of suckling and allosuckling behaviour in captive common hippopotamus	Behaviour	Captive	
Blowers et al.	2012	Female nile hippopotamus (*Hippopotamus amphibius*) space use in a naturalistic exhibit: Hippopotamus exhibit use	Behaviour	Captive	
Fazal et al.	2014	Comparative behavioral study of male Nile hippopotamus (*Hippopotamus amphibius*) after pairing at Lahore Zoo	Behaviour	Captive	
Maust-Mohl et al.	2015	Acoustic and behavioral repertoires of the hippopotamus (*Hippopotamus amphibius*)	Behaviour	Captive	
Prinsloo	2016	Aspects of the spatial and behavioural ecology of *Hippopotamus amphibious* in the Saint Lucia Estuary, KwaZulu-Natal, South Africa	Behaviour	South Africa	St. Lucia
Dudley et al.	2016	Carnivory in the common hippopotamus *Hippopotamus amphibius*: implications for the ecology and epidemiology of anthrax in African landscapes	Behaviour	Various	
Stears et al.	2019	Spatial ecology of male hippopotamus in a changing watershed	Behaviour	Tanzania	Mara River
Inman and Legget	2019	Observations on the response of a pod of hippos to a dead juvenile hippo (*Hippopotamus amphibius* , Linnaeus 1758)	Behaviour	Botswana	Okavango Delta
de Castro et al.	2019	Hippo cannibalism	Behaviour	Zimbabwe	Masuma Dam
Prinsloo et al.	2020	Multiscale drivers of hippopotamus distribution in the St Lucia Estuary, South Africa	Behaviour	South Africa	St. Lucia
Spinage	1959	Hippos galore: The Kazinga channel and its hippo problem	Ecology	Uganda	Kazinga channel
Rice	1963	Birds associating with elephants and hippopotamuses	Ecology	Various	
Pooley	1967	Bird/crocodile and bird/hippopotamus commensalism in Zululand	Ecology	South Africa	KwaZulu-Natal
Laws	1968	Interactions between elephant and hippopotamus populations and their environments	Ecology	Various	

Field	1970	A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Queen Elizabeth National Park, Uganda, with some management implications	Ecology	Uganda	Queen Elizabeth National Park
Lock	1972	The effects of hippopotamus grazing on grasslands	Ecology	Uganda	Queen Elizabeth National Park
Olivier and Laurie	1974	Birds associating with hippopotamuses	Ecology	Kenya	Mara River
Scotcher	1974	A quantitative assessment of the food preferences of *Hippopotamus amphibius* L. in the Ndumu game reserve, Tongaland	Ecology	South Africa	Ndumo Game Reserve
Olivier	1974	Habitat utilization by hippopotamus in the Mara River*	Ecology	Tanzania	Mara River
Eltringham	1974	Changes in the large mammal community of Mweya Peninsula, Rwenzori National Park, Uganda, following removal of hippopotamus	Ecology	Uganda	Ruwenzori National Park
Leyhausen	1976	Erosion and the hippos	Ecology	Congo	Virunga National Park
Taylor	1976	Hippopotamuses at Lake St Lucia	Ecology	South Africa	KwaZulu-Natal
Delvingt	1978	Écologie de l'hippopotame (*Hippopotamus amphibius*. L) au parc national des Virunga (Zaïre)	Ecology	Congo	Virunga National Park
Scotcher et al.	1978	The diet of the hippopotamus in Ndumu Game Reserve, Natal, as determined by faecal analysis	Ecology	South Africa	Ndumo Game Reserve
Taylor	1980	A land capability study for hippopotamuses at Lake St Lucia, Zululand	Ecology	South Africa	St. Lucia
Smuts and Whyte	1981	Relationships between reproduction and environment in the hippopotamus *Hippopotamus amphibius* in the Kruger National Park	Ecology	South Africa	Kruger National Park
Kilham	1982	The effect of hippopotamuses on potassium and phosphate ion concentrations in an African Lake	Ecology	Uganda	Ruwenzori National Park
O'Connor and Campbell	1986	Hippopotamus habitat relationships on the Lundi River, Gonarezhou National Park, Zimbabwe	Ecology	Zimbabwe	Gonarezhou National Park
Mugangu and Hunter	1992	Aquatic foraging by hippopotamus in Zaïre: Response to a food shortage?	Ecology	Congo	Virunga National Park
Viljoen	1995	Changes in number and distribution of hippoptamus (*Hippopotamus amphibius*) in the Sabie River, Kruger National Park, during the 1992 drought	Ecology	South Africa	Kruger National Park

McCarthy et al.	1998	Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius* L.) in the Okavango Delta, Botswana	Ecology	Botswana	Okavango Delta
Wolanski and Gereta	1999	Oxygen cycle in a hippo pool, Serengeti National Park, Tanzania	Ecology	Tanzania	Serengeti National Park
Grey and Harper	2002	Using Stable Isotope Analyses to Identify Allochthonous Inputs to Lake Naivasha Mediated via the Hippopotamus Gut	Ecology	Kenya	Lake Naivasha
Deocampo	2002	Sedimentary structures generated by *Hippopotamus amphibius* in a lake-margin wetland, Ngorongoro Crater, Tanzania	Ecology	Tanzania	Ngorongoro Crater
Noirad et al.	2004	Diets of sympatric hippopotamus (*Hippopotamus amphibius*) and Zebus (*Bos indicus*) during the dry season in the "W" National Park (Niger Republic)	Ecology	Niger	"W" National Park
Payne	2004	Describing the relation between ward structure, forage quality and soil chemistry in grasslands grazed by Hippo (*Hippopotamus amphibius*) in the Eastern Shores region of the Greater St Lucia Wetland Park.	Ecology	South Africa	St. Lucia
Lewison and Carter	2004	Exploring behavior of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus	Ecology	Tanzania	Kavati National Park
Harrison et al.	2008	The ecology of the hippopotamus in Liwonde National Park, Malawi: implications for management	Ecology	Malawi	Liwonde National Park
Cerling et al.	2008	Stable isotope ecology of the common hippopotamus	Ecology	Various	
Kanga et al.	2011	Population trend and distribution of the Vulnerable common hippopotamus *Hippopotamus amphibius* in the Mara Region of Kenya	Ecology	Kenya	Mara Region
Chansa et al.	2011	Influence of river geomorphologic features on hippopotamus density distribution along the Luangwa River, Zambia: River geomorphology and hippo distribution	Ecology	Zambia	Luangwa River
Chansa et al.	2011	The influence of grass biomass production on hippopotamus population density distribution along the Luangwa River in Zambia	Ecology	Zambia	Luangwa Valley
Theophile et al.	2012	Feeding Habits of *Hippopotamus amphibius* and Carrying Capacity in the Biosphere Reserve of "Mare aux Hippopotames" in the South-Sudanian Zone of Burkina Faso	Ecology	Burkina Faso	Mare aux Hippopotames
Valderama	2012	Wild hippos in Colombia.	Ecology	Colombia	Various
Timbuka	2012	The Ecology and Behaviour of the Common hippopotamus, Hippopotamus amphibious L. in Katavi National Park, Tanzania: Responses to Varying Water Resources	Ecology	Tanzania	Kavati National Park

Michez et al.	2013	Preliminary description of the diet of *Hippopotamus amphibius* L. in Loango National Park (Gabon)	Ecology	Gabon	Loango National Park
Kanga et al.	2013	Hippopotamus and livestock grazing: influences on riparian vegetation and facilitation of other herbivores in the Mara Region of Kenya	Ecology	Kenya	Mara Region
Zoeller and Bond	2013	Hippos as ecosystem engineers? Grazing lawns and their determinants in the St Lucia floodplain	Ecology	South Africa	St. Lucia
Subalusky et al.	2014	The hippopotamus conveyor belt: vectors of Carbon and nutrients from terrestrial grasslands to aquatic systems in sub-Saharan Africa	Ecology	Captive	
McCauley et al.	2015	Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river	Ecology	Kenya	Ewaso Ng'iro River
Dawson et al.	2016	Declines in benthic macroinvertebrate community metrics and microphytobenthic biomass in an estuarine lake following enrichment by hippo dung	Ecology	South Africa	St. Lucia
McCauley et al.	2018	Diverse effects of the common hippopotamus on plant communities and soil chemistry	Ecology	Kenya	Mpala Research Centre
Stears and McCauley	2018	Hippopotamus dung inputs accelerate fish predation by terrestrial consumers	Ecology	Tanzania	Mara River
Stears et al.	2018	Effects of the hippopotamus on the chemistry and ecology of a changing watershed	Ecology	Tanzania	Mara River
Dutton et al.	2018	Organic matter loading by hippopotami causes subsidy overload resulting in downstream hypoxia and fish kills	Ecology	Tanzania	Mara River
Driciru et al.	2018	Spatio-temporal epidemiology of anthrax in *Hippopotamus amphibious* in Queen Elizabeth Protected Area, Uganda	Ecology	Uganda	Queen Elizabeth National Park
Subalusky et al.	2019	Potential ecological and socio-economic effects of a novel megaherbivore introduction: the hippopotamus in Colombia	Ecology	Colombia	Various
Dawson	2019	Terrestrial-aquatic transfers by hippopotamus (*Hippopotamus amphibius*)- effects on food web and benthic community structure of the St Lucia Estuary, iSimangaliso Wetland Park, World Heritage Site, South Africa	Ecology	South Africa	St. Lucia
Schoelynck et al.	2019	Hippos (*Hippopotamus amphibius*): The animal silicon pump	Ecology	Tanzania	Mara River

Masese et al.	2020	Hippopotamus are distinct from domestic livestock in their resource subsidies to and effects on aquatic ecosystems	Ecology	Kenya	Mara River
Dawson et al.	2020	Idiosyncratic responses of meiofaunal assemblages to hippo dung inputs in an estuarine lake	Ecology	South Africa	St. Lucia
Dawson et al.	2020	Fatty acid analyses provide novel insights on hippo defecation and consequences for aquatic food webs	Ecology	South Africa	St. Lucia
Clarke	1953	The Hippopotamus in Gambia, West Africa	Human-hippo conflict	Gambia	Various
Sayer and Rakha	1974	The age of puberty of the hippopotamus (*Hippopotamus amphibius* Linn.) in the Luangwa River in eastern Zambia	Human-hippo conflict	Zambia	Luangwa Valley
Mkanda	1994	Conflicts between hippopotamus (*Hippopotamus amphibius* (L.)) and man in Malawi	Human-hippo conflict	Malawi	Various
Mkanda	1997	Relationship between crop damage by hippopotamus (*Hippopotamus amphibius* L.) and farmer complaints in the Elephant Marsh	Human-hippo conflict	Malawi	Elephant Marsh
Post	2000	The hippopotamus: nothing but a nuisance?	Human-hippo conflict	Kenya	Lake Victoria
Kendall	2011	The spatial and agricultural basis of crop raiding by the Vulnerable common hippopotamus *Hippopotamus amphibius* around Ruaha National Park, Tanzania	Human-hippo conflict	Tanzania	Ruaha National Park
Kanga et al.	2012	Human–hippo conflicts in Kenya during 1997–2008: vulnerability of a megaherbivore to anthropogenic land use changes	Human-hippo conflict	Kenya	Various
Ertiban	2016	Population status and human conflict of common hippopotamus (*Hippopotamus amphibius*, Linnaeus, 1758) In Boye Wetland, Jimma, Ethiopia	Human-hippo conflict	Ethiopia	Boye Wetland

González et al.	2017	Preventing crop raiding by the Vulnerable common hippopotamus *Hippopotamus amphibius* in Guinea-Bissau	Human-hippo conflict	Guinea-Bissau	Various
Dossou et al.	2019	Common hippopotamus-human conflicts in Ouémé River area in central Benin Republic	Human-hippo conflict	Benin Republic	Oueme
Haddara et al.	2020	Hippopotamus bite morbidity: a report of 11 cases from Burundi	Human-hippo conflict	Burundi	Various
Pienaar et al.	1966	An experimental cropping scheme of hippopotami in the Letaba River of the Kruger National Park	Population distribution and trends	South Africa	Kruger National Park
Marshal and Sayer	1976	Population ecology and response to cropping of a hippopotamus population in Eastern Zambia	Population distribution and trends	Zambia	Luangwa Valley
Viljoen	1980	Distribution and numbers of hippopotamus in the Olifants and Blyde rivers	Population distribution and trends	South Africa	Kruger National Park
Karstad and Hudson	1984	Census of the Mara River hippopotamus (*hippopotamus amphibius*), southwest Kenya, 1980-1982	Population distribution and trends	Kenya	Mara River
Tembo	1987	Population status of the hippopotamus on the Luangwa River, Zambia	Population distribution and trends	Zambia	Luangwa Valley

Norton	1988	Hippopotamus numbers in the Luangwa Valley, Zambia, in 1981	Population distribution and trends	Zambia	Luangwa Valley
Jacobsen and Kleynhans	1993	The importance of weirs as refugia for hippopotami and crocodiles in the Limpopo River, South Africa	Population distribution and trends	South Africa	Kruger National Park
Eksteen	1993	The determination of acceptable hippopotamus (*Hippopotamus amphibius*) densities in the Crocodile River, Outside the Kruger National Park	Population distribution and trends	South Africa	Kruger National Park
Bhima	1996	Census of hippopotamus (*Hippopotamus amphibius* (L)) in the Upper Shire River, Malawi	Population distribution and trends	Malawi	Liwonde National Park
Viljoen and Biggs	1998	Population trends of hippopotami in the rivers of the Kruger National Park, South Africa	Population distribution and trends	South Africa	Kruger National Park
Manilus	2000	Historical ecology and biogeography of the hippopotamus in Egypt	Population distribution and trends	Egypt	Various
Bennett et al.	2000	Notes and records. The abundance of *Hippopotamus amphibius* in the Black Volta River at Bui National Park, Ghana.	Population distribution and trends	Ghana	Bui National Park
Roth et al.	2004	Distribution and status of the hippopotamids in the Ivory Coast	Population distribution and trends	Ivory Coast	Various

Nchanji and Fotso	2006	Common hippopotamus (*Hippopotamus amphibius*): a survey on the River Djerem, Mbam-Djerem National Park, Cameroon	Population distribution and trends	Cameroon	Mbam-Djerem National Park
Brugière et al.	2006	Population abundance of the common hippopotamus *Hippopotamus amphibius* in the Haut Niger National Park, Republic of Guinea / Abondance de la population d'hippopotame commun *Hippopotamus amphibius* dans le Parc National du Haut Niger, République de Guinée	Population distribution and trends	Republic of Guinea	Haut Niger National Park
Lewison	2007	Population responses to natural and human-mediated disturbances: assessing the vulnerability of the common hippopotamus (*Hippopotamus amphibius*)	Population distribution and trends	Various	
Ngog	2009	Contribution à l'étude de la structure de la population des hippopotames (*Hippopotamus amphibius* L.) au Parc National de la Bénoué (Cameroun)	Population distribution and trends	Cameroon	Benoue National Park
Dibloni et al.	2010	Structure démographique et mouvements saisonniers des populations d'hippopotame commun, *Hippopotamus amphibius* Linné 1758 dans la zone sud soudanienne du Burkina faso	Population distribution and trends	Burkina Faso	Mare aux Hippopotames
Zisadza et al.	2010	Abundance, Distribution and Population Trends of Hippopotamus in Gonarezhou National Park, Zimbabwe	Population distribution and trends	Zimbabwe	Gonarezhou National Park
Wilbroad and Milanzi	2011	Population status of the hippopotamus in Zambia: Population status of the hippopotamus in Zambia	Population distribution and trends	Zambia	
Mackie et al	2013	Current status and distribution of the Vulnerable common hippopotamus *Hippopotamus amphibius* in Mozambique	Population distribution and trends	Mozambique	Various

Chomba	2013	Factors affecting the Luangwa (Zambia) hippo population dynamics within its carrying capacity band – Insights for better management	Population distribution and trends	Zambia	Luangwa Valley
Chomba et al.	2014	Does the Luangwa hippo population size and density distribution vary between upper and lower study blocks? What are the management implications of such distribution pattern?	Population distribution and trends	Zambia	Luangwa Valley
Scholte and Iyah	2016	Declining population of the Vulnerable common hippopotamus *Hippopotamus amphibius* in Bénoué National Park, Cameroon (1976–2013): the importance of conservation presence	Population distribution and trends	Cameroon	Benoue National Park
Scholte et al.	2016	Dry season counts (1976-2016) in the Faro-Bénoué protected area complex (North Cameroon) highlight the continued importance of West-Central Africa's largest population of common hippopotamus	Population distribution and trends	Cameroon	Benoue National Park
Stommel et al.	2016	The effect of reduced water availability in the Great Ruaha River on the Vulnerable Common Hippopotamus in the Ruaha National Park, Tanzania	Population distribution and trends	Tanzania	Ruaha National Park
Scholte et al.	2017	Good news from north-central Africa: largest population of Vulnerable common hippopotamus *Hippopotamus amphibius* is stable	Population distribution and trends	Cameroon	Benoue National Park
Utete et al.	2017	Analysis of the abundance and spatial distribution of the common hippopotamus, (*Hippopotamus amphibius*) in the Manjirenji Dam, Zimbabwe, to inform conservation and detect human-wildlife conflict hot spots	Population distribution and trends	Zimbabwe	Manjirenji Dam
Monsalve Buriticá and Ramírez Guerra	2018	Estado actual de los hipopótamos (*Hippopotamus amphibius*) en Colombia: 2018	Population distribution and trends	Colombia	Various

Utete et al.	2020	A review of some aspects of the ecology, population trends, threats and conservation strategies for the common hippopotamus, *Hippopotamus amphibius* L, in Zimbabwe	Population distribution and trends	Zimbabwe	Various

CHAPTER 2

Evaluation of low-cost consumer-grade UAVs for conducting comprehensive high-frequency population censuses of hippopotamus populations

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Running header: Hippo census methods using a UAV

2.1 Abstract

The hippopotamus *Hippopotamus amphibius* (hereafter referred to as hippo) is classified as vulnerable according to the IUCN Red data list. They play a significant role in aquatic systems as allochthonous nutrient providers, and as facilitators and competitors in grasslands. Traditional census methodologies for hippo are difficult and costly to repeat. Previous research has been conducted on the use of unmanned aerial systems (UASs) to conduct hippo population estimates, however, findings either needed justification through additional field testing or used high-cost UASs that may be unaffordable for management authorities in developing countries in Africa. Therefore, using a low-cost, consumer-grade, DJI Phantom 3 Advanced multi-rotor unmanned aerial vehicle (UAV), 47 surveys were conducted of the hippo population at Ndumo Game Reserve (NGR), South Africa, between August 2016 and July 2017. In addition, comparisons were drawn between the results of and the logistical requirements and costs of respective helicopter and UAV surveys conducted on the same day of the same hippo population. The use of a consumer-grade UAV permitted frequent, accurate, and comparatively low-cost surveys to identify temporal changes in the number of hippos present in NGR and at different locations within NGR. Hippos are a data deficient species, particularly in remote developing countries. UAVs surveys of hippo will allow accurate, highly repeatable, and comparatively low-cost data collection for management of hippos and the ecosystems within which they occur.

Keywords

Hippos, drone, unmanned aerial system, UAS, aerial census, population estimate, Ndumo Game Reserve, South Africa

2.2 Introduction

Applications for unmanned aerial systems (UASs) in wildlife research are increasing, particularly considering their benefit for effective monitoring and managing of species of conservation importance in areas and countries with budgetary limitations (Linchant et al. 2015; Hahn et al. 2017; Bevan et al. 2018; Ezat et al. 2018; Roberts et al. 2020). Population censuses are used by conservation area managers as an overarching indication of species and ecosystem health (Dice 1938; Lancia et al. 2005). Traditional census methods include foot and ground counts as well as manned aerial methods. These methods have been implemented in the monitoring of varieties of species, including large African herbivores like the African elephant (*Loxondonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and the common hippopotamus (*Hippopotamus amphibius*) (hereafter referred to as hippo) (Owen-Smith 1981; Whitehouse et al. 2001; Brockett 2002). The high costs and high effort associated with surveys conducted using traditional methods have provided opportunities for new methods with broader application. UASs have made strides in superseding traditional methods and have been implemented in studies monitoring a variety of species, including Nile crocodiles (*Crocodylus niloticus*), bowhead whales (*Balaena mysticetus*), Sumatran orangutan (*Pongo abelii*), and a number of surface nesting bird species (Schweder et al. 2010; Chabot & Bird 2012; McClelland et al. 2016; Wich et al. 2016; Afán et al. 2018; Ezat et al. 2018). However, few studies have assessed the capabilities of UASs for conducting comprehensive population censuses of large African mammal species of conservation importance or if surveys can be repeated at high frequencies to divulge high-resolution management related data (Vermeulen et al. 2013).

Hippos are a target for conservation management and their predictable diurnal wading behaviour make them detectable and a good pilot species for managers to evaluate and ameliorate

UAS survey methodologies that can later be adapted and applied to other species. The hippo is one of Africa's most iconic species, yet the historic fractionalisation and continued recent global declines of up to 20% in the last 10 years have focused more attention on their conservation (Lewison & Pluhacek 2017). The aforementioned, along with unreliable population estimations and a paucity of research on hippo ecology and behaviour, have contributed to the hippo being classified as vulnerable according to the IUCN (Lewison & Pluhacek 2017). Furthermore, because of the impacts associated with an exponentially expanding human population in sub-Saharan Africa, a growing proportion of the global hippo populations are being displaced and/ or restricted to protected areas (Lewison 2007; Ramesh et al. 2016; Lewison & Pluhacek 2017; Tilman et al. 2017).

Outside of the conservation importance, the role of hippos as ecosystem engineers in African aquatic and grassland environments make them an important species to consider in managed systems (Field 1970; Lock 1972; McCarthy et al. 1998; Moore 2006; Subalusky et al. 2014; Bakker et al. 2016; McCauley et al. 2018). Hippos graze on land and defecate when wading, facilitating the transport of allochthonous carbon, silicates, and nutrients into aquatic systems (Subalusky et al. 2014; Dutton et al. 2018; Schoelynck et al. 2019). Allochthonous nutrient contributions by hippos play a fundamental role in supporting aquatic communities (McCauley et al. 2015). However, excessive inputs by dense congregations can have varying effects, such as eutrophication in systems with highly variable habitat characteristics like flow, discharge, and water quality (Bengis et al. 2016; Stears et al. 2018). Additionally, although periodic grazing by hippos promotes the diversification of grazing areas, unmanaged hippo populations contribute significant inter- and intra- species grazing competition and cause overall deterioration of grazing areas through overgrazing (Field 1970; Bengis et al. 2016). Hippos have few natural predators,

and population numbers are instead controlled naturally by disease and drought or controlled directly with management strategies like culling (Marshall & Sayer 1976; Lewison 2007; Harrison et al. 2008; Bengis et al. 2016). Consequently, the effects of unmanaged hippo populations are endured exponentially in closed systems or in open systems that experience periodic or seasonal influxes of hippos (Lock 1972; Chansa et al. 2011; Bengis et al. 2016).

Hippos are nocturnally active and wade or lie up diurnally in or near water bodies, rivers, or lakes (Chansa et al. 2011; Perissinotto et al. 2013). Where traditional methods would have been limited by varying exposure and submergence of individuals and the remoteness of wading locations, the predictability of hippos diurnal wading activity facilitates surveys that employ the use of a UASs bird's-eye-view (Delvingt 1978; Stuart 2001; Lhoest et al. 2015). Previous studies on the application of UASs for surveying hippo populations have formed the building blocks of the methodology. Studies conducted in the Democratic Republic of Congo outlined census parameters like optimum flight altitude, the impact of environmental conditions, and the importance of observer bias in calculating hippo population estimates from UAV surveys, in addition to the utilisation of algorithms for automatic detection and counting of hippos from infrared UAV imagery (Lhoest et al. 2015; Linchant et al. 2018). Further research in Botswana evaluated the capabilities of a low-cost UAV for collecting census data, including population demographics, under an experimental setting (Inman et al. 2019). However, the afore-mentioned studies have all been conducted under experimental conditions in closed lake or pond systems, without taking into account changing environmental conditions and habitat types, the variability of pod size and number, and have therefore not tested the capabilities of a UAV census conducted in a real-world scenario. Additional research to ameliorate current UAS census methodologies will

help normalise a universally accessible methodology to aid in future management and conservation of hippos, especially in parks and areas with budgetary limitations and data deficiencies.

Therefore our aims were: 1) to contribute to the evaluation of a low-cost, consumer-grade, multi-rotor UAVs for conducting comprehensive population surveys, and particularly if these systems permit surveys at increased frequencies to divulge data at a finer temporal scales; 2) to compare the logistical requirements and the results of a UAV survey to a helicopter survey conducted on the same day of the same hippo population to justify the relevance of UASs amongst current population census methodologies for hippos; and 3) based on our results and previous research on the use of UAS for census of hippos, provide a protocol to be followed when using a low-cost multi-rotor UAV for such censuses of minimum population number.

2.3 Methods

2.3.1 Study area

NGR (26°S, 32°N) is a relatively small 10,117 ha reserve managed by the provincial authority Ezemvelo KwaZulu-Natal Wildlife (EKZNW) in northern South Africa (Figure 1). NGR is situated along South Africa's northern border with Mozambique within the Mozambique Coastal Plain (Whittington et al. 2013). NGR's northern boundary with Mozambique is formed by the Usuthu River, which runs from west to east. The Phongolo River, the other predominant river within the system, runs from south to north through the eastern side of the park. During periods of high rainfall (November-February), these rivers swell, then flood, inundating the Usuthu and Phongolo floodplains, accounting for over 4000 ha of inundated land stretching over 40% of NGR (Calverley & Downs 2014a,b). These two main river courses along with 12 pans, of which

Nyamithi Pan is the largest (157 ha), form the predominant water bodies in NGR (Calverley & Downs 2017).

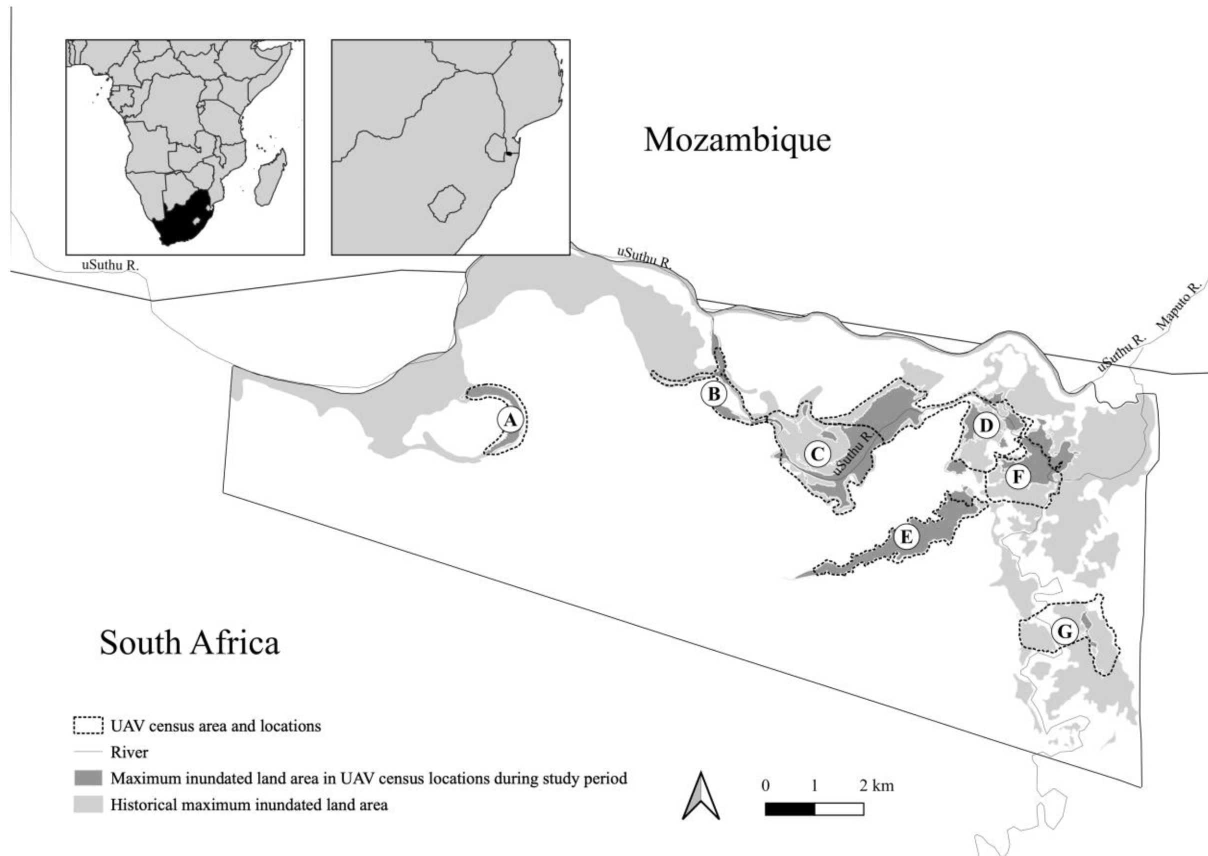

Figure 2.1. Location of Ndumo Game Reserve, South Africa, situated along South Africa's northern border with Mozambique and the UAV census area and locations.

2.3.2 UAV survey locations

We conducted four monthly UAV surveys of the important wading areas in NGR (Figure 1) from August 2016 to July 2017. Surveys were conducted at seven different locations along the uSuthu and Phongolo Rivers and associated floodplains, pans, and lakes (Figure 2.1). The UAV survey area was first designed to account for dry season wading localities as determined from previous years aerial census data as well as by known localities of hippos reported by EKZNW field rangers

and management staff. The large survey area was then strategically broken down into seven survey locations (Figure 2.1) based on the accessibility of the pilot, bandwidth of the UAV, and UAV battery life. Travel between survey locations was also considered. Survey localities were then adjusted or expanded when new wading locations were identified either visually, from spore, by vocalisation, or with the UAV. Surveys were mostly comprehensive of the available wading areas in low-flow season and accounted for most of the expanded inundated area in the wet season. Each of these localities was surveyed once each survey day for four respective surveys per month. Surveys were not conducted outside of the major floodplain system as these areas are dominated by Makatini Clay thicket and Western Maputaland Clay bushveld and do not provide conducive wading environments for hippos (pers. obs.). To account for potential changes in hippo numbers through different times of the day, we surveyed localities according to four different patterns interspersed across the four survey days each month. In order to decrease the amount of time spent travelling between survey locations, these patterns also considered the distance between locations, where locations that were closer together were surveyed together.

2.3.3 Unmanned aerial vehicle used

We employed the use of a DJI Phantom 3 Advanced UAV to collect the images necessary for our surveys (DJI has since discontinued this product, but the description is available at https://www.dji.com/phantom-3-adv/info). Excluding the propellers, the Phantom 3 Advanced UAV had a diagonal breadth of 350 mm and weighed 1280 g. An additional two batteries were purchased to increase the total possible survey time. The maximum flight time was estimated to be approximately 23 min with a top speed of 16 m/s and a maximum flight distance of 6000 m. The UAV is manufactured with a 2.7 K Camera and 3-Axis Gimbal with the capacity for shooting

12 megapixel JPEG files, a 1/2.3" sensor, fast f/2.8 prime lens, and a pre-set focus optimised for aerial images. All image global positioning system (GPS) locations were automatically embedded as part of every image.

2.3.4 UAV survey protocol

The UAV was controlled by a pilot on the ground via the DJI GO app on an Apple iPhone 6 and operated through the DJI Phantom 3 Advanced remote controller. An example flight path is shown in Figure 2.2. The operator used a live video feed from the UAV to manoeuvre the UAV to, from, and around the survey locations. Only aquatic habitat was surveyed, and surveys were completed once all possible wading locations in the survey area were surveyed. The breadth of the survey areas was first determined by the distribution of dry season wading habitat; accounting for potential increases in the survey area in the wet season, and second by connectivity with the UAV, where if bandwidth was limited, then survey areas were split so that all available habitat could be surveyed. An effort was made to conduct all flights at a consistent altitude of 30 m and a constant speed of between 8-10 m/s; however, some increases in altitude of up to 60 m were required to compensate for low bandwidth during surveys. The flight height was determined based on the lowest flight altitude possible above the highest tree canopy to increase detection and achieve the highest count precision and accuracy. Although the floodplain was generally uniform in topography, the flight altitude of the UAV was gauged based on the height of the UAV above the take-off location and not the actual altitude during flight, and therefore images taken during flight were taken from unknown altitudes. Although the pilot made an effort to search for hippos with the camera facing forward to identify targets on the horizon, the pilot was sometimes forced to adapt to environmental conditions and changes in survey area characteristics. Single individuals

as well as large pods, were distinguishable during surveys. Once a target was located, the piloted hovered the drone above with the camera facing directly below and took at least three sequential photographs of each hippo or group of hippos. These photographs were taken from different angles to avoid glare and to ensure the best photographic quality. The number of photographs taken of each group of hippos depended on the number, the level of submergence, and level of disturbance of hippos. Increased numbers of images were taken of large congregations, pods that were either entirely or partially submerged, and groups that were disturbed by the presence of the UAV. An effort was made to capture as many hippos in each photograph as possible. If congregations of pods did not allow for all hippos to be captured in a single photograph, sets of photographs were taken of different portions of hippo congregations so that all individuals could be accounted for. It was necessary that UAV batteries be fully charged before each survey. Therefore, batteries were charged in a research vehicle between survey locations using a car-charging adapter.

2.3.5 UAV image processing and hippo counts

Images were processed using Apple Preview (https://support.apple.com/en-za/guide/preview/welcome/mac) (Figure 2.1). Each image taken during the survey was captured, assuming that it contained at least one hippo. However, some images contained only objects that resembled hippos and no actual hippos and were therefore removed from the data set. We grouped images containing hippos based on date and survey area. We then sorted images of the same pod containing different numbers of visible individuals, and we kept the photographs that contained the highest minimum number of individuals for the data set. Each hippo was counted and marked using the 'sketch' tool in the 'mark-up toolbar' to prevent multiple counts of single individuals. Each photograph was counted and marked twice; if there were discrepancies between counts, the

image was counted a third time or until a consistent total was determined. Once we counted all hippos, we calculated a total for each location as well as a total for the survey. All recordings and calculations were done in Microsoft Excel.

Figure 2.2. A selection of imagery representing the UAV census process (a) a sample flight path of a UAV census of Nyamiti Pan in August 2016 (b) a screenshot of a UAV image taken at Dephini showing the interface used to count hippos (c-f) a selection of photographs from the UAV census conducted in August 2016 exemplifying differences in ease of detection of hippos at four different survey locations (c) a single hippo at Bhakabhaka (d) a large congregation of hippos in muddy water at Banzi (e) a small pod well-hidden at Shabathan (f) a set of hippos basking in shallow water on the periphery of Nyamiti Pan.

2.3.6 EKZNW helicopter survey

EKZNW conducted their annual survey of the hippo population at NGR on August 22, 2016, using a Bell Jetranger III helicopter. These surveys are typically conducted during the dry season between July and August when water levels are lowest and were designed to cover the entire wading habitat in the reserve, targeting previously known wading habitat. Four observers were aboard the aircraft, two in the front and two in the rear. One observer in the front of the aircraft was equipped with a Canon 30D camera with an 18-135 zoom lens used to capture photographs of the hippo. The hippo count was carried out from 10h:00 to 11h:30. Flight height was approximately 30 - 90 m at a speed of 30 knots. When a congregation of hippos was spotted, the helicopter hovered until a satisfactory number of quality images could be taken. The images were processed by EKZNW staff, and the results recorded in Microsoft Excel.

2.4 Results

A total of 47 of the 48 planned UAV surveys were conducted from August 2016-July 2017. Mean total census area was $2.26 km^2 \pm 1.79 km^2$ with a maximum of $6 km^2$. The mean flight distance covered by the UAV in a single census survey 5.28 km ± 3.15 km with a maximum of 22.08 km. Mean UAV survey time at a single survey location was 13:57 min ± 6:56 min with a maximum of 49:17 min. The ground sampling distance (GSD) realised while flying the UAV at 30 m altitude was 1.3cm/px. The maximum distance attained between the UAV and remote during flight was 3.6 km flying over open water at Nyamiti Pan. The maximum number of flights required to cover the census area in a single survey was 13 flights. Battery life and connectivity from the UAV to the remote were the greatest limitations and determined UAV census area. Increases in forest density decreased connectivity between the UAV and remote. UAV surveys enabled us to identify

temporal changes in density, distribution, and minimum hippo population. This manuscript aims to highlight the capabilities and methodologies resulting from implementing UAS based censuses of a hippo population, and therefore the behavioural and ecological findings that resulted from these censuses are reported in a separate manuscript (Fritsch et al. in prep.). We were able to use the UAV to survey areas where hippo localities were known, as well as at discovering new localities through changing distribution of wading locations. A total of 7435 images of hippos were processed (Figure 2.2). The mean number of hippos detected in a census was 145.6 ± 54.5, with a maximum number of 246 hippos and a minimum of 26 hippos.

On 22 August 2019, the total census areas for the UAV and helicopter censuses were 0.77 km^2 and 50.54 km^2, respectively (Table 2.1). The maximum attained UAV survey area in the study period was 5.99 km^2 (Table 2.1). The costs for the UAV census included the fuel costs for vehicle travel between survey take-off locations and excluded initial costs: UAV purchase (~$1500) and, although it was not relevant to this study, UAV pilot hire (~$150/hour) or UAV pilot licensing (~$1500-$8000) (South African Civil Aviation Authority 2019). The cost of the helicopter census was determined based on an hourly rate of $756/h that included the fuel, pilot hours, and cost of utilisation of helicopter but excluded initial purchase of a helicopter, its maintenance, and the cost of travel to and from the census take-off location. In August 2016, the UAV census accounted for approximately 43% of the cost/km^2 of the helicopter census (Table 2.1). The maximum flight area UAV census in the study period (November 2016) was 4% of the cost/km^2 of the helicopter survey in August 2016. The person-hours required are also documented in Table 2.1, where the August 2016 UAV census required 7.25 h from one person, while the helicopter census required 1.5 h from 4 people (6 total person h) (Table 2.1). The total minimum population estimate derived from the August UAV survey was 227 hippos, and the total derived from the helicopter survey was 255

hippos (Table 2.1). The UAV census accounted for all the same localities as the helicopter within the UAV flight area (Table 2.2). The UAV census detected a higher number of hippos at 2/7 survey locations (Banzi and Dephini), an equal amount was detected at 3/7 survey locations (Shokwe, Shabathan, and Nyamiti), and less were detected at 2/7 locations (Bhakabhaka and Pholwe) (Table 2.2).

Table 2.1. Cost and effort comparisons between UAV and helicopter survey methodologies for counting hippos in Ndumo Game Reserve, South Africa.

Parameter	**UAV (Aug. 2016)**	**UAV (Nov. 2016)**	**Helicopter (Aug. 2016)**
Elapsed survey time (hours)	7.25	7.5	1.5
Person hours required (hours)	7.25	7.5	6
Approximate total survey area (km^2)	0.77	6.00	50.54
Cost per survey (US Dollars)	4.07	4.07	756
Census cost per km^2 surveyed (US Dollars)	6.49	0.68	14.96

*Note: Fuel costs were calculated using March 2019 exchange rates between South African Rands and US Dollars and March 2019 fuel prices

Table 2.2. The total number of hippos counted by location during the UAV and helicopter censuses conducted in August 2016 in Ndumo Game Reserve, South Africa.

	UAV	Helicopter
Shokwe	0	0
Dephini	37	31
Shabathan	0	0
Banzi	49	47
Nyamiti	8	8
Bhakabhaka	38	67
Pholwe	95	99
Outside UAV census area	-	3
Total	**227**	**255**

*Note: Helicopter disturbed hippo leading to underestimates by UAV

2.5 Discussion

Large government-run conservation authorities in South Africa, namely South African National Parks (SANParks) and EKZNW, generally conduct hippo population surveys using helicopters. At a fraction of the cost and skill-level required, low-cost multi-rotor UAV surveys provided accurate population estimations that could be easily repeated over diel and annual timescales to identify temporal changes in the number and distribution of hippos. Although some discrepancies in counts were realised between the helicopter and the UAV, the UAV resulted in comparable data (Table 2.2). The underestimate of the minimum population at least 1/7 locations (Bhakabhaka)

was attributed to the disturbance caused by the helicopter, which instigated the retreat of the hippos to deeper water where they submerged, and later in the day, went undetected during the UAV survey (Table 2.2). Normal shifts in the distribution of hippos through wading localities may have also contributed to the discrepancies between counts, even though both surveys occurred on the same day. In August 2016, the helicopter census was more than two times more expensive per km^2 surveyed than the UAV census. Although the helicopter covered far more area, most of the area covered can be attributed to taxiing between census locations and did not account for areas with viable hippo habitat (Table 2.1). On the contrary, the UAV census was designed to focus on known aquatic wading sites and surrounds, and the only costs incurred were related to commuting by car between survey locations. An even larger discrepancy in cost per km^2 surveyed was realised when the maximum attained UAV flight area in the study period was compared with the helicopter census in August 2016 (Table 2.1).

Hippos are the last remaining large herbivore (>1000kg) that occur outside of protected areas in South Africa (Eksteen et al. 2016; Lewison & Pluhacek 2017). South Africa has the third-largest population in the world accounting for 5-6% of global numbers, of which roughly 90% occur in managed protected areas (Eksteen et al. 2016; Lewison & Pluhacek 2017). NGR's estimated 250-300 hippo in 2017 accounted for the second-largest population managed by EKZNW, after iSimangaliso Wetland Park (iSWP), and the third-largest remaining natural population in South Africa (the largest being in Kruger National Park). In the 2016-2017 fiscal year, across more than 120 parks (> 6,750km^2), EKZNW spent approximately 1% (~$50,200) of their annual budget on logistics related to game counts utilising methods including walked transects, fixed-wing aircraft, and helicopter censuses (pers. comm.). Even so, a number of the planned annual censuses could not be completed because of monetary constraints and over-booked

aircrafts. To add to the problem, in 2017-2018, EKZNW experienced dramatic budget cuts, and funding towards censuses and logistics were reduced by a further 40% (pers. comm.). Assuming the hippo censuses in NGR and iSWP covered 50km^2 and 750km^2, respectively, our cost estimates indicate that EKZNW could save between ~$6,776-11,424 annually by replacing helicopters with UAS based survey methodologies at these two locations. These cost-saving opportunities are not only relevant in South Africa as, according to the IUCN, 1-2% of the global population occurs in nine African countries with unknown or data-deficient populations, the majority of which are budget-related (Eksteen et al. 2016; Lewison & Pluhacek 2017).

Other challenges remain ahead before UAS survey methods are adapted in conservation management and scientific research in South Africa. The South African Civil Aviation Authority (SACAA) has established some of the most stringent laws in the world for remotely piloted aerial systems (RPAS), and licensing comes at a relatively high financial cost (≤ ~$15,000), even for research and conservation management entities (South African Civil Aviation Authority 2019). These entities, which, at first glance, neither fall under 'personal or private use' nor 'commercial outcome, interest, or gain', are blanketed under the 'commercial' category and are required to jump through a number of very expensive hoops before implementing UAS methodologies (South African Civil Aviation Authority 2019). In a different setting, these stringent laws and licensing requirements lead to better overall public safety. However, many of these precautions are less relevant in remote, expansive, protected areas, away from tourists and people. Across EKZNW protected areas, there is a growing concern about the potential application of UAS's as part of illegal poaching activities, particularly rhino poaching. Although there are additional security and logistical concerns that arise when piloting UASs in protected areas with elevated security

protocols, conservation management and scientific research should be afforded a different level of scrutiny than outside entities and members of the public.

In addition, although the data are not presented here, this study is the first to collect high resolution population-level behavioural and demographic data for hippos and demonstrates the management as well as the scientific opportunities that arise from high-frequency population censuses. The pilot had no experience flying a UAV before the study, yet the surveys were easy to conduct and yielded important results. The multi-rotor UAV offered advantages in manoeuvrability and permitted active detection and approximation of hippo numbers during the course of survey flights. The manoeuvrability and ease of piloting of the UAV enabled sustained relevance of the methodology through changing ecosystem-level characteristics like increases in inundated land surface area. In addition, when hovering, multiple images could be captured of targets. The most significant hurdle we encountered with the implementation of the multi-rotor UAV was restricted flight range because of limited bandwidth.

Some ameliorations to the UAV census protocol used in this study can be made to increase its quality and efficiency. The UAV offered relatively low levels of disturbance compared to the helicopter; however, we did encounter some disturbance of hippos dependent on pod size and water level through our surveys (pers. obs.). A hippo's eyesight is generally less sensitive than it's hearing. In addition, the UAV was of diminutive size, and therefore any disturbance during surveys was more likely to be caused by noise disturbance rather than visual disturbance (pers. obs.). Hippos were more difficult to count where deeper water allowed them to submerge once disturbed by the sound of the UAV. We did not quantify the impact of a potential change in altitude on the quality of a census, but did at some points increase our flight altitude to compensate for low bandwidth, and believe an increase in survey altitude to 40-50 m (GSD: 1.73-2.16) will still result

in effective and informative surveys as individual hippo and large pods were still distinguishable. We acknowledge that the implementation of UAS-based census methods will be dependent on several variables, including 1) the population size where populations with <1000 hippo will be easier to survey, 2) the behaviour and particularly the level of disturbance or persecution of the population where a previously undisturbed population will be more favourable, 3) the system type where rivers, dams, and lakes will be much easier to survey than floodplain systems and systems with open grasslands will be easier to survey than forested, 4) the road access and remoteness of target survey areas where less remote localities will allow enough bandwidth between the UAV and pilot and decrease the time needed for surveys, 5) the level of cover and water depth at survey locations where hidden or submerged hippos will be more difficult to account for, 6) the presence and flexibility of drone regulations, 7) the available budget. We recommend that low-cost multirotor UASs are effective for intensive surveying of known wading areas and surrounds. If wading areas are unknown, then we rather recommend the use of a more powerful multi-rotor UAS or the use of a multi-rotor UAS system in unison with fixed-wing UAS, or a helicopter, first to locate hippo wading locations as they are more adept to surveys covering large areas, e.g. 10-30 km^2 (Guo et al. 2018). Some unforeseen advantages of using a multi-rotor UAV was that it permitted the identification and investigation of targets, and increased adaptability during flight and provided immediate feedback without needing to download or process imagery. In terms of management, the multi-rotor UAV also allowed the collection of finite data on groups of animals, like the identification of individuals, group-level social structures, and the identification of snared or injured animals. This is a useful tool in protected areas in Africa where management scenarios on the ground require constant and adaptable surveillance techniques.

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Conflict of interest

The authors declare no potential conflict of interest.

Authors' contributions

C.F. and C.T.D conceptualised this research and found funding. C.F. collected the data, conducted the analyses and wrote the manuscript. C.T.D. edited and reviewed subsequent drafts.

Ethics statement

No ethics approval was required for this research.

Data availability statement

All data used in this manuscript are available on request and are stored at the University of KwaZulu-Natal.

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Evaluation of low-cost consumer-grade UAVs for conducting comprehensive high-frequency population censuses of hippopotamus populations

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Abstract

The hippopotamus Hippopotamus amphibious (hereafter referred to as hippo) is classified as vulnerable according to the IUCN Red data list. They play a significant role in aquatic systems as allochthonous nutrient providers, and as facilitators and competitors in grasslands. Traditional census methodologies for hippo are difficult and costly to repeat. Previous research has been conducted on the use of unmanned aerial systems (UASs) to conduct hippo population estimates; however, findings either needed justification through additional field testing or used high-cost UASs that may be unaffordable for management authorities in developing countries in Africa. Therefore, using a low-cost, consumer-grade, DJI Phantom 3 Advanced multi-rotor unmanned aerial vehicle (UAV), 47 surveys were conducted of the hippo population at Ndumo Game Reserve (NGR), South Africa, between August 2016 and July 2017. In addition, comparisons were drawn between the results of and the logistical requirements and costs of the respective helicopter and UAV surveys conducted on the same day of the same hippo population. The use of a consumer-grade UAV permitted frequent, accurate, and comparatively low-cost surveys to identify temporal changes in the number of hippos present in NGR and at different locations within NGR. Hippos are a data deficient species, particularly in remote developing countries. UAVs surveys of hippo will allow accurate, highly repeatable, and comparatively low-cost data collection for management of hippos and the ecosystems within which they occur.

KEYWORDS
aerial census, drone, hippos, Ndumo game reserve, population estimate, South Africa, UAS

1 | INTRODUCTION

Applications for unmanned aerial systems (UASs) in wildlife research are increasing, particularly considering their benefit for effective monitoring and managing of species of conservation importance in areas and countries with budgetary limitations (Bevan et al., 2018; Ezat, Fritsch, & Downs, 2018; Hahn et al., 2017; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015; Roberts et al., 2020). Population censuses are utilized by

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conservation area managers as an overarching indication of species and ecosystem health (Dice, 1938; Lancia, Kendall, Pollock, & Nichols, 2005). Traditional census methods include foot and ground counts as well as manned aerial methods. These methods have been implemented in the monitoring of a variety of species including large African herbivores like the African elephant (*Loxondonta africana*), white rhinoceros (*Ceratotherium simum*), black rhinoceros (*Diceros bicornis*), and the common hippopotamus (*Hippopotamus amphibius*) (hereafter referred to as hippo) (Brockett, 2002; Owen-Smith, 1981; Whitehouse, Hall-Martin, & Knight, 2001). The high costs and high effort associated with surveys conducted using traditional methods have provided opportunities for new methods with broader application. UASs have made strides in superseding traditional methods and have been implemented in studies monitoring a variety of species including Nile crocodiles (*Crocodylus niloticus*), bowhead whales (*Balaena mysticetus*), Sumatran orangutan (*Pongo abelii*), and several surface nesting bird species (Afán, Máñez, & Díaz-Delgado, 2018; Chabot & Bird, 2012; Ezat et al., 2018; McClelland, Bond, Sardana, & Glass, 2016; Schweder, Sadykova, Rugh, & Koski, 2010; Wich, Dellatore, Houghton, Ardi, & Koh, 2016). However, few studies have assessed the capabilities of UASs for conducting comprehensive population censuses of large African mammal species of conservation importance or if surveys can be repeated at high frequencies to divulge high-resolution management related data (Vermeulen, Lejeune, Lisein, Sawadogo, & Bouché, 2013).

Hippos are a target for conservation management and their predictable diurnal wading behavior make them detectable and a good pilot species for managers to evaluate and ameliorate UAS survey methodologies that can later be adapted and applied to other species. The hippo is one of Africa's most iconic species, yet the historical fragmentation of their habitats and continued recent global declines of up to 20% in the last 10 years have focused more attention on their conservation (Lewison & Pluhacek, 2017). The aforementioned, along with unreliable population estimations and a paucity of research on hippo ecology and behavior, have contributed to the hippo being classified as vulnerable according to the IUCN (Lewison & Pluhacek, 2017). Furthermore, because of the impacts associated with an exponentially expanding human population in sub-Saharan Africa, a growing proportion of the global hippo populations are being displaced and/or restricted to protected areas (Lewison, 2007; Lewison & Pluhacek, 2017; Ramesh, Kalle, Rosenlund, & Downs, 2016; Tilman et al., 2017).

Outside of the conservation importance, the role of hippos as ecosystem engineers in African aquatic and grassland environments make them an important species to consider in managed systems (Bakker, Pagès, Arthur, & Alcoverro, 2016; Field, 1970; Lock, 1972; McCarthy, Ellery, & Bloem, 1998; McCauley et al., 2018; Moore, 2006; Subalusky, Dutton, Rosi-Marshall, & Post, 2014). Hippos graze on land and defecate when wading, facilitating the transport of allochthonous carbon, silicates, and nutrients into aquatic systems (Dutton, Subalusky, Hamilton, Rosi, & Post, 2018; Schoelynck et al., 2019; Subalusky et al., 2014). Allochthonous nutrient contributions by hippos play a fundamental role in supporting aquatic communities (McCauley et al., 2015). However, excessive inputs by dense congregations can have varying effects such as eutrophication in systems with highly variable habitat characteristics like flow, discharge, and water quality (Bengis et al., 2016; Stears et al., 2018). Additionally, although periodic grazing by hippos promotes the diversification of grazing areas, unmanaged hippo populations contribute significantly to inter- and intra-species grazing competition and cause overall deterioration of grazing areas through overgrazing (Bengis et al., 2016; Field, 1970). Hippos have few natural predators, and population numbers are instead controlled naturally by disease and drought, or controlled directly with management strategies like culling (Bengis et al., 2016; Harrison, Kalindekafe, & Banda, 2008; Lewison, 2007; Marshall & Sayer, 1976). Consequently, the effects of unmanaged hippo populations are endured exponentially in closed systems or in open systems that experience periodic or seasonal influxes of hippos (Bengis et al., 2016; Chansa, Milanzi, & Sichone, 2011; Lock, 1972).

Hippos are nocturnally active and wade or lie-up diurnally in or near water bodies, rivers, or lakes (Chansa, Senzota, Chabwela, & Nyirenda, 2011; Taylor., 2013). Where traditional methods would have been limited by varying exposure and submergence of individuals and the remoteness of wading locations, the predictability of hippos diurnal wading activity facilitates surveys that employ the use of a UASs birds-eye-view (Delvingt, 1978; Lhoest, Linchant, Quevauvillers, Vermeulen, & Lejeune, 2015; Stuart, 2001). Previous studies on the application of UASs for surveying hippo populations have formed the building blocks of the methodology. Studies conducted in the Democratic Republic of Congo outlined census parameters like optimum flight altitude, the impact of environmental conditions, and the importance of observer bias in calculating hippo population estimates from UAV surveys, in addition to the utilization of algorithms for automatic detection and counting of hippos from infrared UAV imagery (Lhoest et al., 2015; Linchant et al., 2018). Further research in Botswana evaluated the capabilities of a low-cost UAV

for collecting census data, including population demographics, under an experimental setting (Inman, Kingsford, Chase, & Leggett, 2019). However, the abovementioned studies have all been conducted under experimental conditions in closed lake or pond systems, without taking into account changing environmental conditions and habitat types, the variability of pod size and number, and have therefore not tested the capabilities of a UAV census conducted in a real-world scenario. Additional research to ameliorate current UAS census methodologies will help normalize a universally accessible methodology to aid in future management and conservation of hippos, especially in parks and areas with budgetary limitations and data deficiencies.

Therefore our aims were: (a) to contribute to the evaluation of a low-cost, consumer-grade, multi-rotor UAVs for conducting comprehensive population surveys, and particularly if these systems permit surveys at increased frequencies to divulge data at a finer temporal scales; (b) to compare the logistical requirements and the results of a UAV survey to a helicopter survey conducted on the same day of the same hippo population to justify the relevance of UASs amongst current population census methodologies for hippos; and (c) based on our results and previous research on the use of UAS for census of hippos, provide a protocol to be followed when using a low-cost multi-rotor UAV for such censuses of minimum population number.

2 | METHODS

2.1 | Study area

NGR (26°S, 32°N) is a relatively small 10,117 ha reserve managed by the provincial authority Ezemvelo KwaZulu-Natal Wildlife (EKZNW) in northern South Africa (Figure 1). NGR is situated along South Africa's northern border with Mozambique within the Mozambique Coastal Plain (Whittington, Malan, & Panagos, 2013). NGR's northern boundary with Mozambique is formed by the Usuthu River, which runs from west to east. The Phongolo River, the other predominant river within the system, runs from south to north through the eastern side of the park. During periods of high rainfall (November–February) these rivers swell, then flood, inundating the

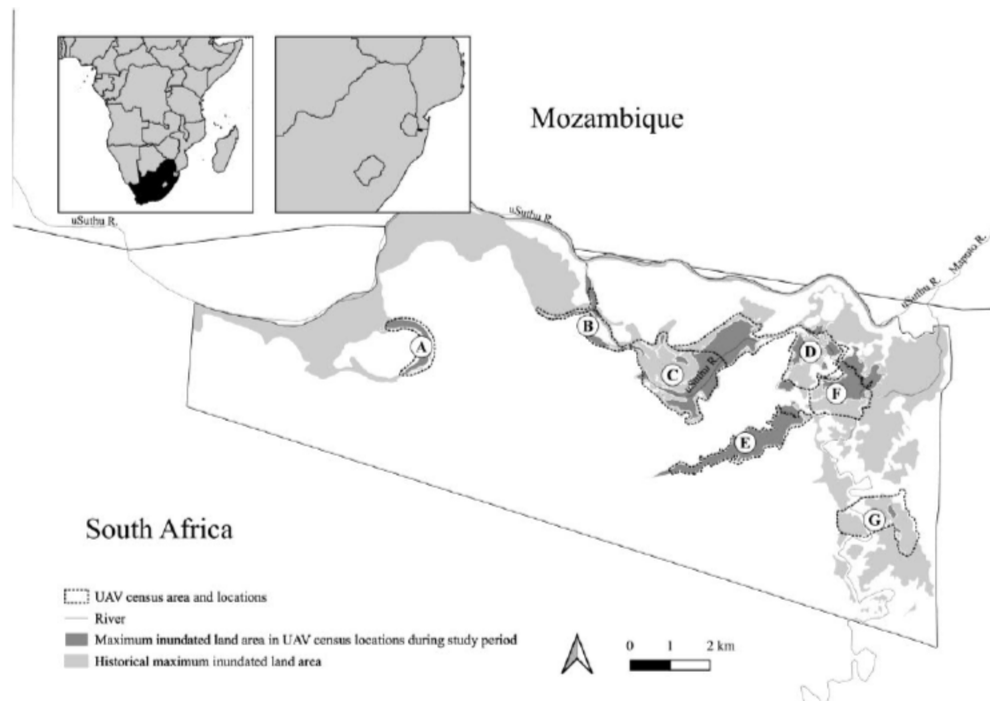

FIGURE 1 Location of Ndumo Game Reserve, South Africa, situated along South Africa's northern border with Mozambique and the UAV census area and locations

Usuthu and Phongolo floodplains accounting for over 4,000 ha of inundated land stretching over 40% of NGR (Calverley & Downs, 2014a, 2014b). These two main river courses along with 12 pans, of which Nyamithi Pan is the largest (157 ha), form the predominant water bodies in NGR (Calverley & Downs, 2017).

2.2 | UAV survey locations

We conducted four monthly UAV surveys of the important wading areas in NGR (Figure 1) from August 2016 to July 2017. Surveys were conducted at seven different locations along the Usuthu and Phongolo Rivers and associated floodplains, pans, and lakes (Figure 1). The UAV survey area was first designed to account for dry season wading localities as determined from previous year's aerial census data as well as by known localities of hippos reported by EKZNW field rangers and management staff. The large survey area was then strategically broken down into seven survey locations (Figure 1) based on the accessibility of the pilot, bandwidth of the UAV, and UAV battery life. Travel between survey locations was also considered. Survey localities were then adjusted or expanded when new wading locations were identified either visually, from spore, by vocalization, or with the UAV. Surveys were mostly comprehensive of the available wading areas in low-flow season and accounted for most of the expanded inundated area in the wet season. Each of these localities was surveyed once each survey day for four respective surveys per month. Surveys were not conducted outside of the major floodplain system as these areas are dominated by Makatini Clay thicket and Western Maputaland Clay bushveld and do not provide conducive wading environments for hippos (pers. obs.). To account for potential changes in hippo numbers through different times of the day, we surveyed localities according to four different patterns interspersed across the four survey days each month. In order to decrease the amount of time spent travelling between survey locations, these patterns also considered the distance between locations, where locations that were closer together were surveyed together.

2.3 | Unmanned aerial vehicle used

We employed the use of a DJI Phantom 3 Advanced UAV to collect the images necessary for our surveys (DJI has since discontinued this product but the description is available at https://www.dji.com/phantom-3-adv/info). Excluding the propellers, the Phantom 3 Advanced UAV had a diagonal breadth of 350 mm and weighed 1,280 g. An additional two batteries were purchased to increase the total possible survey time. The maximum flight time was estimated to be ~23 min with a top speed of 16 m/s and a maximum flight distance of 6,000 m. The UAV is manufactured with a 2.7 K Camera and 3-Axis Gimbal with the capacity for shooting 12 megapixel JPEG files, a 1/2.3″ sensor, fast f/2.8 prime lens, and a preset focus optimized for aerial images. All image global positioning system (GPS) locations were automatically embedded as part of every image.

2.4 | UAV survey protocol

The UAV was controlled by a pilot on the ground via the DJI GO app on an Apple iPhone 6 and operated through the DJI Phantom 3 Advanced remote controller. An example flight path is pictured in Figure 2. The operator used a live video feed from the UAV to manoeuvre the UAV to, from, and around the survey locations. Only aquatic habitat was surveyed, and surveys were completed once all possible wading locations in the survey area were surveyed. The breadth of the survey areas was first determined by the distribution of dry season wading habitat; accounting for potential increases in the survey area in the wet season, and second by connectivity with the UAV, where if bandwidth was limited, then survey areas were split so that all available habitat could be surveyed. An effort was made to conduct all flights at a consistent altitude of 30 m and a constant speed of between 8 and 10 m/s; however, some increases in altitude of up to 60 m were required to compensate for low bandwidth during surveys. The flight height was determined based on the lowest flight altitude possible above the highest tree canopy to increase detection and achieve the highest count precision and accuracy. Although the floodplain was generally uniform in topography, the flight altitude of the UAV was gauged based on the height of the UAV above the take-off location and not the actual altitude during flight, and therefore images taken during flight were taken from unknown altitudes. Although the pilot made an effort to search for hippos with the camera facing forward to identify targets on the horizon, the pilot was sometimes forced to adapt to environmental conditions and changes in survey area characteristics. Single individuals, as well as large pods, were distinguishable during surveys. Once a target was located, the piloted hovered the drone above with the camera facing directly below and took at least three sequential photographs of each hippo or group of hippos. These photographs were taken from different angles to avoid glare and to ensure the best photograph quality. The number of photographs taken of each group of hippos depended on the number,

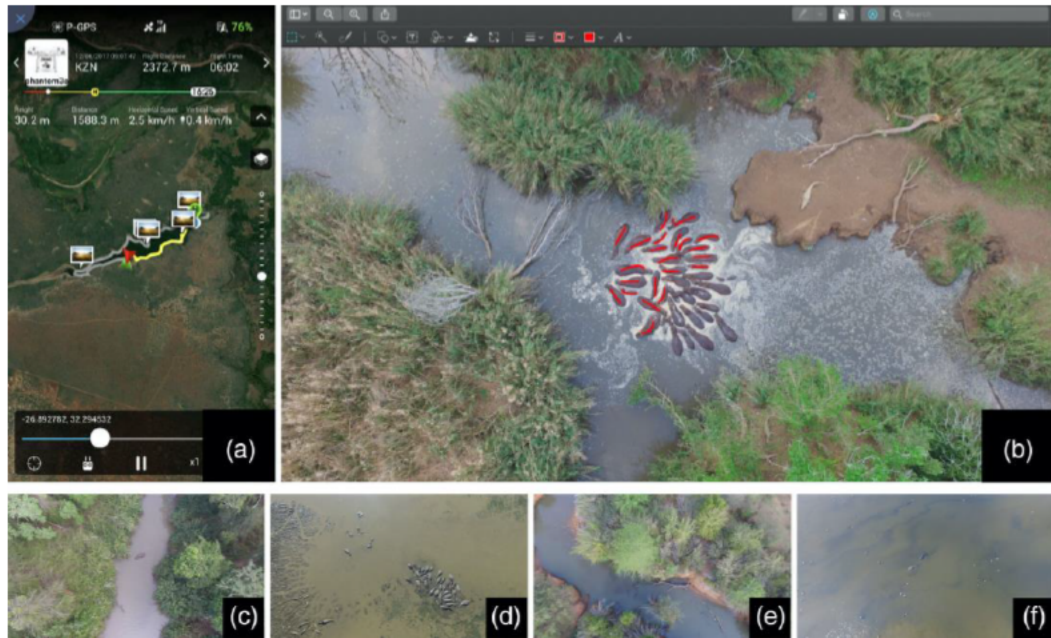

FIGURE 2 A selection of imagery representing the UAV census process (a) a sample flight path of a UAV census of Nyamiti Pan in August 2016 (b) a screenshot of a UAV image taken at Dephini showing the interface used to count hippos (c-f) a selection of photographs from the UAV census conducted in August 2016 exemplifying differences in ease of detection of hippos at four different survey locations (c) a single hippo at Bhakabhaka (d) a large congregation of hippo's in muddy water at Banzi (e) a small pod well-hidden at Shabathan (f) a set of hippos basking in shallow water on the periphery of Nyamiti Pan

the level of submergence, and level of disturbance of hippos. Increased numbers of images were taken of large congregations, pods that were either entirely or partially submerged, and groups that were disturbed by the presence of the UAV. An effort was made to capture as many hippos in each photograph as possible. If congregations of pods did not allow for all hippos to be captured in a single photograph, sets of photographs were taken of different portions of hippo congregations so that all individuals could be accounted for. It was necessary that UAV batteries be fully charged before each survey. Therefore, batteries were charged in a research vehicle between survey locations using a car-charging adapter.

2.5 | UAV image processing and hippo counts

We processed images using Apple Preview (https://support.apple.com/en-za/guide/preview/welcome/mac) (Figure 1). Each image taken during the survey was captured, assuming that it contained at least one hippo. However, some images contained only objects that resembled hippos and no actual hippos and were therefore removed from the data set. We grouped images containing hippos based on date and survey area. We then sorted images of the same pod containing different numbers of visible individuals, and we kept the photographs that contained the highest minimum number of individuals for the data set. Each hippo was counted and marked using the "sketch" tool in the "markup toolbar" to prevent multiple counts of single individuals. Each photograph was counted and marked twice, and if there were discrepancies between counts, the image was counted a third time or until a consistent total was determined. Once we had counted all hippos, we calculated a total for each location as well as a total for the survey. All recordings and calculations were done in Microsoft Excel.

2.6 | EKZNW helicopter survey

EKZNW conducted their annual survey of the hippo population at NGR on August 22, 2016, using a Bell Jetranger

III helicopter. These surveys are typically conducted during the dry season between July and August when water levels are lowest and were designed to cover the entire wading habitat in the reserve targeting previously known wading habitat. Four observers were aboard the aircraft; two in the front and two in the rear. One observer in the front of the aircraft was equipped with a Canon 30D camera with an 18–135 zoom lens used to capture photographs of the hippo. The hippo count was carried out from 10 hr:00 to 11 hr:30 min. Flight height was ~30–90 m at a speed of 30 knots. When a congregation of hippos was spotted, the helicopter hovered until a satisfactory number of quality images could be taken. The images were processed by EKZNW staff and the results recorded in Microsoft Excel.

3 | RESULTS

A total of 47 of the 48 planned UAV surveys were conducted from August 2016 to July 2017. Mean total census area was 2.26 ± 1.79 km^2 with a maximum of 6 km^2. The mean flight distance covered by the UAV in a single census survey 5.28 ± 3.15 km with a maximum of 22.08 km. Mean UAV survey time at single survey location was 13:57 ± 6:56 min with a maximum of 49:17 min. The ground sampling distance (GSD) realized while flying the UAV at 30 m altitude was 1.3 cm/px. The maximum distance attained between the UAV and remote during flight was 3.6 km flying over open water at Nyamiti Pan. The maximum number of flights required to cover the census area in a single survey was 13 flights. Battery life and connectivity from the UAV to the remote were the greatest limitations and determined UAV census area. Increases in forest density decreased connectivity between the UAV and remote. UAV surveys enabled us to identify temporal changes in density, distribution, and minimum hippo population. This manuscript aims to highlight the capabilities and methodologies resulting from implementing UAS based censuses of a hippo population, and therefore the behavioral and ecological findings that resulted from these censuses are reported in a separate manuscript (Fritsch et al. in prep.). We were able to use the UAV to survey areas where hippo localities were known, as well as at discovering new localities through changing distribution of wading locations. A total of 7,435 images of hippos were processed (Figure 2). The mean number of hippos detected in a census was 145.6 ± 54.5 with a maximum number of 246 hippos and a minimum of 26 hippos.

On August 22, 2019, the total census areas for the UAV and helicopter censuses were 0.77 and 50.54 km^2, respectively (Table 1). The maximum attained UAV survey area in the study period was 5.99 km^2 (Table 1). The costs for the UAV census included the fuel costs for vehicle travel between survey take-off locations and excluded initial costs: UAV purchase (~\$1,500) and, although it was not relevant to this study, UAV pilot hire (~\$150/hr) or UAV pilot licensing (~\$1,500–\$8,000) (South African Civil Aviation Authority, 2019). The cost of the helicopter census was determined based on an hourly rate of \$756/hr that included the fuel, pilot hours, and cost of utilization of helicopter but excluded initial purchase of a helicopter, its maintenance, and the cost of travel to and from the census take-off location. In August 2016, the UAV census accounted for ~43% of the cost/km^2 of the helicopter census (Table 1). The maximum flight area UAV census in the study period (November 2016) was 4% of the cost/km^2 of the helicopter survey in August 2016. The person-hours required are also documented in Table 1, where the August 2016 UAV census required 7.25 hr from one person, while the helicopter census required 1.5 hr from 4 people (6 total man-hour) (Table 1). The total minimum population estimate derived from the August UAV survey was 227 hippos, and the total derived from the helicopter survey was 255 hippos (Table 1). The UAV census accounted for all the same localities as the helicopter within the UAV flight area (Table 2). The UAV census detected a higher number of hippos at 2/7 survey locations (Banzi and

TABLE 1 Cost and effort comparisons between UAV and helicopter survey methodologies for counting hippos in Ndumo Game Reserve, South Africa

Parameter	UAV (Aug. 2016)	UAV (Nov. 2016)	Helicopter (Aug. 2016)
Elapsed survey time (hours)	7.25	7.5	1.5
Person hours required (hours)	7.25	7.5	6
Approximate total survey area (km^2)	0.77	6.00	50.54
Cost per survey (US dollars)	4.07	4.07	756
Census cost per km^2 surveyed (US dollars)	6.49	0.68	14.96

Note: Fuel costs were calculated using March 2019 exchange rates between South African Rands and US dollars and March 2019 fuel prices.

TABLE 2 The total number of hippos counted by location during the UAV and helicopter censuses conducted in August 2016 in Ndumo Game Reserve, South Africa

	UAV	Helicopter
Shokwe	0	0
Dephini	37	31
Shabathan	0	0
Banzi	49	47
Nyamiti	8	8
Bhakabhaka	38	67
Pholwe	95	99
Outside UAV census area	–	3
Total	**227**	**255**

Note: Helicopter disturbed hippo leading to underestimate by UAV.

Dephini), an equal amount was detected at 3/7 survey locations (Shokwe, Shabathan, and Nyamiti), and less were detected at 2/7 locations (Bhakabhaka and Pholwe) (Table 2).

4 | DISCUSSION

Large government-run conservation authorities in South Africa, namely South African National Parks (SANParks) and EKZNW, generally conduct hippo population surveys using helicopters. At a fraction of the cost and skill-level required, low-cost multi-rotor UAV surveys provided accurate population estimations that could be easily repeated over diel and annual timescales to identify temporal changes in number and distribution of hippos. Although some discrepancies in counts were realized between the helicopter and the UAV, the UAV resulted in comparable data (Table 2). The underestimate of the minimum population at least 1/7 locations (Bhakabhaka) was attributed to the disturbance caused by the helicopter, which instigated the retreat of the hippos to deeper water where they submerged, and later in the day, went undetected during the UAV survey (Table 2). Normal shifts in the distribution of hippos through wading localities may have also contributed to the discrepancies between counts, even though both surveys occurred on the same day. In August 2016, the helicopter census was more than two times more expensive per km^2 surveyed than the UAV census, and although the helicopter covered far more area, most of the area covered can be attributed to taxiing between census locations and did not account for areas with viable hippo habitat (Table 1). On the contrary, the UAV census was designed to focus on known aquatic wading sites and surrounds, and the only costs incurred were related to commuting by car between survey locations. An even larger discrepancy in cost per km^2 surveyed was realized when the maximum attained UAV flight area in the study period was compared with the helicopter census in August 2016 (Table 1).

Hippos are the last remaining large herbivore (>1,000 kg) that occur outside of protected areas in South Africa (Eksteen, Goodman, Whyte, Downs, & Taylor, 2016; Lewison & Pluhacek, 2017). South Africa has the third-largest population in the world accounting for 5–6% of global numbers, of which roughly 90% occur in managed protected areas (Eksteen et al., 2016; Lewison & Pluhacek, 2017). NGR's estimated 250–300 hippo in 2017 accounted for the second-largest population managed by EKZNW, after iSimangaliso Wetland Park (iSWP), and the third-largest remaining natural population in South Africa (the largest being in Kruger National Park). In the 2016–2017 fiscal year, across more than 120 parks (> 6,750km^2), EKZNW spent ~1% (~$50,200) of their annual budget on logistics related to game counts utilizing methods including walked transects, fixed-wing aircraft, and helicopter censuses (pers. comm.). Even so, a number of the planned annual censuses could not be completed because of monetary constraints and over-booked aircraft. To add to the problem, in 2017–2018 EKZNW experienced dramatic budget cuts, and funding towards censuses and logistics were reduced a further 40% (pers. comm.). Assuming the hippo censuses in NGR and iSWP covered 50 and 750 km^2 respectively, our cost estimates indicate that EKZNW could save between ~$6,776 and 11,424 annually by replacing helicopters with UAS based survey methodologies at these two locations. These cost-saving opportunities are not only relevant in South Africa as according to the IUCN, nine African countries have unknown or data-deficient populations, the majority of which are budget-related (Eksteen et al., 2016; Lewison & Pluhacek, 2017).

Other challenges remain ahead before UAS survey methods are adapted in conservation management and scientific research in South Africa. The South African Civil Aviation Authority (SACAA) has established some of the most stringent laws in the world for remotely piloted aerial systems (RPAS) and licensing comes at a relatively high financial cost (≤ ~ $15,000), even for research and conservation management entities (South African Civil Aviation Authority, 2019). These entities, which, at first glance, neither fall under "personal or private use" nor "commercial outcome, interest, or gain," are blanketed under the "commercial" category, and are required to jump through a number of costly hoops before implementing UAS methodologies (South African Civil Aviation Authority, 2019). In a different setting,

these stringent laws and licensing requirements lead to better overall public safety; however, many of these precautions are less relevant in remote, expansive, protected areas, away from tourists and people. Across EKZNW protected areas, there is a growing concern about the potential application of UAS's as part of illegal poaching activities, particularly rhino poaching. Although there are additional security and logistical concerns that arise when piloting UASs in protected areas with elevated security protocols, conservation management, and scientific research should be afforded a different level of scrutiny than outside entities and members of the public.

In addition, although the data are not presented here, this study is the first to collect high-resolution population-level behavioral and demographic data for hippos and demonstrates the management as well as the scientific opportunities that arise from high-frequency population censuses (Fritsch et al. in prep.). The pilot had no experience flying a UAV prior to the study, yet the surveys were easy to conduct and yielded important results. The multi-rotor UAV offered advantages in manoeuvrability and permitted active detection and approximation of hippo numbers during the course of survey flights. The manoeuvrability and ease of piloting of the UAV enabled sustained relevance of the methodology through changing ecosystem-level characteristics like increases in inundated land surface area. In addition, when hovering, multiple images could be captured of targets. The most significant hurdle we encountered with the implementation of the multi-rotor UAV was restricted flight range because of limited bandwidth.

Some ameliorations to the UAV census protocol used in this study can be made to increase its quality and efficiency. The UAV offered relatively low levels of disturbance compared with the helicopter; however, we did encounter some disturbance of hippos dependent on pod size and water level through our surveys (pers. obs.). A hippo's eyesight is generally less sensitive than it's hearing. In addition, the UAV was of diminutive size, and therefore any disturbance during surveys was more likely to be caused by noise disturbance rather than visual disturbance (pers. obs.). Hippos were more difficult to count where deeper water allowed them to submerge once disturbed by the sound of the UAV. We did not quantify the impact of a potential change in altitude on the quality of a census, but did at some points increase our flight altitude to compensate for low bandwidth, and believe an increase in survey altitude to 40–50 m (GSD: 1.73–2.16) will still result in effective and informative surveys as individual hippo and large pods were still distinguishable. We acknowledge that the implementation of UAS-based census methods will be dependent on several variables including (a) the population size where populations with <1,000 hippo will be easier to survey, (b) the behavior and particularly the level of disturbance or persecution of the population where a previously undisturbed population will be more favorable, (c) the system type where rivers, dams, and lakes will be much easier to survey than floodplain systems and systems with open grasslands will be easier to survey than forested, (d) the road access and remoteness of target survey areas where localities that are less remote will allow enough bandwidth between the UAV and pilot and decrease the time needed for surveys, (e) the level of cover and water depth at survey locations where hidden or submerged hippos will be more difficult to account for, (f) the presence and flexibility of drone regulations, (g) the available budget. Our recommendations are that low-cost multirotor UASs are effective for intensive surveying of known wading areas and surrounds. If wading areas are unknown, then we rather recommend the use of a more powerful multi-rotor UAS or the use of a multirotor UAS system in unison with fixed-wing UAS, or a helicopter, to first locate hippo wading locations as they are more adept to surveys covering large areas, for example, 10–30 km^2 (Guo et al., 2018). Some unforeseen advantages of using a multi-rotor UAV was that it permitted the identification and investigation of targets, and increased adaptability during flight and provided immediate feedback without needing to download or process imagery. In terms of management, the multi-rotor UAV also allowed the collection of finite data on groups of animals, like the identification of individuals, group-level social structures, and the identification of snared or injured animals. This is a useful tool in protected areas in Africa where management scenarios on the ground require constant and adaptable surveillance techniques.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Camille J. Fritsch and Colleen T. Downs conceptualized this research and found funding. Camille J. Fritsch collected the data, conducted the analyses and wrote the manuscript. Colleen T. Downs edited and reviewed subsequent drafts.

DATA AVAILABILITY STATEMENT

All data used in this manuscript are available on request and are stored at the University of KwaZulu-Natal.

ETHICS STATEMENT

No ethics approval was required for this research.

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CHAPTER 3

Inundation levels drive hippo fission-fusion social dynamics in a floodplain system

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Running header: Hippo population characteristics change with floodplain inundation

3.1 Abstract

Common hippopotamus (*Hippopotamus amphibius)* (hereafter hippos) are iconic and understudied ecological engineers in African aquatic and terrestrial systems. Fission-fusion dynamics (temporal changes in the size and composition of sub-groups as individuals separate (fission) or come together (fusion) while balancing the costs and benefits of group living) have been described for other large-bodied African herbivores but remain unquantified for hippos. We used monthly census data collected with an unmanned aerial vehicle from August 2016-July 2017 to identify changes in hippo distribution, density, and pod composition at the most used wading areas in Ndumo Game Reserve (NGR), South Africa. We found on average, most of the population (74.0%) occupied large nursery pods (≥ 20 individuals), with 15.3% of the population occupying very large nursery pods (≥ 60 individuals) when the inundation area was below average. Whereas, when the inundation area was above the mean, most (59.9%) pods were small (≤ 20 individuals; isolated individuals, bachelor herds, family groups, and small nursery pods) with no nursery pods > 60 individuals. Our findings suggest that hippos are forced into large pods in perennial wading areas in the dry season when food resources are scarce, likely catalyzing natural cycles of population regulation. Hippos drive ecological processes, and spatial and temporal changes in hippo abundance and density dependence on inundation area may affect the distribution and intensity of their ecological impacts. The results of our study provide additional information necessary for the conservation and management of hippos and the systems in which they exist.

Keywords: *Hippopotamus amphibius*, large mammal behavioral ecology, water resource management, drone, Ndumo Game Reserve

3.2 Introduction

Anthropogenic and climate-induced stressors threaten freshwater ecosystems globally (Fouchy et al. 2019; Grantham et al. 2019). The impacts of pollution, unmanaged water abstraction, spatiotemporal shifts in rainfall patterns, and habitat loss have been studied extensively for freshwater taxa of socio-economic importance, such as fish (Dutton et al. 2018; O'Brien et al. 2019; Burnett et al. 2020). However, few studies have focused on understanding the repercussions for aquatic and semi-aquatic mammalian species (Tockner and Stanford 2002; King et al. 2003; O'Brien et al. 2019).

Common hippopotamus (*Hippopotamus amphibius,* hereafter hippo) are listed as a species vulnerable to extinction according to the IUCN Red List of Threatened Species (Lewison and Pluhacek 2017). Historically hippos occurred in nearly all in-land aquatic habitat types in sub-Saharan Africa (Lewison and Pluhacek 2017). Currently, however, populations in Africa are mostly restricted to larger, intact ecosystems and public and private protected areas (Sidney 1965; Lewison and Pluhacek 2017). Research on hippo behavioral ecology is scarce, particularly in the context of above mentioned environmental change (Dawson et al. 2016; Stears et al. 2019). In the last ten years, novel research has provided additional understandings of hippos role as ecological engineers, particularly the consequences of hippo-vectored nutrients in aquatic systems (Subalusky et al. 2014; Schoelynck et al. 2019; Dawson et al. 2020; Dutton et al. 2020). Yet hippo behavior remains poorly studied, and further knowledge is required to give context to their ecology for the benefit of their conservation and the management of systems in which they occur (Lewison and Carter 2004; Dawson et al. 2016; Stears et al. 2019).

Fission-fusion societies can be defined as populations that experience changes in the size and composition of sub-groups over time as individuals separate (fission) or

come together (fusion) while balancing the costs and benefits of group living (Aureli et al. 2008; Renan et al. 2018). Group sizes typically change in response to spatio-temporal shifts in variables including; resource availability and competition (Wielgus et al. 2020), predation risk (Kelley et al. 2011), group demographics (Ramos-Fernández and Morales 2014), and activity synchronization (Conradt and Roper 2000). Varying levels of fission-fusion society dynamics have been described for several species, including other large-bodied African herbivores such as Cape buffalo (*Syncerus caffer*; Wielgus et al. 2020), giraffes (*Giraffa camelopardalis thornicrofti*, Lydekker 1911; Bercovitch and Berry 2013), and African elephants (*Loxodonta africana cyclotis*; Fishlock and Lee 2013). However, hippo fission-fusion social dynamics remain unquantified.

Hippos are mostly sedentary when wading and occupy relatively small home ranges (~8 km^2) driven almost exclusively by nocturnal foraging bouts to and from aquatic refuges (Field 1970; Lewison and Carter 2004; Stears et al. 2019). When wading, hippos congregate in pods (1-100 individuals) and select wading areas with decreased flows in depths of 1-2 m (Chansa et al. 2011). Five loose social unit types within hippo populations have been described in the literature and are delineated as the following: 1) solitary males which can be found throughout the year and are either roaming or claim dominion over territory that is not occupied by other hippos and are therefore solitary for at least part of the year; 2) solitary female or female with an infant calf: expecting females that normally make up part of a nursery pod and seasonally seek solitude before and just after giving birth for a total period estimated at 14 days; 3) bachelor pods: a relatively small pod with no permanent members, of a maximum of five nomadic younger and older males that share a wading area but have no strong ties between individuals; 4) a family group: a small pod of closely related individuals

usually comprising of up to three females with strong ties and their offspring, numbering a total of no more than 6-10 individuals and may have temporarily separated from a nursery pod; 5) a nursery pod: the most recognizable pod form numbering 2-200 individuals and is a conglomeration of a number of family groups and subordinate males all under the dominion of one dominant bull where the largest pods are realized when dry season wading resources force surrounding sub-units into congregations in suitable perennial wading habitat (Klingel 1979; Smuts and Whyte 1981; Karstad and Hudson 1986; Dibloni et al. 2010). Seasonal shifts in population distribution in response to spatiotemporal changes in aquatic wading habitat availability (merging in reduced flows and dispersals in high flow) have been identified across several systems in Africa (Klingel 1979; Viljoen 1980; Smuts and Whyte 1981; Karstad and Hudson 1986; O'Connor and Campbell 1986; Jacobsen and Kleynhans 1993; Viljoen and Biggs 1998; Zisadza et al. 2010; Kanga et al. 2012; Kanga et al. 2013; Mackie et al. 2013; Scholte et al. 2017; Prinsloo et al. 2020). However, previous studies have not defined the drivers nor identified the degree of shifts in hippo population pod structure (Viljoen 1995; Stommel et al. 2016).

There are significant obstacles when attempting to identify social interactions between hippos because individuals are only discernible by obscure markings and scarring on their backs and haunches that are rarely visible when partially or completely submerged in murky water during diel wading activities (Linchant et al. 2018; Fritsch and Downs 2020). New data collection methods, such as unmanned aerial vehicles (UAVs), present novel opportunities to understand the drivers of hippo fission-fusion society dynamics without requiring individual identification. Therefore, the goal of our study was to identify changes in hippo population distribution, density, and social structure in response to seasonal changes in the inundated land surface area using a

river-floodplain system as a case study. Our aims were to test a) how changes in inundated surface area affected population abundance, distribution, and density; b) whether changes in inundation surface area prompted a shift in population pod structure; and c) provide insights as to how the observed population-level changes impact the management of freshwater systems and protected areas with hippos. We predicted that wet-season increases in inundated land surface area would be associated with a decrease in population density and abundance in the census area, likely driven by individual dispersal. In turn, this would increase the number of pods and decrease the number of individuals in each pod.

3.3 Methods

3.3.1 Study area

This study took place in Ndumo Game Reserve (NGR), South Africa, (26°53'12.2"S 32°14'53.2"E). Ndumo Game Reserve is a relatively small (10 117 ha) Ezemvelo KwaZulu-Natal Wildlife (EKZNW) managed protected area situated along South Africa's northern border with Mozambique. NGR was originally established in 1924 as a hippo sanctuary after colonial hunting in the late 1800's severely depleted South Africa's hippo population, and in 1997 was distinguished as a wetland of international importance (Ramsar site number 887; (Blackmore 2017). NGR forms an important component of the Maputaland Centre of Endemism, protected under the international protocol between South Africa, Mozambique, and Eswatini named the Lubombo Transfrontier Conservation and Resource Area (Blackmore 2017). NGR has fenced boundaries on 2/4 sides, making it an open system, where wild animals, livestock, and people can move across its boundaries. During the study period, NGR hosted an estimated ~250 hippos, accounting for roughly 5-10% of the national population

(Lewison and Oliver 2008; Eksteen et al. 2016). Average annual rainfall is typically 638 mm p.a. with the heaviest rains generally falling in the middle of summer (December-February) and lighter rains in early summer (Kyle 1996). Temperatures in the summer regularly exceed 40°C, with average minimum temperatures at 9°C (Kyle 1996).

3.3.2 Flooding regime

Ndumo Game Reserve is situated at the junction of two perennial river systems: the Phongolo and uSuthu Rivers, which seasonally flood and inundate up to 40% of the reserve (Fig. 3.1). These systems also consist of several oxbow lakes, bowed wetlands and 12 associated seasonal and perennial pans, of which Nyamithi Pan (157 ha) is the largest when full. Our data collection was conducted during a severe drought period from 2014 - 2017 (deJager 2016). In 2014, annual October releases from the Phongolopoort Dam (or Jozini Dam)—which are asynchronous to natural flooding patterns—were halted because of drought-induced depleted reservoir levels (Birkhead et al. 2018). Although the floodplains experienced seasonal periods of inundation during these drought years (2014-2017), the inundation of the floodplain was driven primarily by the uSuthu River. The areas along the Phongolo River that the backwater from the uSuthu River did not reach were inundated less than would have occurred historically. During the period of our study, the floodplains experienced two periods of inundation each year: the first in November, mainly driven by increases in the flow in both the uSuthu and Phongolo Rivers, and the second longer period from January-February, where the flooding of the uSuthu caused most of the inundation.

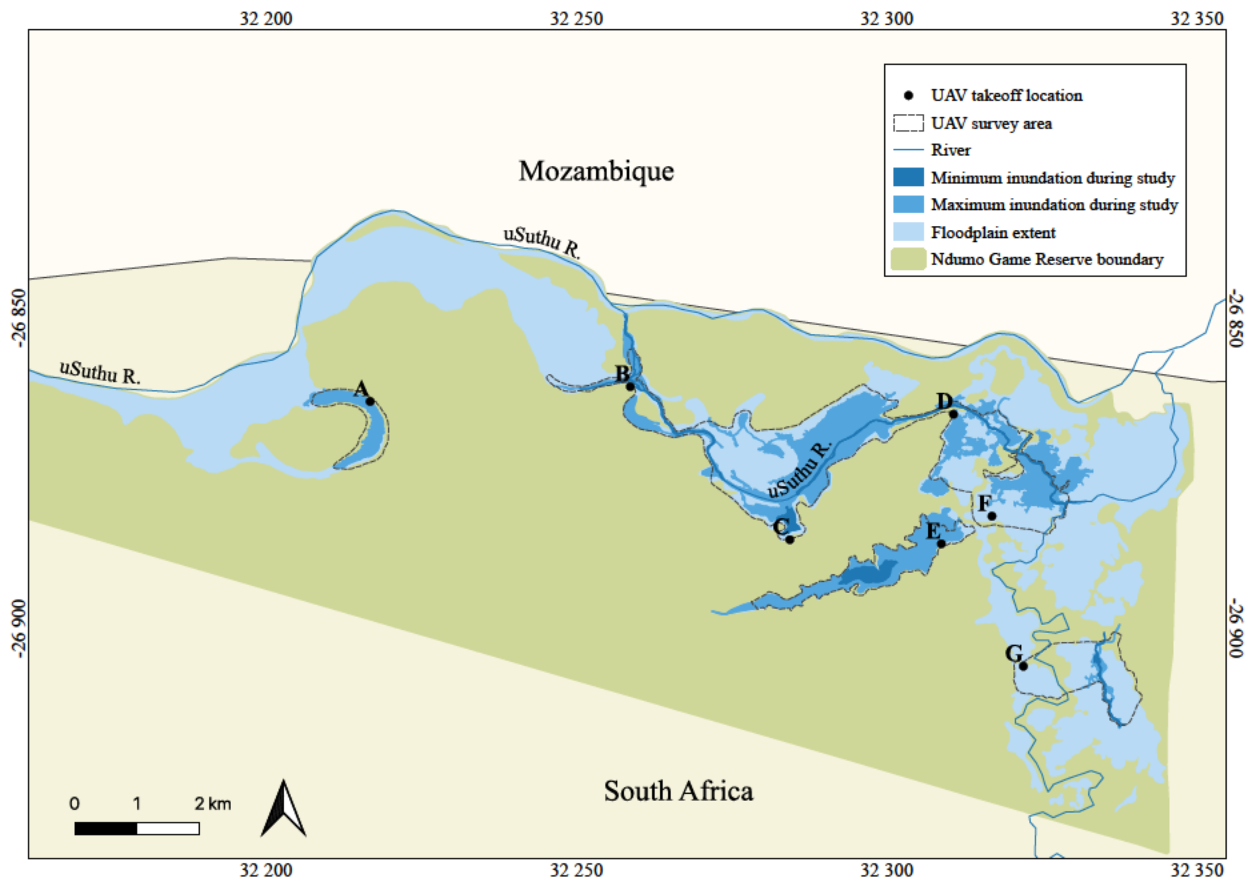

Figure 3.1 A map of Ndumo Game Reserve, South Africa, and the survey locations as well as maximum and minimum inundation areas during the study period. (Location A: Shokwe; B: Dephini; C: Banzi; D: Shabathan; E: Nyamithi Pan; F: Bhakabhaka).

3.3.3 Survey methods

We conducted a year-long UAV survey of the hippo population at NGR, beginning in August 2016 and ending in July 2017. Detailed descriptions of the UAV survey methods used are presented in Fritsch and Downs (2020). We conducted four UAV censuses every month for 12 months at seven different locations along the uSuthu and Phongolo Rivers and associated pans. Dephini, Banzi, Shabathan and Bhakabhaka (locations B-D and F) are along the uSuthu River and make up most of the uSuthu floodplain (Fig. 1). Shokwe (location A) is a seasonal pan fed by the uSuthu River, and Nyamithi Pan (location E) is a perennial brackish pan historically fed primarily by the

Phongolo River but now also fed by the uSuthu River. Polwe (location G) is along the main Phongolo River channel (Fig. 3.1). We made an effort to conduct all surveys at 30 m altitude above the take-off location and at speeds of 8-10 m/s. The UAV model used was a DJI Phantom 3 Drone with 2.7 K Camera and 3-Axis Gimbal with the following features: a capacity for shooting 12-megapixel JPEG files, a 1/2.3” sensor, fast f/2.8 prime lens, a pre-set focus optimized for aerial images, and a battery life of up to 22 min. Using the UAV, we obtained geo-referenced photographs of each hippo pod encountered during each survey. We made an effort to photograph pods in their entirety. On a few occasions (<1%), because of complications from weather, we conducted hippo surveys on foot. In these instances, we recorded the geographic locations and number of individuals using a hand-held GPS, and if possible, we also recorded pod demographics.

3.3.4 UAV image processing

We counted hippos in images using Apple Preview (see Fritsch and Downs, 2020 for a detailed description of the image processing methods used). We assigned GPS locations to pods based on UAV image metadata. We assigned hippos that were separated by >100 m to different pods. We determined the number of hippos and, where possible, the age class (juvenile or adult) of each hippo in each pod.

3.3.5 Water surface area

We downloaded 12 monthly satellite images of NGR from Planet imagery using the Planet Explorer tool (Planet Labs, San Francisco, United States of America), which allows free access to four band multispectral satellite imagery to researchers. Because clear imagery was not always available for the dates of our hippo censuses, we chose

the clearest images that encompassed all census locations closest to the survey (<14 days). Using the digitize tool in ArcGIS 10.4 (ESRI, Redlands, CA, USA) and QGIS 2.8 (QGIS Geographic Information System. Open-Source Geospatial Foundation Project, www.qgis.osgeo.org), we then extracted the inundated area from each satellite image to create a monthly inundation area in km^2 for each hippo census location in NGR (Fig. 3.1).

3.3.6 Statistical analyses

We analyzed the changes in hippo abundance and density, pod abundance and density, pod size, and inter-pod distance in relationship to inundation area using a mixed-effect approach. We tested for correlation between each response variable and inundation area using Poisson-distributed mixed-effect models. The random-effect part of each model initially included an autocorrelation term to account for repeated measures, a random-effect term for locality, and a random effect term for survey month. While the temporal autocorrelation term was always retained, the informative value of locality and survey month was evaluated by comparing the second-order Akaike Information Criterion (AICc) of each model, and the simplest model with lowest AICc was retained. To test for the correlation between the mean distance between pods and inundation area we first calculated the pairwise distances between all hippo pods, then we calculated the mean inter-pod distance at each location on each sample date. Finally, we tested for correlation between mean distance between pods (hereafter: inter-pod distance) and inundation area using a Poisson-distributed mixed-effect model. In the model, each value of mean inter-pod distance was weighed by the number of pods it was calculated for. Otherwise, model specification and model selection was performed as described previously. All statistical analyses were performed using R version 3.6.3 (R Core Team

2020). We calculated the pairwise distances between pods using the function distGeo from the R package Geosphere version 1.5-10. We performed linear models with function lm from the R package stats. We performed mixed-effect models with function glmmTMB from the R package glmmTMB version 1.0.2.1 (Brooks et al. 2017). We calculated AICc with the R package MUMIn version 1.43.17 (Bartoń 2009). Descriptive statistics were calculated using Microsoft Excel.

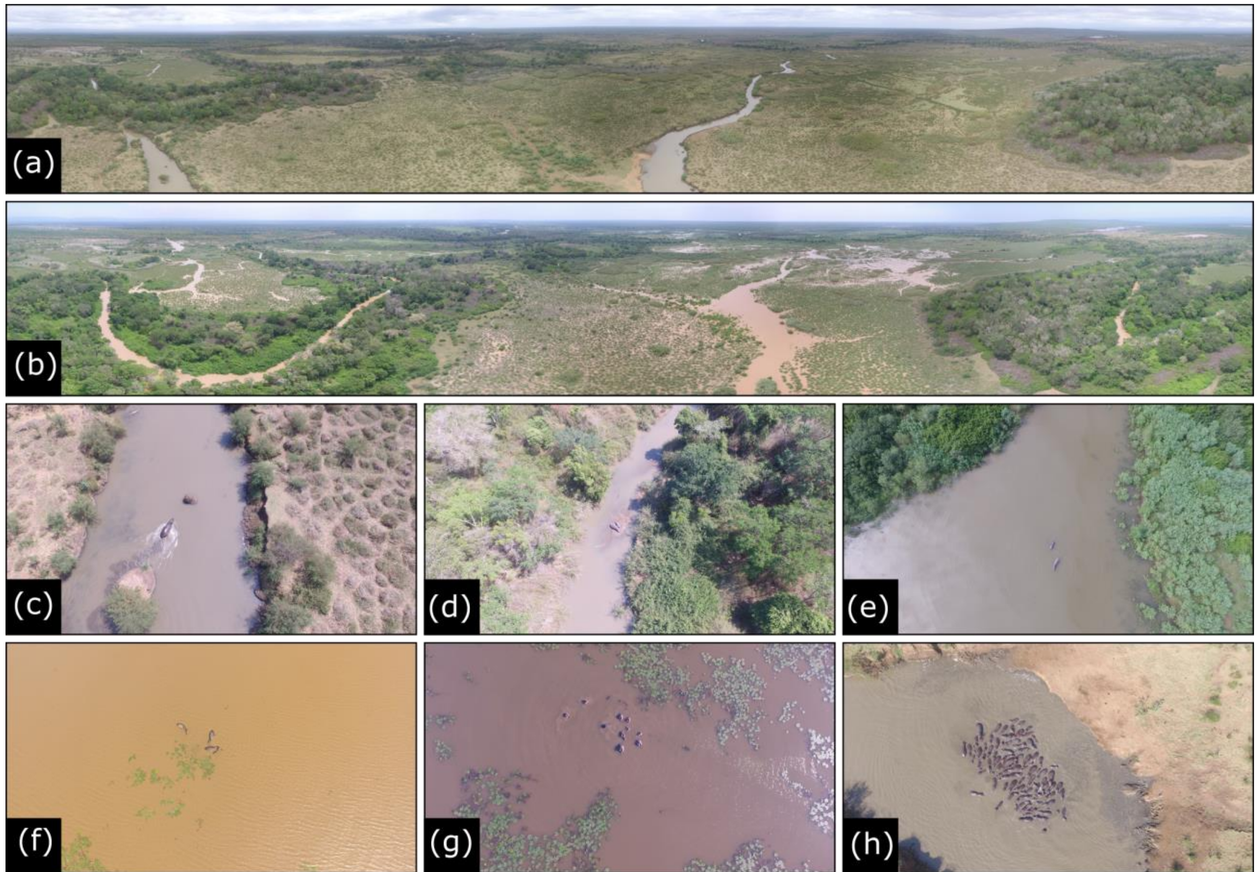

Figure 3.2 Changes in the inundation of Ndumo Game Reserve and hippo presence in the present study where a) is high inundation at Bhakabhaka in November 2016; b) low inundation at Bhakabhaka in October 2016; c) a solitary bull at Bhakabhaka in September 2016; d) an adult female and her calf basking at Bhakabhaka in September 2016; e) a bachelor pod at Polwe in February 2020; f) a family group at Banzi in December 2016; g) a small nursery pod at Shokwe in April 2017; and h) a large nursery pod at Bhakabhaka in September 2016.

3.4 Results

The inundation area of NGR changed seasonally between the wet and dry seasons (Fig. 3.2). The mean (± SD) inundation area across all survey locations in NGR for the study period was 2.26 ± 1.79 km^2, where the minimum was 0.48 km^2 in October 2016, and

the maximum was 6.0 km^2 in February 2017. We noticed a relationship between inundation area and water depth while conducting drone censuses where water depth increased with increased inundation area.

The total number of hippos detected in the study area ranged from a minimum of 23 individuals (November 2016) to a maximum of 246 individuals (August 2016). Large discrepancies in minimum population estimates are believed to be at least partly due to a reduction in the accuracy of population estimates when water depth and inundated area were increased. This is because hippos were able to submerge themselves completely and were only seen intermittently. In addition, censuses were not comprehensive of all possible wading areas, so some individuals may have moved into areas that were not included. However, search effort increased significantly as the number of hippos decreased ($p = 0.009$), while changes in the number of pods did not affect the amount of search effort ($p = 0.59$). This suggests that we did not underestimate the number of hippos and pods even when their rarity made them hard to detect. The total abundance of hippos did not decrease significantly with increasing inundation area, and neither did the number of adult and juvenile hippos when analyzed separately (Table 3.1).

The density of hippos and pods in NGR were all at their maximum when inundation areas were at a minimum (Fig. 3.3; Fig. 3.4; Table 3.1). Hippo density declined significantly with increasing inundation area, reaching a plateau close to their minimum density for inundation areas of ~0.5 km^2. The same trend held when adult and juvenile hippos were examined separately. Pod density also displayed a significant, negative correlation with inundation area, reaching a plateau close to its minimum density for inundation areas of ~0.8 km^2 (Fig. 3.4b). Hippo density based on length of

river surveyed (as it is traditionally reported) peaked in August 2016 at 16.5 ± 1.03 hippo/km over a total of 14 km of river surveyed.

The total number of hippo pods did not decrease significantly with increasing inundation area (Fig. 3.4b; Table 3.1). Hippo pod size decreased significantly with increasing inundation area (Fig. 3.4c, Table 3.1). Mean (± SD) hippo pod size for the study period was 12.2 ±16.2 individuals with a minimum pod size of 1 and a maximum of 103. During periods of below-average inundation, mean pod size was 15.6 ± 19.37 hippos, whereas in periods of above-average inundation, mean pod size was 8.1 ± 9.7 hippos. When the inundation area was above average, a larger proportion of the population occupied pods with ≤20 individuals than when the inundation area was below average. Conversely, a larger proportion of the population occupied pods with >20 individuals when the inundation area was below average than when inundation was above average (Fig. 3.4a).

The mean distance between hippo pods increased significantly with increasing inundation area (Fig. 3.4d, Table 3.1). Detection effort was not related to the number of hippo pods, and it increased significantly as the number of hippos detected decreased (Supplementary information Fig. S3.1; Supplementary information Table S3.1).

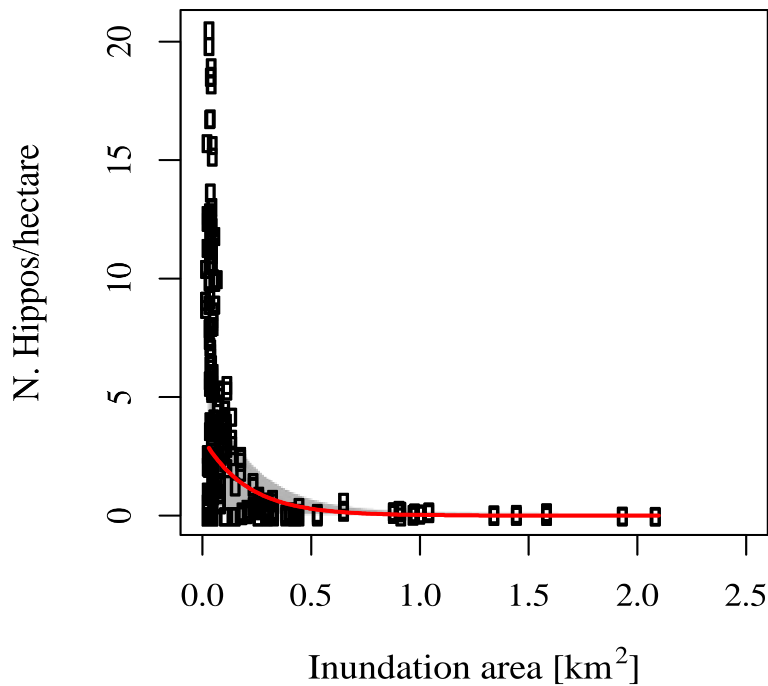

Figure 3.3 Relationship between hippo density and inundation area in Ndumo Game Reserve in the present study.

Table 3.1 Correlation between hippo and pod abundance, hippo and pod density, and inundation area in the present study. (Significant p values in bold).

Variable	Exponent	SE	z value	p value
Hippo abundance [N]	-0.55	0.33	-1.673	0.0943
Adult abundance [N]	-0.57	0.32	-1.761	0.0782
Juvenile abundance [N]	-0.86	0.52	-1.669	0.0951
Pod abundance [N]	0.08	0.16	0.482	0.6298
Hippo density [N/ha]	-4.87	0.78	-6.267	**< 0.0001**
Adult density [N/ha]	-4.98	0.8	-6.203	**< 0.0001**
Juvenile density [N/ha]	-7.26	2.93	-2.481	**0.0131**
Pod density [N/km2]	-1.85	0.13	-6.147	**< 0.0001**
Pod size [N]	-0.71	0.27	-2.617	**0.0089**
Inter-pod distance [m]	0.59	0.22	2.728	**0.0064**

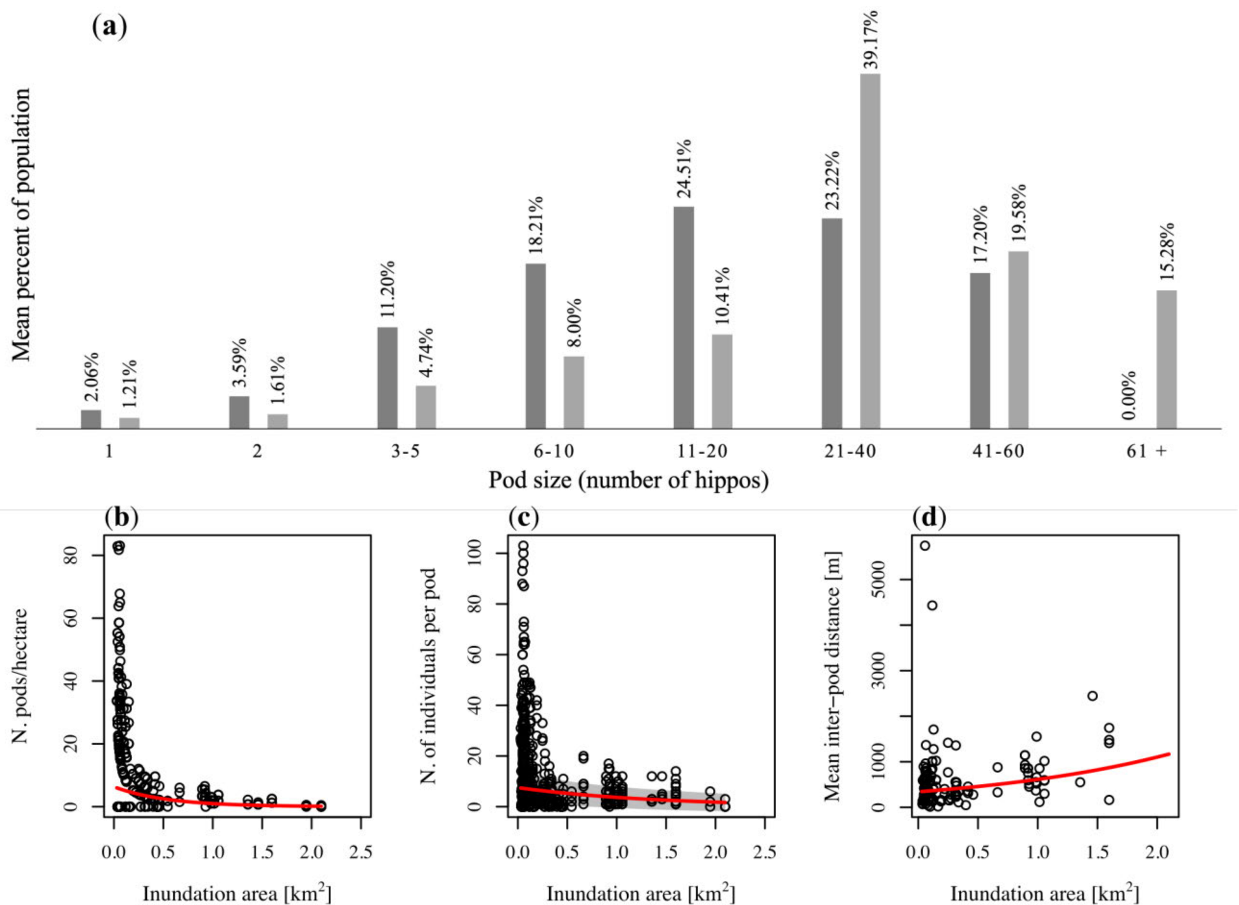

Figure 3.4 a) Distribution of the mean proportion of the hippo population in different pod sizes during periods with inundation area below (light grey) and above-average (dark grey); b) hippo pod density versus inundation area; c) hippo pod size versus inundation area; and d) inter-pod distance versus inundation area in the present study.

3.5 Discussion

Our findings suggest that hippo populations undergo drastic temporal and spatial changes in population social structure (fission-fusion dynamics; Aureli et al. 2008) driven by aquatic habitat availability. We found that, on average, when the inundation area was below the mean, most of the population (74.0%) occupied large nursery pods (≥ 20 individuals), with 15.3% of the population occupying relatively large nursery

pods (≥ 60 individuals). Comparatively, with above-average inundation area, the majority (59.9%) occupied smaller pods (≤ 20 individuals: isolated individuals, bachelor herds, family groups, and small nursery pods) with none in very large nursery pods (> 60 individuals). We found that as the inundation area increased, overall individual and pod density decreased, and hippo abundance decreased as hippos likely dispersed outside the study area. These results provide the first detailed description of hippo population fission-fusion social dynamics and are of prime interest for conservation efforts and the management of systems with hippos.

Hippos are a K-selected species that adopt a low reproductive rate and high offspring survival rate. Previous studies on the physiology of hippos have suggested that in systems with a single rainy season, mating coincides with dry season congregations, and births are correlated with wet-season rainfall (Laws and Clough 1966; Smuts and Whyte 1981). Increased aquatic wading habitat permits females to seek seclusion for the birthing process, and reduced pod sizes decrease the risk of calves being trampled or drowned (Klingel 1979). In NGR, we observed mating in May 2017 and then saw births correlate with the peak of NGR's rainy season (pers. obs.). Although we would have liked to identify seasonal increases in juveniles and secluded females, calves were difficult to identify from the UAV imagery (pers. obs.). Nevertheless, our results support that elements of hippo reproductive behavior benefit from seasonal changes in population social structure and the quality and timing of flow and flooding events.

Adult hippos are subjected to relatively little predation risk, and hippo populations are instead regulated by stochastic die-off events driven by disease and drought (Smuts and Whyte 1981; Chansa et al. 2011; Smit et al. 2020). Hippos are spatially constrained to forage near to wading habitat; therefore, bigger pods create

increased competition for food, particularly as increased densities of sympatric grazers use these areas during periods of resource scarcity (Smit et al. 2020). In addition, large pods in unfavourable wading conditions are characterized by direct intraspecific stress from increased exposure, aggressive behavior, and disease transmission risk (Attwell 1963; Olivier and Laurie 1974; Smuts and Whyte 1981). Conversely, in periods of favourable resource availability, hippo populations can increase relatively fast and recover numbers following die-off events (Smit et al. 2020). Previous research has shown that nutrient levels before pubescence influences the calving rate and the age at which hippos become sexually mature, where populations under low levels of resource stress reach sexual maturity earlier and reproduce more quickly (Laws and Clough 1966; Pienaar et al. 1966; Sayer and Rakha 1974; Smuts and Whyte 1981). The introduction of artificial watering holes and impoundments in Kruger National Park in the 1950's and 1960's created a surplus of wading habitat and subsequently catalyzed substantial unanticipated increases in hippo population numbers (Bengis et al. 2016; Smit et al. 2020). Similarly, for hippo populations with access to increased perennial wading habitat, the absence of seasonal dry periods poses significant issues for managing population numbers (Dembitzer 2017; Subalusky et al. 2019; Castelblanco-Martínez et al. 2021). Therefore, contrary to other species like elephant and giraffe that come together in periods of superior resource availability in the wet season (Bercovitch and Berry 2013), our findings suggest that hippos are forced into congregations in perennial wading areas in the dry season when food resources are scarce. These changes in population social structure drive natural cycles of population regulation (Smit et al. 2020).

Hippos drive ecological processes in their environment. Spatial and temporal changes in hippo abundance and density dependence on changes in inundation area

influence the distribution and intensity of their ecological effect both on land and in water. Allochthonous nutrient contributions by hippos via their dung have significant positive and negative influences depending on the type and condition of aquatic systems (Leyhausen 1976; Kilham 1982; McCarthy et al. 1998; Subalusky et al. 2014; McCauley et al. 2015; Dawson et al. 2016; Dutton et al. 2018; Stears et al. 2018; Dawson et al. 2020). Our findings show that nutrient inputs introduced into NGR's river-floodplain system by hippo dung will differ seasonally in location and concentration. In the dry season, hippo dung inputs from large pods are concentrated in the perennial river channels and are likely flushed downstream. Conversely, in periods of high inundation, hippo pods are dispersed across the landscape, and the nutrients they introduce into the system are taken up and recycled more easily. In terrestrial systems, dense congregations of hippos can degrade and erode grazing areas and cause increased inter- and intra-species grazing competition and eventual overgrazing of pastures (Field 1970; Lock 1972; Zoeller and Bond 2013; McCauley et al. 2018; Smit and Archibald 2019). Typically, scarcity of grazing resources reaches its peak in the dry season; however, in NGR, the grazing pastures of scutch grass (*Cynodon dactylon* L.) are inundated during periods of flooding and only become available once floodwaters recede. Hippos are likely forced to forage on elevated stands of low nutrient grasses outside the floodplain and introduce added grazing pressure to species in those areas. Future studies addressing seasonal changes in hippo effects on ecological processes in river-floodplain systems will provide valuable information for the management of NGR and similar river-floodplain systems, especially those experiencing rapid human and climatic induced changes.

Conservation of hippos requires an in-depth understanding of the environmental variables that drive population ecology and behavior. Although hippos occur in various

inland aquatic systems, their physiological, behavioral, and ecological requirements within these discrete system types are not the same and are not well understood. The results of our study, together with future studies that identify hippo population environmental requirements, will provide managers with the information necessary to develop informed environmental flow requirements for hippos and other taxa in river-floodplain systems. Hippos are sensitive to rapid environmental change because of their dependence on water, reproductive reliance on seasonal flooding, and high grazing requirements. The presence of hippos in a system indicates some level of landscape connectivity, and the loss of hippos in a system may be one of the first indications of landscape discontinuity. Hippos physiologically require wading areas. The ebb and flow of inundation coincide with aspects of hippo behavior and biology, and the inundation area determines the distribution of wading and grazing resources and whether hippos can access these resources. South African aquatic systems are under anthropogenic pressures, with the majority (>57%) of river ecosystem types occurring in threatened or unstable ecological states (Driver et al. 2012; O'Brien et al. 2019). Changes in water quality, flow timing, duration, and quantity, and landscape connectivity will impact hippo populations as well as impact the ecological role they play in aquatic and terrestrial systems. This is particularly relevant in the Phongolo River system, where changes in the ecological role hippos play may have implications on socioecologically important fish species and water resources.

Our study shows that hippo social dynamics are highly sensitive to changes in water availability and that flooding in the wet season drives population dispersal. We hope that these findings stimulate future behavioral work to explain grouping patterns, range use, mating behavior, dispersal tendencies, and social relationships in response to changes in features of the ecological environment (Aureli et al. 2008). In this regard,

one limitation of our study approach is that UAV did not allow us to identify and track individuals and pods univocally. Future studies that use UAVs to track individuals and pods will address this gap and improve our understanding of hippo movement and migration patterns. Tracking individuals and pods will provide insights on the nature of hippo pod structure, e.g., whether they are haphazard or organized social structure and whether they coincide with family groups. Furthermore, while our study examines seasonal fission-fusion dynamics, future work examining diel fission-fusion dynamics will allow quantifying behavioral and social changes at the pod level during the day versus night and in the dry versus wet season (Field 1970; Stears et al. 2019).

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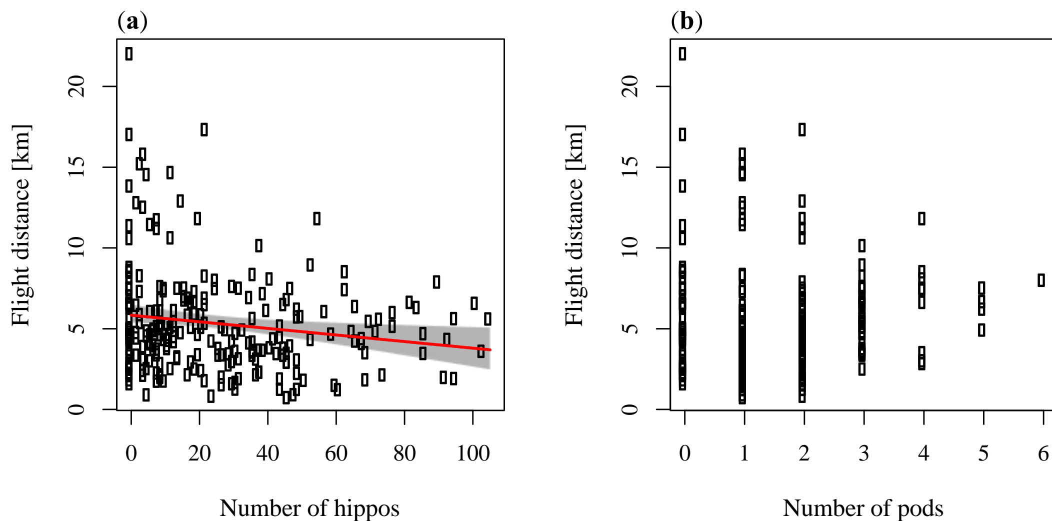
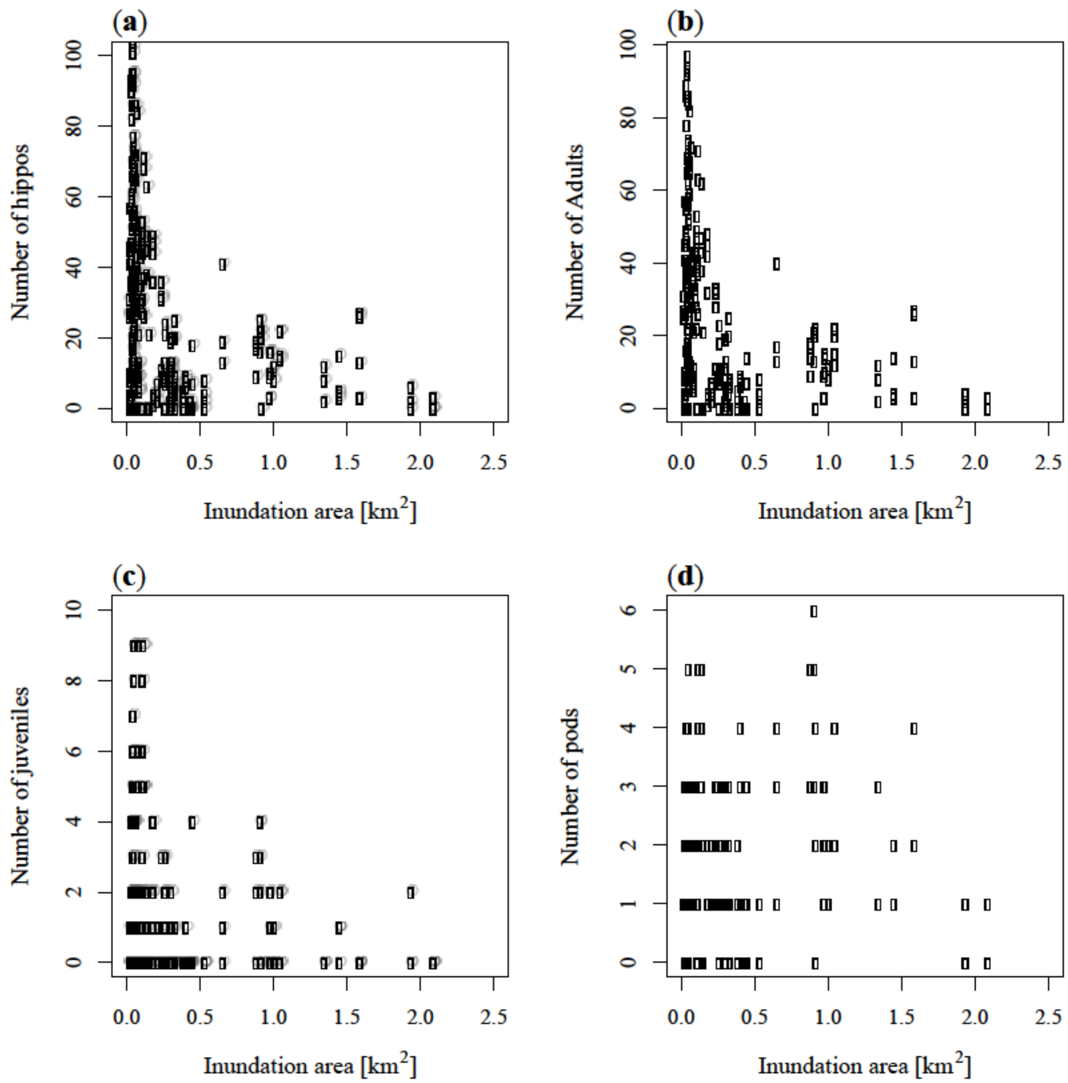
3.8 Supplementary information

The abundance of hippos and hippo pods might have affected the search effort. To verify that we did not reduce the search effort when hippos and pods were few (thus underestimating their number), we used linear regression to assess the correlation between drone flight distance (a proxy for search effort) and the number of hippos and the number of pods observed, respectively. As a measure of search effort, we used drone flight distance.

Search effort increased significantly as the number of hippos decreased, while changes in the number of pods did not affect the amount of search effort (Supplementary Fig. S1; Table S1). This suggests that we did not underestimate the number of hippos and pods even when their rarity made them hard to detect.



Supplementary Figure S3.1. Drone flight distance was negatively correlated with the number of hippos (a) but showed no significant correlation with the number of hippo pods observed (b) in the present study. Statistical details are presented in Table S1.



Supplementary Figure S3.2. Number of hippos (a), adults (b), juveniles (c), and hippo pods (d) versus inundation area in the present study.

Supplementary Table S3.1. Summary statistics for the correlation between drone flight distance and number of hippos and hippo pods in the present study.

Predictor	**Slope**	**SE**	**t value**	**p value**
Number of hippos	-0.02	0.01	-2.62	0.0094
Number of pods	0.09	0.17	0.53	0.5957

Supplementary Table S3.2. Monthly minimum and maximum hippo counts at each location throughout the present study. The overall mean counts at each location throughout the study ("Mean count per location") and monthly sum of the mean counts across localities ("Sum of means") are also shown.

Year	2016					2017							Mean count
	August	September	October	November	December	January	February	March	April	May	June	July	per location
Banzi	27-49	9-49	44-50	0-6	36-49	3-27	0-3	3-15	0-8	0	0-21	0	17
Bhakabhaka	38-86	66-105	36-93	8-12	39-82	26-71	0-22	30-44	38-63	66-69	63-77	13-95	54
Dephini	8-46	0-20	26-31	0-9	18-30	5-13	0-5	7-24	2-7	0-14	5-17	9-31	14
Nyamithi	6-9	4-5	1-4	NA	11-20	1-2	2-12	14-22	3-10	10-16	16-25	9-19	10
Pholwe	69-95	13-68	26-61	11-36	27-47	39-56	46-53	12-84	36-53	32-46	41-57	32-38	45
Shabathan	0-17	0-2	0	0-18	0-9	5-34	13-41	9-33	5-21	6-12	0-11	0-10	9
Shokwe	NA	NA	NA	0-2	0-13	1	0	0-9	4-25	0-19	8-9	0	5
Sum of means	231	175	193	55	187	144	98	146	130	143	172	148	

CHAPTER 4

Human and climatic drivers of hippopotamus population trends in Ndumo Game Reserve, South Africa, and its associated wading areas from 1951-2017

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Running header: Hippo population trends in Ndumo Game Reserve, South Africa

4.1 Abstract

Understanding trends in species population dynamics is an important factor when trying to better manage species in protected areas. The common hippopotamus, *Hippopotamus amphibius* (hereafter hippo), is an iconic African species, yet is mainly restricted to protected areas where they are important ecosystem engineers. Ndumo Game Reserve (NGR), South Africa, was established as a sanctuary for hippos in 1924. Ndumo Game Reserve and its hippo population are under increased anthropogenic threat, outlining the importance of published research on changes in the hippo population dynamics. We conducted monthly surveys for a year using an unmanned aerial vehicle to obtain hippo numbers and locations in the various water bodies in NGR. Significant differences in hippo numbers and distribution through different locations in NGR were observed, with 85-95% of the population using the uSuthu and Phongolo Rivers and associated floodplains. When compared with historical data, a significant decrease in the hippo population in the past 40 years was evident. Although recent increases in the population have been seen since 2014, this increase is likely because of hippos seeking refuge in NGR from drought and hunting outside the reserve. Areas in NGR experiencing the greatest human land invasions are also the areas that represent the best hippo habitat in NGR. We recommend that serious consideration be taken by the conservation management authority to work with sections of the South African government like the Department of Land Affairs to reinstate the complete boundary of NGR to protect hippo and other wildlife.

Keywords: hippo, UAV, drone, census, large mammal conservation, population dynamics

4.2 Introduction

Developing countries, like South Africa, are experiencing widespread environmental deterioration caused by accelerated climate change and anthropogenic impacts like land-use alterations, habitat fragmentation, overhunting, invasive species, and pollution (Steffen, 2007; Tilman et al., 2017). Large mammals are innately susceptible to rapid landscape-level modifications because of their high individual energy requirements (large home range sizes), low reproductive rate, and increased vulnerability to illegal hunting and poaching (Cardillo & Bromham, 2001; Cardillo et al., 2005; Barnes et al., 2016; Tilman et al., 2017). In the past, conservation organisations in South Africa, like Ezemvelo KwaZulu-Natal Wildlife (EKZNW; previously known as Natal Parks Board), have been at the forefront of successful conservation initiatives (Sas-Rolfes, 2012). However, recent political unravelling in South Africa and generally across Africa has reduced the receptivity of government policies to conservation needs, impacting the accruement of funding and limiting the capabilities of these organisations to fulfil conservation initiatives of national and international importance (Daitz, 2003; Bruner et al., 2004; Meer & Schnurr, 2013; Lindsey et al., 2018).

The common hippopotamus, *Hippopotamus amphibius* (hereafter hippo), plays an important and understudied role as ecosystem engineers in aquatic and terrestrial systems in South Africa (Field 1970; Subalusky et al. 2015). Hippos improve aquatic habitat connectivity and diversity by wallowing and physically engineering paths and channels in riparian environments (Field, 1970). They deposit valuable allochthonous nutrients into aquatic systems later used by fish and other aquatic micro and macroinvertebrates (Dawson et al. 2016). They create grazing lawns that promote increased grass species diversity, in turn facilitating foraging for other grazing herbivores (Field, 1970; McCarthy et al., 1998; Grey & Harper, 2002; Zoeller & Bond, 2013;

Kanga et al., 2013; Subalusky et al., 2014; McCauley et al., 2015). Historically, hippos occupied many of the inland aquatic systems in sub-Saharan Africa; however, unmanaged hunting and direct and indirect human-induced habitat loss have caused dramatic global declines in the last 200 years (Eksteen et al., 2016; Lewison & Pluhacek, 2017). Today, climate change impacts (e.g., global warming, flood/drought rainfall patterns) and various indirect symptoms of a growing impoverished human population in Africa, including unmanaged subsistence hunting practices, unsustainable water abstraction practices, and outdated freshwater policy, have continued to drive global declines of >20% over the past 10-20 years and have left the majority of the remaining hippo populations restricted to protected areas (McCracken, 2008; Lewison & Pluhacek, 2017). Consequently, hippos are listed on CITES as a Schedule II species and have a Red Data classification of Vulnerable (VU A4cd) (Lewison and Pluháček 2017). The loss of this species may have detrimental cascading effects through already vulnerable grassland and wetland environments. Therefore, labelling hippos as vulnerable may be an understatement of the immediate concern surrounding the loss of members of the species across systems continental Africa.

Hippos require access to suitable dial wading conditions to thermoregulate and to avoid trans-epidermal water loss (Wright, 1987; Miller et al., 2014). Therefore, populations are vulnerable to drought events or unnatural reductions in the availability of acceptable wading conditions (Smuts & Whyte, 1981; Viljoen, 1995). Temporal changes (i.e., seasonal, annual, or longer) in wading habitat availability play a fundamental role in determining hippo population distribution and social structure and ultimately impact population dynamics (Olivier & Laurie, 1974; Smuts & Whyte, 1981; Viljoen, 1995; Lewison & Carter, 2004). These events force hippos

to form dense congregations (>100 hippos) in perennial wading areas where significant die-offs can occur as a result of intraspecific competition and feeding and wading resource stress (Smuts & Whyte, 1981). Male to female sex ratios within a population are typically 1:1, and sexes reach sexual maturity at 6-8 years and 9-13 years respectively, with females calving every 2-3 years (Pienaar et al., 1966; Sayer & Rakha, 1974; Smuts & Whyte, 1981). There is no strict mating season; however, most calves are born in the wet 6 months (October-March) after an 8 month gestation period, and consummation is facilitated by seasonal increases in density in the dry season (Field, 1970; Smuts & Whyte, 1981). The age of sexual maturity and calving rates realised within a population are subject to the environmental conditions experienced by the population, where both can be accelerated to 1-2 years and 2-3 years respectively in growing populations, or the age of reproduction can be delayed to as late as 17 years in populations when females undergo pre-pubescent nutrient deficiencies as a product of population resource stress (Laws & Clough, 1966; Pienaar et al., 1966; Sayer & Rakha, 1974; Smuts & Whyte, 1981).

South Africa currently has one of the largest hippopotamus populations in Africa (Eksteen et al., 2016; Lewison & Pluhacek, 2017). Ndumo Game Reserve (NGR), South Africa, was established in 1924 and is one of South Africa's oldest game reserves. Ndumo Game Reserve was originally established as a hippo sanctuary in 1924 after hunting in the late 1800's severely depleted South Africa's hippo population (McCracken 2008; Meer and Schnurr 2013). The hippo population in NGR is ~300 hippo making it one of the largest and densest populations in South Africa (Eksteen et al., 2016). Recent land claim bouts over NGR's floodplain could put the population in jeopardy. Population counts have historically been accepted as being the preferred method for estimating population size and give an indication as to the overall population health of

species (Dice, 1938; Lancia et al., 2005). Ground counts and other traditional methods have been used in the past to estimate population size and densities; however, the introduction of more modern methods, like the application of Unmanned Aerial Vehicles (UAV) for ecological surveys of certain species has gained popularity more recently (van Gemert et al., 2015; Hodgson et al., 2016; Ezat et al., 2018; Fritsch & Downs, 2020). The most recent detailed hippo studies in NGR were conducted in the 1970s (Hancock, 1978; Scotcher, 1978). Therefore, the aim of this study was to a) identify the seasonal importance of wading areas in NGR based on monthly UAV census data from 2016-2017 b) compare current EKZNW annual census data to historical EKZNW annual census data collected using various methodologies from 1951-2017 to identify population trends and temporal changes in the importance of various wading areas d) provide recommendations for future management of NGR's hippo population. We predicted that currently and historically, hippos preferentially utilise the river-floodplain systems in NGR. We also predicted that although historical data were collected using various methodologies, they would reveal an overall population decline in the last 70 years and that trends over time can be attributed to increased anthropogenic disturbance, particularly in the important wading areas.

4.3 Methods

4.3.1 Study site

The NGR (26 S, 32 N) is a relatively small (10,117 ha) protected area managed by EKZNW and situated along South Africa's north-eastern border with Mozambique within the Mozambique Coastal Plain (Fig. 4.1). The NGR's northern boundary is denoted by what historically was the main uSuthu River channel, which ran from west to east between South Africa and Mozambique.

The uSuthu River has since changed course and now flows south and then east, through the centre of NGR. The Phongolo River, the other predominant river within the system, runs from south to north through the eastern half of the park and joins the new uSuthu River channel in the northeastern corner of NGR. During periods of high rainfall, these rivers swell, then flood creating the uSuthu and Phongolo floodplains (~4,000 ha). In addition, these rivers also fill 12 pans, of which Nyamiti is the largest perennial pan, and Shokwe is the largest seasonal pan.

The NGR falls within the Maputoland Center of Endemism, is an internationally recognised Important Birding Area (IBA), and a Ramsar site (proclaimed Ramsar site No. 887 in 1997) (Hancock 1978, Calverley and Downs 2014, 2017). NGR hosts South Africa's densest Nile crocodile *Crocodylus niloticus* population (>800 individuals), the densest avifaunal diversity of any protected area in South Africa (>420 species), and South Africa's third-largest hippo population after Kruger National Park and the iSimangaliso Wetland Park (Hancock 1978, Calverley and Downs 2014, 2017). In the 1980's, NGR was also a stronghold in the fight for the conservation of black *Diceros bicornis* and white rhinoceros *Ceratotherium simum*. However, these populations were virtually poached out before the last individuals were relocated to other protected areas (Conway & Goodman, 1989; EKZNW pers. comm.).

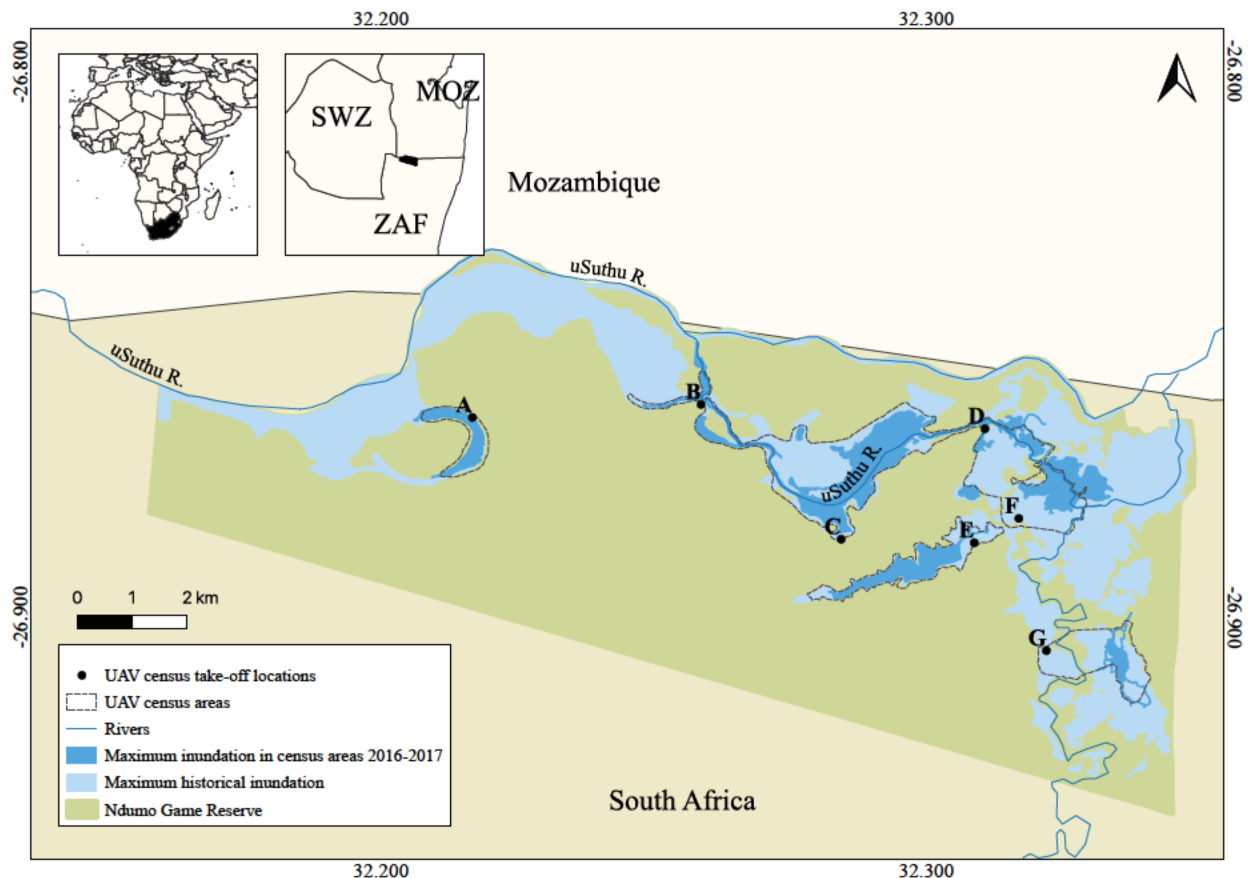

Figure 4.1 The UAV census take-off and survey area locations (A-G) along the uSuthu and Phongolo Rivers and floodplains in Ndumo Game Reserve, South Africa, in the present study where A) is Shokwe Pan, B-D) is Diphini, Banzi Pan, Sabatana within the uSuthu River floodplain, and E) is Nyamiti Pan, F-G) Bhakabhaka and Polwe within the Phongolo River floodplain, in the present study.

The NGR has within it a wide range of soils; sandy and silty alluvial soils in the uSuthu and Phongolo floodplains, Quartenary Red Sands of the Zwartfontein Series on Ndumo Hill, and red sandy clay soils on the Mahemane and Bunguzane Flats (Hancock, 1978). These create a variety of different habitats (Riverine Forest, Floodplains, Fever Tree Forest, "Pan-edge"

community, Sand Forest, Deciduous broad-leafed Woodland, *Vachellia nigrescens* Woodland, and Mahemane Thicket) that support a dense amalgamation of fauna and flora (Hancock, 1978). The NGR has a hot, humid tropical climate with seasonal summer rainfall and a dry winter season (Hancock, 1978). Mean annual rainfall is 630-640 mm, with the majority of rainfall occurring during the wet summer season from November to March (Wadeson, 2006). However, rainfall can be erratic, and annual precipitation has been recorded lower than 500 mm. Mean annual temperatures fall at approximately 22.9 ºC, and maximum temperatures exceed 40 ºC (Wadeson, 2006).

4.3.2 UAV census methods and image processing

A detailed description of UAV census methods can be found in Fritsch and Downs (2020). We conducted a total of 47 UAV censuses of the hippo population in NGR from August 2016 to July 2017. We used a DJI Phantom 3 Standard Drone (2.7 K Camera; 3-Axis Gimbal; capacity for shooting 12 megapixel JPEG files; a 1/2.3” sensor, f/2.8 prime lens; a pre-set focus for aerial images; and battery life of up to 22 min.). Censuses were conducted on four sequential days each month with the exception of May 2017 when only three censuses were completed. Each census was comprised of seven different flight locations (Banzi, Bhakabhaka, Dephini, Nyamiti, Pholwe, Shabathan, Shokwe) covering the main wading locations (as reported in previous annual aerial census data from EKZNW) within the uSuthu and Phongolo River floodplains, and Nyamiti and Shokwe Pans. Temporal expansions in the inundated habitat that hippos could have or were observed using through the study period were also adaptively included in each census (Fig. 4.1a). Although these censuses covered the vast majority of the possible wading habitat, they were not

comprehensive of NGR as they excluded remote areas that could not be accessed because of limitations in the possible flight distance of the UAV. Photographs were taken of all hippos encountered with the UAV in flight, and all photographed hippos were then counted using Apple Preview Version 11.0 (Fritsch & Downs, 2020).

4.3.3 EKZNW census methods

Historical peak dry season (July-August) hippo population census data (1951-2017) gathered by EKZNW used a variety of methods. Foot counts were conducted from 1951-1957 until they were replaced by a mix of fixed-wing and helicopter-based aerial counts until 1979 when helicopter census methods superseded all methodologies and continue to be used today. The transition to aerial methods permitted censuses that covered the entirety of NGR and typically combined the collection of monitoring data for hippos and other species like Nile crocodiles as well as noted sightings and numbers of Cape buffalo *Syncerus caffer*, and black and white rhinoceros. All flights flew the lengths of the uSuthu and Phongolo Rivers in NGR, Nyamiti and Shokwe Pans and were comprehensive of all inundated area in NGR. Additional details on helicopter-based census methods can be found in Fritsch and Downs (2020).

4.3.4 Statistical analyses

We used descriptive statistics and the function ‘kruskal.test’ provided with the library ‘stats’ (R Core Team, 2020) in R-studio version 4.0.2 to determine any significant differences in mean hippo counts between each survey month during the yearlong survey period. The data were not normally distributed; therefore, a Kruskal-Wallis test was used to determine the effect of survey month on

the mean total number of hippo detected. Similarly, a Kruskal-Wallis test was used to determine if the change in total adult and total juvenile hippo differed significantly between surveys. A Kruskal-Wallis test was also used to identify if there was a significant difference in the number of hippo between each location. We also used a one-way analysis of variance (ANOVA) run in STATISTICA 7.0 (Statsoft, Tulsa, Oklahoma) to determine if there was a significant difference in the mean UAV flight distance and flight time between survey months.

4.4 Results

Four sequential censuses were conducted each month during the study period (August 2016 - July 2017), excluding May 2017, where only three surveys were conducted, for a total of 47 UAV surveys.

The end of 2016 saw the end of an extreme drought period that began in 2012. This drought affected the majority of South Africa where 2015 was the lowest rainfall level recorded in South Africa since 1904 (de Jager, 2016). Water levels inside NGR increased from an extreme low in late 2016 to adequate and normal levels through 2017. The monthly total number of hippo per census location in NGR differed significantly between months (Kruskal-Wallis chi-squared = 156.35, df = 6, $p < .001$). Bhakabhaka and Pholwe were the locations that had the highest monthly total mean hippo numbers throughout the survey period. In contrast, Shokwe generally had the least monthly total mean numbers of hippo, mainly because of the fact the pan only held water from November 2016- June 2017 (Fig. 4.2). The importance of different wading areas in NGR is represented by the proportion of the population that used them over seasonal and annual timescales. The mean monthly ($\pm$ SD) population proportion of hippos amongst the wading areas

in NGR from 2016-2017 was 66.7 ± 9.1%) for Phongolo River and floodplain, 24.7 ± 9.6% for the uSuthu River and floodplain, 6.6 ± 5% at Nyamiti Pan, and 2 ± 2.7% at Shokwe Pan (Fig. 4.2). Nyamiti Pan (which was at extremely low levels in the dry season and with irregularly high salinity levels) and the seasonal pan Shokwe increased in use in the months with increased inundation (December 2016 - June 2017).

There was a significant difference in the mean monthly total number of hippos in NGR from August 2016 to July 2017 (Kruskal-Wallis chi-squared = 35.782, df = 11, $p < 0.001$). Because the rivers are not fenced, and the eastern boundary fence no longer exists, hippos were also able to distribute throughout the inundated habitat available inside and outside of NGR. These distributions may have been driven by the inundation of the majority of the grazing areas in the floodplain. In addition, seasonal increases in inundation permitted hippos to distribute in small pods throughout the floodplain, making detection with the UAV more difficult even with significant increases in census effort (flight time and flight distance) compared with the drier months when pods were >100 individuals in size. There was a significant difference per location per month in drone flight distance (GLM ANOVA, $F(57, 184) = 3.328$, $p < 0.05$), as well as drone flight time (GLM ANOVA, $F(57, 184) = 2.165$, $p < 0.001$). A Posthoc Tukey showed that Banzi and Bhakabhaka, which encountered the most substantial expansions in seasonal inundation, were flown significantly further in distance and time in February and March 2017 compared with the other survey months.

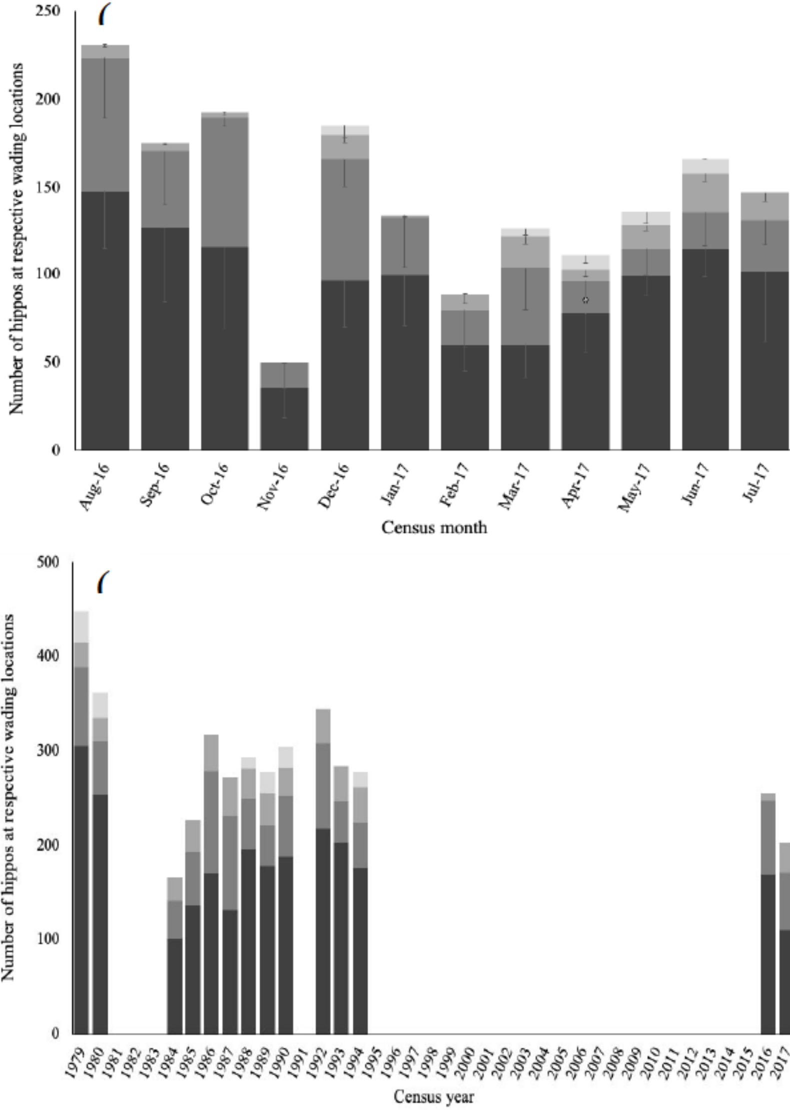

Figure 4.2 Trends in populations census numbers within the different wading areas in NGR with a) the monthly changes in population number at different wading areas from August 2016 – July 2017, and b) the historical distribution of hippos across the same wading areas in dry season censuses (usually conducted in July or August) from 1979 – 2017. (From dark to light: Phongolo River area, uSuthu River area, Nyamiti Pan, Shokwe Pan).

The mean monthly total number of adults did not differ significantly with month (Kruskal-Wallis chi-squared = 19.319, df = 11, $p < 0.05$, mean max 215 $\pm$ 14.1 in August, mean min 47 $\pm$ 14.1 in November) but the mean monthly number of juveniles was significant (Kruskal-Wallis chi-squared = 24.626, df = 11, p = 0.01, mean max 16 $\pm$ 2.0 in August, mean min 1 $\pm$ 2.0 in February). The seasonal changes in the prevalence of juveniles were apparent; however, because juveniles were much more difficult to detect in increased inundation with the UAV, the reduced number in the wet season may not reflect the actual number of juveniles present in the population. It would have rather been because of detection error. Juveniles are much smaller and tend to stay underwater for long periods when disturbed, making detection difficult. In addition, turbid water in the rainy season also hampered their detection.

Historical dry-season census data from 1979-2017 were collected using a variety of methods, and therefore only observed trends can be reported but cannot be identified statistically. Historical trends showed the past importance of the same wading sites where the mean ($\pm$ SD) proportion of the population was 62.2 ± 6.5% for Phongolo River and floodplain, 23.5 ± 7.2% for the uSuthu River and floodplain, 11.3 ± 3.8% at Nyamiti Pan, and 2.9 ± 3.4% at Shokwe Pan. These consistencies exist even with increases in people and their domestic livestock living and utilising the Phongolo floodplain since 1994 (although more recent accelerated impacts from 2017-2020 (pers. comm. EKZNW) have not been quantified in the present study).

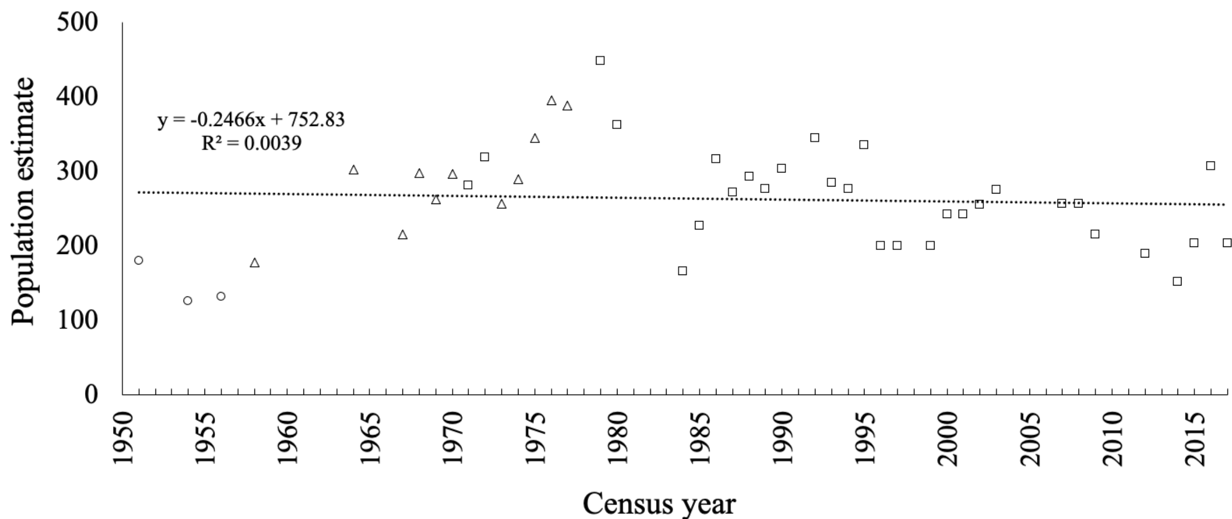

Figure 4.3 The results of annual hippo censuses conducted by EKZNW from 1951-2017 using three different methods (circles = ground count, triangles = fixed-wing aircraft, squares = helicopter).

The hippo population numbers in NGR have fluctuated dramatically in the last 70+ years, although the mean (± SD) population size across this time period is 263 ± 71 individuals, which was closely related to the recommended ~250 hippos as the carrying capacity developed by Hancock (1978). The observed trends showed a steady increase in hippo in NGR from the 1950's-1970's and a steady decline of hippo along the Phongolo floodplain outside and to the south of NGR during the same time period (Scotcher, 1978). This has previously been attributed to immigration of hippo from outside NGR as the decline outside the reserve was driven by increased anthropogenic presence and impacts (Scotcher, 1978). The damming of the Phongolo River in 1968 altered the timing, frequency, and duration of floods where the length of time the floodplain was inundated doubled and the floodplain was often inundated in the dry season (Hancock 1978).

The availability of wading habitat catalysed growth in the hippo population to a maximum of 448 individuals in 1979 (Fig. 4.3). To reduce the pressure on the grazing areas in NGR, a culling regime was established following Hancock's (1978) established carrying capacity for hippos. Relatively soon after, a succession of droughts in the 1980's and again in the 1990's instigated a series of population reductions and subsequent recoveries with a reported 200 individuals remaining in 1999 (Richard et al., 2001; Fauchereau, 2003). Meanwhile, the population on the Phongolo River outside NGR reportedly fell to 0 through the 1980s, only recovering to a reported maximum number of 29 individuals in 1989. The forced removal of the eastern boundary in 2008 and again in 2011 facilitated the increased use of the Phongolo floodplain by hippos and probably also helped reduce numbers in NGR. In 2014 hippo population numbers had reportedly decreased to 152, the lowest population count recorded for NGR since the initiation of aerial counts in 1958. This decrease was attributed to poaching, habitat loss, and resource competition caused the communities given access to NGR. However, the inflated population numbers from the 1970's and 1980's were unnaturally high, and alterations of the flooding regime from the Jozini Dam in the 1990's as well as the altered course of the uSuthu River through Banzi Pan, draining what was once the largest pan in NGR, reducing perennial wading habitat availability. Therefore, an overall reduction in the maximum attainable population was expected. An increase in hippo in NGR was then seen from 2014-2016 (Fig. 4.3). This sharp increase may be because of a drought from 2012-2016 that forced hippo from outside NGR to seek refuge in NGR during low water levels and high competition with people outside the northern and eastern boundaries of the reserve, especially in the floodplains in Mozambique (EKZNW pers. comm.). Similar increases in detection were seen in response to the droughts in the 1980's and 1990's. By 2017, hippo numbers in the floodplains

south of NGR were again reduced to virtually zero as anthropogenic development and farming dominated the area (pers. obs.).

4.5 Discussion

The migration of hippos into NGR highlights its importance as a hippo 'safe-haven' within a rapidly changing landscape. Trends in the monthly drone census data have shown the importance of the wading areas within and along Phongolo and uSuthu Rivers and associated floodplains. Historically, these same areas have also been the most used wading areas, although comparisons in minimum population do not account for different census methodologies (Fig. 4.2). The persistent preference of these areas can be attributed to the suitable wading environment they provide in meandering rivers and tributaries in the dry season and inundated floodplain in the wet, as well as their proximity to perennial grazing offered by the alluvial floodplain soils. In addition to unnatural flooding regimes instigated by the Jozini Dam, observed population declines across NGR over the past ~40 years have been attributed to the direct and indirect impacts of encroaching communities and livestock on the Phongolo floodplain along the eastern boundary of NGR (pers. comm. EKZNW). The negative impact of the presence of communities on the distribution of hippos have been outlined across Africa as well as in previous research in NGR and more recently in the nearby iSWP (Scotcher, 1978; Kanga et al., 2012; Scholte et al., 2016; Lewison & Pluhacek, 2017; Prinsloo et al., 2020; Utete, 2020). In NGR, the most substantial impacts come from the ~2,500 head of cattle grazing in the floodplain causing grazing competition and bush encroachment. However, when compared to historical data, the increased presence of people and livestock in the Phongolo floodplain in NGR in the last 25 years has made relatively little impact

on the reported proportion of the hippo population utilising these areas, although these data were collected using different data collection methods. Similar results were found in Gonarezhou National Park (GNP), Zimbabwe, where the hippo population appeared to be growing alongside increased human disturbance as opposed to showing symptoms of population stress (Zisadza et al., 2010). The sustained use of the disturbed areas in NGR by hippos indicated that although these areas were presently being changed unfavourably, they were still preferentially used over other parts of NGR. This highlighted the importance of these areas for the continued persistence of the hippo population.

Observed hippo population trends in NGR are believed to be a product of a combination of drivers. However, the availability of wading resources, either artificially or as a result of natural fluctuations in rainfall, played an apparent role in both the reduction and recovery of hippo population numbers in NGR. Inundation areas over seasonal and annual timescales also appear to drive hippo use of different wading areas in NGR (Fig 4.2a-b).

Population die-offs are common across species and are particularly common amongst large mammal species in savannah ecosystems in southern Africa, which endure highly variable rainfall patterns and droughts (Young, 1994; Richard et al., 2001; Smit et al., 2020). Because of their semi-aquatic nature, hippo populations are more vulnerable to drought-induced reductions in wading and grazing resource shortages than they are to predation or disease (Smuts & Whyte, 1981; O’Connor & Campbell, 1986; Viljoen, 1995). Studies from Kruger National Park (KNP), South Africa and GNP have detailed the impacts of the droughts in the 1980’s and 1990’s on their respective populations (Smuts & Whyte, 1981; Viljoen, 1995; Zisadza et al., 2010). Similarly, in the drought from 2012-2016, KNP lost close to 50% of its 7,000 hippo population (SANParks

Scientific Services, pers. comm.). Nonetheless, with a high calving rate, early age sexual maturity, and low rates of offspring fatality, hippo populations have a demonstrated ability to recuperate numbers following a die-off event (Kanga et al., 2011). The KNP saw massive increases in grazing resource pressure across the park because of the proliferation of the hippo population following the construction of numerous artificial watering holes that were intended to facilitate increases in prey densities but instead permitted hippos to distribute to otherwise remote areas of the park (SANParks unpublished data). A recent study of the invasive hippo population in Columbia has shown an introduced hippo population of 4 individuals has grown to more than 65 individuals in 26 years (exponential population growth rate of 11% per year), and individuals have dispersed >150 km from the site of introduction (Shurin et al., 2020). The sensitivity of hippo populations to climate or human-induced changes in wading and grazing resources are apparent; however, the abilities of hippo populations to recover from die-off events has relieved tremendous pressure on conservation initiatives, though the viability of isolated populations with increased chances of inbreeding requires additional investigation.

At the core of NGR's distinction as a wetland of international importance, was the recognition of the unique aquatic habitat created by the joining of the uSuthu and Phongolo floodplains and the subsequent increased biological diversity present within its boundaries. The social importance of these systems, which has perhaps been more readily overlooked in the past, are evident as a growing impoverished population (currently estimated as >400,000 people along the Phongolo River system alone). They are socio-economically dependent on these systems for water resources for consumption and agriculture, thatch and reeds used in the construction of homes and fish traps, the highly productive floodplain alluvial soils for agriculture, associated

grasslands for livestock fodder, and dietary protein from fish (Heeg et al., 1980; Merron et al., 1993; Mosai, 2004; Meer & Schnurr, 2013; Blackmore, 2017; Acosta et al., 2020). Aquatic biodiversity, particularly fish (~46 species) and invertebrates, along the Phongolo River is highest within NGR; however, alterations in the timing, frequency, and quantity of flows have already shown to decrease biodiversity along stretches of the system (Acosta et al., 2020). Although the aquatic impacts of the hippo population in NGR remain under-quantified, it is no coincidence that the densest population along the Phongolo River coincides with heightened aquatic biodiversity. The vast majority of NGR's hippo population (85-95%) occurs along the Phongolo and uSuthu Rivers, where they have a tremendous influence on the characteristics of the aquatic system, particularly when these river systems are subject to growing human manipulation (Stears et al., 2018; McCauley et al., 2018; Dutton et al., 2018; Schoelynck et al., 2019; Shurin et al., 2020). Future investigations of socio-ecological risk along these systems must account for potential impacts of hippos, particularly concentrations of allochthonous hippo inputs and their associated repercussions on water quality and aquatic biodiversity.

Bulk grazing by hippos accounts for substantial grazing resource consumption, and in addition, close-crop grazing by hippos facilitates grazing for other species like nyala *Nyala angasii* and impala *Aepyceros melampus*, in turn accelerating the use of grazing pastures (Hancock, 1978). Both impala and nyala occur at considerably high densities (no formal census data available), and in comparison, few large predatory species occur in NGR (in order of density: spotted hyena *Crocuta crocuta*; leopard *Panthera pardus*; side-striped jackal *Canis adustus*; black-backed jackal *Canis mesomelas*) to help mitigate their effects (Hancock, 1978; Ramesh et al., 2016). Therefore, management programs require constant monitoring of grazing resources and responses in the form

of culling when threats to grazing resources are observed (Hancock, 1978). Pasture depletions in NGR are accelerated again by a large number of domestic livestock (cattle and goats) sharing the grazing resources, particularly along the Phongolo River. These impacts have expanded every year since the forced removal of NGR's eastern boundary in 2008 and the impacts beyond the period investigated as part of this study show further signs of deterioration of natural habitat and over-use of resources (EKZNW pers. comm.).

In the face of accelerated climate change, resource partitioning, especially of freshwater resources, will become more and more difficult, particularly with the estimated 1.6 billion person increase in sub-Saharan Africa by 2060 (Tilman et al., 2017). The human population along the Phongolo River has grown from 30,000 to over 400,000 in the last 40 years (Acosta et al., 2020). Because of an unjust and exploitative political history and current continued political instability, impoverished communities surrounding NGR are socio-economically reliant on the resources provided by the natural systems surrounding them (Heeg & Breen, 1982; Merron et al., 1993; Meer & Schnurr, 2013; Dube et al., 2015). Therefore, these communities are more susceptible to climate-driven resource depletions exerting additional pressure on surrounding ecological systems (Merron et al., 1993; Dube et al., 2015). In the droughts in 1982-83 when cattle died and crops failed, people along the Phongolo River derived 60-70% of meat meals from fish with an estimated total of over 400 tonnes harvested from the river during the period (Merron et al., 1993). Conservation areas in Africa have static boundaries and are often isolated within otherwise disturbed landscapes, and therefore are highly susceptible to symptoms of rapid climatic change and increased human disturbance. Modern adaptive management approaches for conservation area management provide managers with tools that are accessible, even to conservation authorities in Africa with budgetary

limitations, that account for socio-ecological stochasticity (Sinclair & Walker, 2003; Rogers & Luton, 2016). Recent accelerated impacts have not been quantified; however, the hippo population in 2020 is down to ~80 individuals, the lowest it has ever been in over 70 years of management (EKZNW pers. comm.). Without understanding and accounting for all the drivers threatening the hippo population at NGR, the long-term persistence of the population will remain uncertain. Therefore, future management of NGR must use risk models that involve and consider the perspectives held by all stakeholders to inform immediate and impactful management interventions.

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CHAPTER 5

Home range size of the common hippopotamus in perennial river systems in the Kruger National Park, South Africa

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Running header: Hippo home range sizes in South Africa

5.1 Abstract

The common hippopotamus *Hippopotamus amphibius* (hereafter hippos), because of their unique biology and equal dependence on both aquatic and terrestrial environments, are drivers of important ecological processes in African savannah ecosystems. Recent studies have highlighted the ecological impacts of hippos in these systems; however, few have behavioural data to better quantify hippo inputs. We fitted GPS-GSM UHF transmitter collars on adult, male hippos (n = 4) in Kruger National Park, South Africa. These allowed novel movement data collection in 2019 and 2020. We interpreted space-use data using three home range estimation methods (MCP, KDE, *a*-LoCoH) to identify different patterns in overall and seasonal space use of hippos and understand hippo-driven ecological processes. Mean home range size (~6 km^2) of hippos was smaller than previously documented. Our results highlighted how home range size and shape vary between a perennial river system and one with an impoundment important for the future management of hippos in Kruger National Park and the management of the Olifants River socioecological system.

Keywords: hippo, space use, Olifants River, large mammal behaviour and ecology

5.2 Introduction

Ecological systems have evolved as diverse communities of players, with different ecological requirements, all biologically inter-linked; where the persistence of a community is tied to the persistence of all individuals and groups of individuals, at some level, in a system (McNaughton et al., 1988; Polis et al., 1997; Leibold et al., 2004; Fortin et al., 2005; Morin, 2009; Lamperty et al., 2020). Recent human-induced environmental changes have spatially constrained and fragmented natural systems, and because of the loss of natural habitats globally, are also

manifested with the intention to conserve disproportionately inflated levels of biodiversity (Fahrig and Merriam, 1994; Fahrig, 1997; Brooks et al., 2002; Ramesh et al., 2016; Taubert et al., 2018).

In Africa, intact ecological systems exist almost exclusively within the boundaries of protected areas (Thiollay, 2006; Newmark, 2008; Pettorelli et al., 2012). Although the aim of these altered systems is to retain highly diverse functional ecological systems, generally, there is a lack of understanding of the components and interactions in self-regulating systems within these modern constraints (Ramesh et al., 2016; Alexander et al., 2019; Fahrig, 2019). Therefore, it becomes essential for research to unravel the role of the individuals and populations to better understand 3their contributions to the resilience and future management of these manipulated systems (Alexander et al., 2019; Ehlers Smith et al., 2019; Lacher et al., 2019).

Common hippopotamus *Hippopotamus amphibius* (hereafter hippo) populations are predominantly restricted to protected areas in South Africa, with very few subpopulations occurring outside (Eksteen et al., 2016; Lewison and Pluhacek, 2017). Due to recent habitat loss across continental Africa, gaps in national population monitoring data, and a general lack of behavioural and ecological research in comparison to other large African mammal species, hippos are listed as vulnerable on the IUCN Red List of endangered species (Lewison and Carter, 2004; Lewison and Pluhacek, 2017). Hippos are semi-aquatic and are dependent on the diel use of both aquatic and terrestrial systems for wading and feeding resources, respectively (Smuts and Whyte, 1981; Taylor, 2013; Prinsloo et al., 2020). Although other large herbivore species, namely the African elephant *Loxodonta africana* and Cape buffalo *Syncerus caffer caffer* are arguably equally dependent on and contribute to these system types through their own interactions, hippos are unique in the amount of time they spend and the physical and allochthonous nutrient contributions

they make in African aquatic systems and are therefore regarded as ecological engineers (Subalusky et al., 2014; McCauley, 2015; Dawson et al., 2016; Schoelynck et al., 2019). Several recent studies (Dutton et al., 2018; McCauley et al., 2018; Stears and McCauley, 2018; Schoelynck et al., 2019; Dawson et al., 2020a, 2020b; Masese et al., 2020; Shurin et al., 2020; Voysey et al., 2020) have made strides in quantifying the ecological inputs of hippos in aquatic and terrestrial systems. However, because of a lack of data, few studies have included aspects of hippo behaviour to accurately quantify their ecological role in investigations of ecological resilience.

Detailed home range studies are still relatively new, and recent amelioration of methods for collecting movement data using global positioning systems (GPS) technology have provided opportunities to gain a more in-depth understanding of animal space use. An animal's home range is defined as the 'known' area, encompassing the animal's territory as well as the areas outside that are used as part of normal activities, including gathering food, mating, and caring for young (Burt, 1943; Powell and Mitchell, 2012; Spencer, 2012). The characteristics and size of animal home ranges are typically species-specific but often differ between populations of the same species, between individuals of the same species in the same population, and within the same individual over space and time (Burt, 1943; Schoener, 1981). These differences are related to a number of aspects, including intrinsic physiological constraints like body size or feeding strategy, population structure and social interactions like population density, competition, and territoriality, or environmental factors like spatial and temporal shifts in the availability, presence, and quality of resources (Schoener, 1981; Ofstad et al., 2016). Therefore, animal movements in response to the aforementioned forms one of the most fundamental animal behaviours and are used to understand how animals interact with their habitat, with the other taxa around them, and with other

members of their species (Burt, 1943; Schoener, 1981). The most deterministic drivers of hippo home range are thought to be wading habitat, then access to grazing, and finally mating rights (Chansa et al., 2011; Prinsloo et al., 2020).

Hippos are semi-aquatic, and therefore the availability of suitable wading habitat is the primary determinant of hippo landscape distribution. Hippos wade gregariously diurnally and are primarily active nocturnally when they leave the water to graze between and around wading sites (Field, 1970; Lewison and Carter, 2004; Stears et al., 2019). Despite being an iconic African species, very little data have been obtained on hippo space use particularly because they are widely regarded as one of the most difficult animals to capture and handle in Africa (Pienaar, 1967; Stears et al., 2019; Prinsloo et al., 2020). Recent research by Stears et al. (2019) provided novel insights into hippo space use for hippo in the Ruaha River, a seasonal river system in Tanzania. The mean individual home range size was 8 ± 3 km^2 ($\pm$ SE) (individual range: 1.6–37.6 km^2) with foraging boughts (< 5 km from the river) extending perpendicularly on either side of the river (Stears et al., 2019). Hippos utilized smaller home ranges in the wet six months than they did in the dry (Stears et al., 2019). Additional data using similar methodologies investigating hippo home range size in response to different environments, resource availabilities, and population structures will provide more context to questions regarding patterns in hippo space-use and ecology.

Kruger National Park (KNP), South Africa, is one of Africa's oldest and largest protected areas (Carruthers, 1995; Sinclair and Walker, 2003). Although the ecological systems within KNP remain relatively intact in comparison with many of the more fragmented conservation areas globally, human-induced environmental changes outside and on the periphery of the park boundaries have impacts inside (Carruthers, 1995; Turpie and Joubert, 2001; Sinclair and Walker,

2003; Botha et al., 2011). For example, these effects are evident in KNP's river systems, which traverse vast areas of anthropogenically modified landscapes before entering KNP. The Olifants River, the largest of KNP's six large river systems, is host to KNP's largest hippo population and is also widely regarded as South Africa's most polluted river (De Villiers and Mkwelo, 2009; Botha et al., 2011; De Lange et al., 2012; Dabrowski and De Klerk, 2013). The deteriorating water quality in the Olifants River has raised conservation concerns inside KNP, especially after a series of mass Nile crocodile *Crocodylus niloticus* mortality events (Ashton, 2010; Ferreira and Pienaar, 2011; Woodborne et al., 2012). These concerns are compounded with additional concerns surrounding water quality related to human consumption and use as an estimated 4.2 million people live along and are dependent on the Olifants River (John et al., 2014; Kyei and Hassan, 2019; Mirzabaev et al., 2019). Hippos are drivers of fundamental ecological processes yet, ecological contributions by hippos in this system and their impact on the resilience of the Olifants River ecological system are unknown and require quantification to provide insights for the management inside as well as outside KNP.

The aims of our study were to a) collect novel spatial use data for hippos in perennial river systems in KNP; b) analyse these hippo home range data using several methods to provide additional context to hippo home range patterns, and c) use these hippo home range data to reflect on the resilience of the Olifants socioecological system. We predicted hippo home range size and shape would differ between individuals from different systems, between individuals occupying different roles in the population social hierarchy and differ seasonally in response to the spatial distribution of resources.

Figure 5.1 Habitat type and surrounding vegetation in the two study sites in Kruger National Park, South Africa, which varied considerably where a) is the Olifants River offered hippos wading pools with sandy banks and grazing areas that existed almost exclusively within the riverbed; and b) the Skukuza Golf Course Dam which was occupied by a single pod of (< 30) individuals and had substantial amounts of grazing available year-round as a consequence of artificial maintenance of the golf course.

5.3 Methods

5.3.1 Study area

This study was conducted at two sites within Kruger National Park (KNP), South Africa: Skukuza Golf Course area within the Sabie River system (Golf Course) (24°59'04.7"S 31°34'38.9"E) and the Olifants River (24°03'19.8"S 31°40'41.8"E; Fig. 5.1). Kruger National Park (19,485 km^2) extends more than 360 km north to south in South Africa’s low-lying savannah. The climate in

KNP is separated into two distinct seasons, i.e. a wet, or rainy, summer season from October to March/April where temperatures can reach over 40°C, and a dry winter season from April/May to August/September with milder temperatures and lows reaching 0°C (Sinclair and Walker, 2003). Precipitation increases from north to south with mean annual rainfall from 450-750 mm, respectively (Maruping-Mzileni et al., 2020).

The Olifants River flows through the centre of KNP and is the largest of six major perennial river systems inside the park, including the Sabie. In the west of KNP, the Olifants River passes through the Mopane bioregion characterised predominantly by Lowveld Rugged Mopaneveld and Mopane Basalt Shrubland and in the east passes through the Lebombo Uplands ecoregion characterised by Tshokwane-Hlane Basalt Lowveld and Northern Lebombo Bushveld (South African National Biodiversity Institute, 2006). The Olifants River is predominantly bedrock with sandy banks, and the surrounding habitats are rugged and mostly dry. Therefore, grazing mammalian species are dependent on the broad riparian zone where moderate amounts of grazing can be found within and along its periphery (Fig. 5.1a). In the driest parts of the year, nutrient-poor grazing also remains available on the crests of the small hills that run along the Olifants River (pers. obs.).

The Skukuza Golf Course impoundment/dam (~4 ha) is the smaller of two person-made dams near to each other and to the Sabie River in close proximity to the small town of Skukuza within KNP (Fig. 5.1b). Including the dam, the golf course covers between 25-30 ha and is watered year-round creating artificial grazing lawns habitually used by wildlife. Skukuza village (~450 ha) has a northern ~3 km boundary that runs along the Sabie River, and serves as a residential base for park management and research staff, and represents KNP’s main tourism hub. Anthropogenic

structures are mostly unfenced, and wildlife is free to move in and out of the village. Surrounding Skukuza village is a network of wallows, small rivers, and streams leading into the larger Sabie River. The natural vegetation types are predominantly Savanna Grasslands and Mixed Broadleaf Woodland (South African National Biodiversity Institute, 2006).

5.3.2 Data collection

This study formed part of a registered project under both KNP and South African National Parks (SANParks) Scientifics Services and therefore followed strict ethical standards for both capture and handling of hippos. All permits required to complete this project were obtained as well as ethics committee approvals from both the University of KwaZulu-Natal and SANParks. All captures and processing of hippos were conducted under the supervision of SANParks Veterinary Wildlife Services (VWS).

As part of this study, a total of seven male hippos were captured and immobilised using several capture methodologies (Chapter 6). Once immobilised, we took morphological measurements for each hippo, including the body length (tip of snout to the base of tail). Along with on-site observations, we used these to separate hippos into age categories ("Old Adult", "Adult", and "Sub-Adult"). Social stage categories ("Dominant", "Sub-dominant") were determined based on observations and, when possible, camera-trap imagery from passive capture locations, before, during, and post-capture. Dominant bulls were observed to be the largest male members of family groups, exhibited dominant behaviour, and dominated passive capture baiting stations. Sub-dominant males were observed engaging in territorial bouts and wading alone in isolated pools on the periphery of large family pods (>25 hippos). Detailed descriptions of capture

methods and procedures can be found in Chapter 6. We fitted GPS-GSM UHF telemeter collars (Wireless Wildlife, Potchefstroom, South Africa and Animal Trackem, Pietermaritzburg, South Africa; mass ~800 g) on four male hippos (one at the Golf Course and three in the Olifants River) that were immobilised using a combination of Butorphanol, Medetomidine, and Azaperone (Wildlife Pharmaceuticals, White River, South Africa and Kyron Laboratories, Johannesburg, South Africa) and captured using either vehicle or helicopter-based active capture methodologies. Each collar was fitted around the ankle and had a corrosion-based mechanical release system that was designed to last 2 years.

To test capture methods, to ensure GPS collar functionality, and to justify GPS fix rates for subsequent captures, we first conducted a pilot study where we captured one individual at Skukuza Golf Course dam. This site was favourable for our pilot study because a) hippos that occupied this dam were semi-habituated to people and therefore were likely easier to capture, b) consistent maintenance of the golf course greens provided substantial grazing year-round, and we believed the captured individual would then favour this area, and c) the collared individual could be actively and passively monitored, from photography and with the help of the golfers, staff members, and tourists that visited the golf course on a daily basis. Monitoring occurred over 2 months, and photographs were taken periodically to identify if any injuries, i.e. open sores, were being caused by the telemetry unit, and all images were then reviewed by SANParks VWS before proceeding. GPS fixes from this individual were collected hourly, and upon deployment, the battery life of the collar was estimated to last no more than 12 months. Fix rate success was substantially lower during the day when the hippo was wading and the telemetry unit was submerged. We identified a window with higher fix success between 19:00 and 5:00 when the hippo left the water to graze.

Therefore, the assessments of the home range that resulted from this study were derived from nocturnal movements of hippos during foraging bouts.

Subsequent captures and deployment of telemeter collars were conducted in the Olifants River system. Based on the results of the pilot study, these telemetry units recorded bi-hourly GPS locations between 17:00 and 10:00 and had a maximum estimated battery life of 2 years.

GPS data were collected and downloaded remotely via a network of relay and base stations (Wireless Wildlife, Potchefstroom, South Africa and Animal Trackem, Pietermaritzburg, South Africa) that were erected, prior to captures, on six meter-tall poles at the Golf Course and along a ~20 km stretch of the Olifants River. The network distribution was adjusted following GPS telemeter deployment and initial analysis of space-use patterns of collared individuals, and a download station was erected near to each individuals' most used wading location. When necessary, data were also collected using a portable base-station in the field.

5.3.3 Home range analyses

Before home range analyses, hippo spatial data were screened for repeated or inaccurate fixes in R software version 4.0.2 using packages 'adehabitatLT' version 0.3.25, 'adehabitatMA' version 0.3.14. Due to the range of applications, a number of home range estimation methods are currently used to estimate species' home ranges. Therefore, based on recommendations by Laver and Kelly (2008), three home range estimation methods were used to estimate hippo home ranges and core areas, namely; Maximum Convex Polygon (MCP), Kernal Density Estimation (KDE), and Adaptive Local Convex Hull (*a*-LoCoH). We used the "adehabitatHR' version 0.4.18, "rgdal" version 1.5-15, "sp" version 1.4-2, and "leaflet" version 2.0.3 packages in the R studio (1.0.153)

interface to estimate 50% (core area use estimates) and 95% home range, using the three home range estimation methods. We used the reference bandwidth smoothing parameter (href) for KDE to prevent over-smoothing and excessive fragmentation of home ranges (Walter, 2011). We used the furthest distance between two points for the parameter in a-A-LoCoH following the minimum spurious holes rule (Getz and Wilmers, 2004; Getz et al., 2007).

We performed analyses of variance in Microsoft Excel (version 16.40) to identify differences in measured home range size using the different home range estimation methods at 50% and 95% isopleths.

5.4 Results

Details of capture methods used and varying success are presented in (Chapter 6). A total of four adults, male hippos were successfully collared. In July 2019, one dominant individual was captured and collared at Skukuza Golf Course dam that is part of the Sabie River system (Fig. 5.2c). Three subdominant male hippos; 1 large subadult, and 2 adults, were captured and collared in the Olifants River system in October 2019. Data for analyses were only successfully retrieved from two of the individuals in the Olifants River system (Fig. 5.2a,b). Hippos ranged in size from 3.1 - 3.45 m.

A total of 884 global GPS locations were collected across all individuals. The number of GPS fixes collected per individual ranged from 232-342 fixes across a period of between 94-113 days (Table 5.1). GPS locations were collected at a higher fix rate on hippo Glf5 than on hippos in the Olifants system, and therefore a shorter lifespan for the collar was anticipated. This individual went out of range for an extended period, and the collar battery likely died, leaving a

substantial amount of data gathered, but were not retrieved. Although the anticipated battery life for the individuals in the Olifants River system was substantially longer, the system connectivity allowed for a larger 'playing field', and so individuals went out of range before all data were retrieved from collars. Logistical issues and delays caused by the onset of COVID-19, compounded these issues.

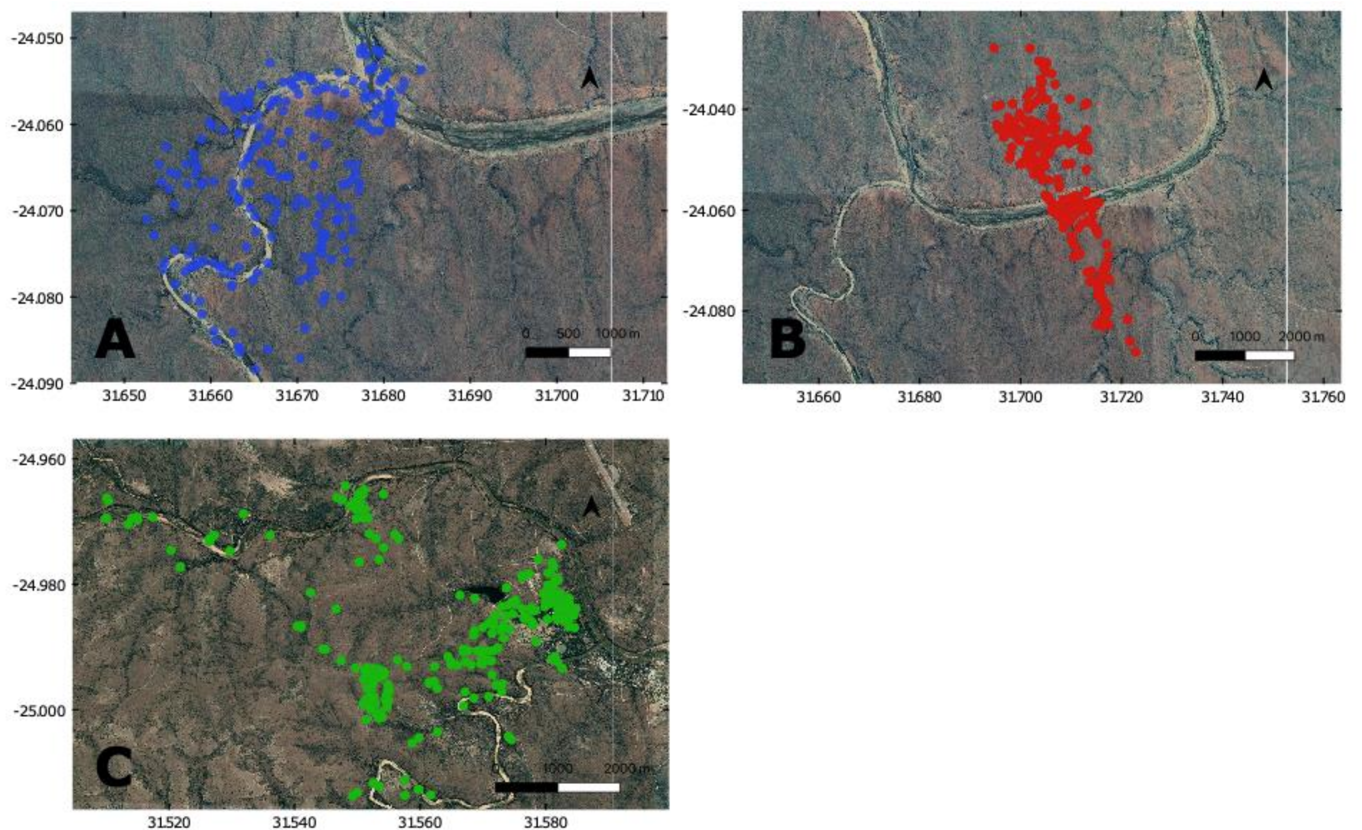

Figure 5.2 The localities and all GPS points collected for the three telemeter collared hippos in the Olifants System (a,b) and near the Skukuza Golf Course (c) in Kruger National Park in the present study using Google Earth (2020).

We accumulated a total of 542 and 342 GPS fixes in the Olifants River and the Skukuza Golf Course dam systems, respectively. Home range estimates using 95% confidence for MCP, KDE, and *a*-LoCoH showed an overall larger 95% home range size for the hippo in the Skukuza Golf Course dam area than for hippos in the Olifants River system irrespective of the home range estimation method. The 95% home range size for the hippo on the golf course was the largest (MCP = 18.7 km^2, KDE = 31.6 km^2, *a*-LoCoH = 8.2 km^2). The mean (± SD) 95% home range size for hippos in the Olifants system were smaller (MCP = 6.6 ± 0.71 km^2, KDE = 13.3 ± 0.85 km^2, *a*-LoCoH = 5.6 ± 1.07 km^2). Overall mean 95% home range estimates using the three different estimation methods were MCP = 10.7 ± 7.0 km^2, KDE = 19.4 ± 10.6 km^2, and *a*-LoCoH = 6.4 ± 1.7 km^2. Sample size and the different data collection period did not permit statistical comparisons based on the site, age class, social status, nor seasonality between individuals. Home range sizes did not differ significantly based on the estimator used for 95% home range estimates (ANOVA, $F(2,6) = 2.39$, $p = 0.172$).

The mean (± SD) core area sizes differed between the two sites. Hippos in the Olifants had smaller core areas for MCP and KDE but were larger when estimated with *a*-LoCoH (MCP = 2.8 ± 1.09 km^2, KDE = 3.8 ± 0.45 km^2, *a*-LoCoH = 1.8 ± 0.83 km^2, Fig. 5.3a). The hippo at the golf course occupied the largest core area for MCP and KDE but the smallest for *a*-LoCoH (MCP = 8.7 km^2, KDE = 5.9 km^2, *a*-LoCoH = 0.7 km^2, Fig. 5.3b). Again sample size and different data collection periods did not permit statistical comparisons based on the site, age class, social status, nor seasonality. Home range sizes did not differ significantly based on the estimator used for core area estimates (ANOVA, $F(2,6) = 2.16$, $p = 0.196$).

Home range shapes using MCP and KDE estimates varied between system types. Hippos in the Olifants System had elongated home ranges that extended perpendicularly on either side of the Olifants River. Wading areas in the Olifants River system were almost exclusively available in the river. The hippo on the golf course revisited at least four wading sites within a larger and more intricate network of small wallows, dams, and riverine based wading sites across its home range area and for periods targeted anthropogenically modified areas (golf course, cricket pitch, residential roads and gardens).

Hippo movement was predominantly restricted to 6 h in the day, and the remaining 18 h spent wading. Hippo daily movement could be categorised in two predominant patterns a) a foraging loop, where the individual vacated a wading site and eventually returned to the same wading location and b) a displacement, where the individual left one wading site and travelled to a different wading site. The distance hippos travelled during foraging ‘loops’ never exceeded 3.5 km in either system. Displacement movement patterns were generally further than foraging loops were only exhibited by the Golf Course hippo. The maximum displacement movement identified was 4.83 km.

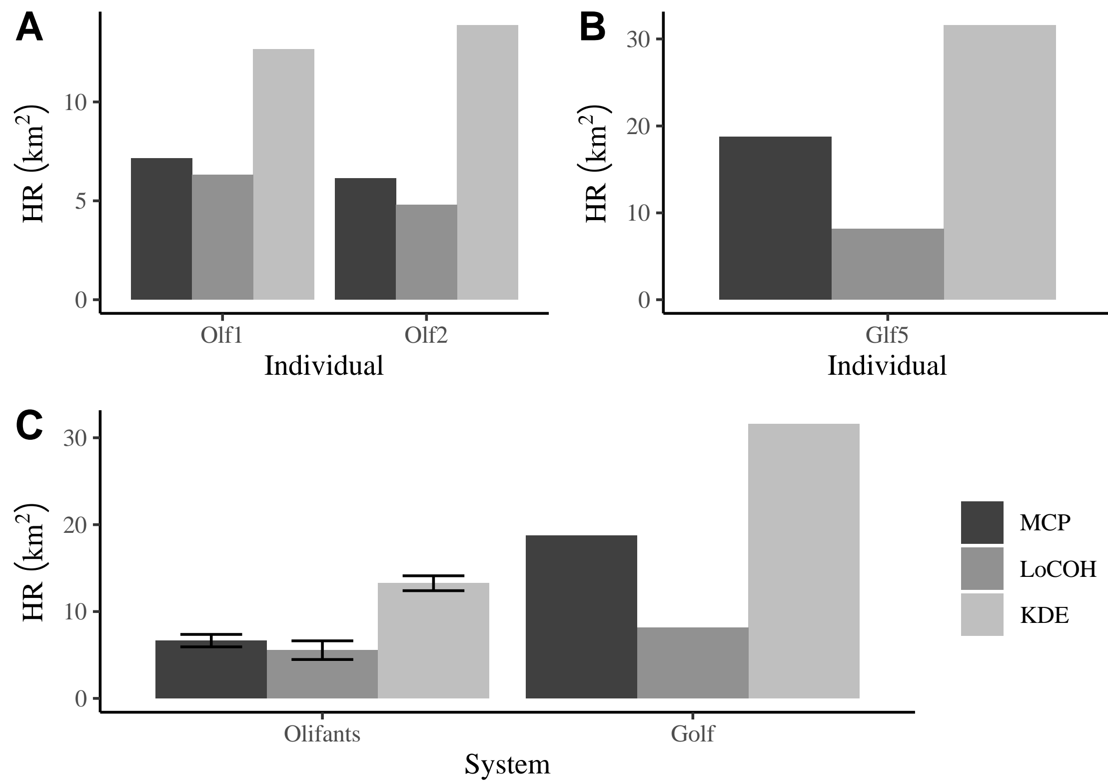

Figure 5.3 Individual home ranges of the three male hippos in a) the Olifants River (Olf, n = 2), b) Skukuza Golf Course (Glf, n = 1) and C) the overall mean home range (± SD) size for the respective location using the 95% confidence interval of the three home range estimates (MCP, KDE, *a*-LoCoH) in the present study

Table 5.1 The 95% home range area of hippos collared with GPS/UHF transmitters at two locations (Olifants River: Olf, Skukuza Golf Course: Glf) within Kruger National Park, South Africa

Individual	System	Sex	Age class	Social status at time of capture	Start date	End date	No. of GPS fixes	No. of days	Nose to base of tail length (m)	95% home range (km^2)		
										MCP	KDE	LoCoH
Olf1	Olifants River	M	Large sub-adult	Sub-dominant	10/10/2019	30/1/2020	232	113	3.1	7.153615812	12.66143605	6.313135164
Olf2	Olifants River	M	Adult	Sub-dominant	11/10/2019	12/1/2020	310	94	3.4	6.143631589	13.86964024	4.795723753
Glf5	Skukuza Golf Course	M	Adult	Dominant	16/07/2019	30/10/2019	342	107	3.45	18.726411	31.5676113	8.1569642

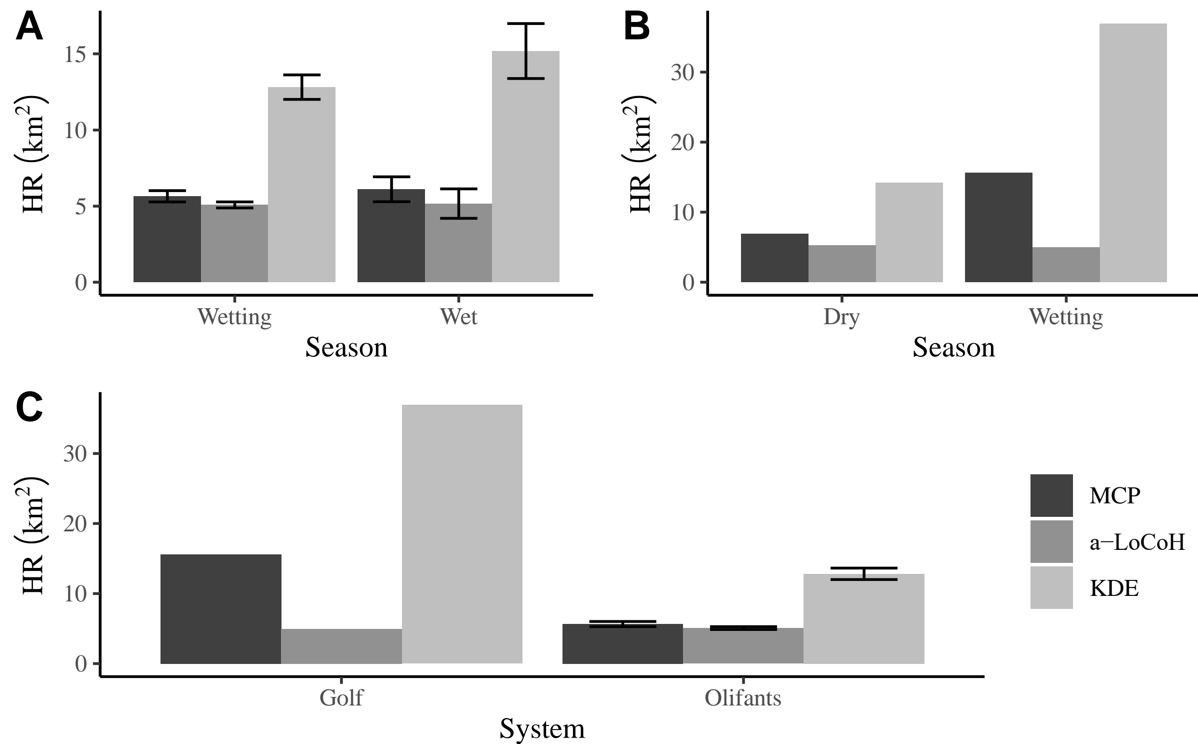

Figure 5.4 Seasonal (Dry = June-Aug, Wetting = Sep-Nov, Wet = Dec-Feb, Drying = Mar-May) home range sizes across the two system types a) the Olifants River (Olf, n = 2), b) Skukuza Golf Course (Glf, n = 1) and c) a comparison of mean home range (± SD) size in the 'Wetting' season for the respective locations using the 95% confidence interval of the three home range estimates (MCP, KDE, *a*-LoCoH) in the present study

5.5 Discussion

Although the data collected as part of this study was relatively short term (~4 months/individual) and across a small sample size (3 individuals), we believe that this study makes an important contribution. It is the second successful GPS home range study of hippos and the first in South

Africa. It was the first GPS hippo home range study along a perennial river system. Consequently, it provides important, novel spatial use data for hippos and contributes valuable data for the future management of the Olifants River socioecological system.

Overall, our study provides some consistencies as well as some different findings to the previous GPS study on hippo space-use along the highly seasonal Ruaha River in Tanzania. Although the estimation method differed, the overall mean 95% home range sizes were similar (*a*-LoCoH = 6.4 km^2 in this study; *T*-LoCoH = 8 km^2 in Stears et al. 2019). The range in body length of hippos in this study (310-345 cm) was smaller than was reported by Stears et al. (2019) (310-490 cm). All individuals in this study would have been grouped into the 'small sub-adult' life stage category (< ~370 cm) prescribed by Stears et al. (2019). However, different age classes and social standings were identified amongst the sample that was captured as part of this study (Table 5.1). All hippos in this study had overall home range sizes that were larger than hippos in the same size class in Stears et al. (2019), and the range in home range size within this single size class was larger in this study than was seen along the Ruaha River (Stears et al., 2019). Therefore, there appeared to be discrepancies in home range sizes between the two study sites amongst smaller sized hippos, indicating that there may be a fundamental underlying difference in space-use patterns between the two populations, or it may indicate that body length may not play as large of a role in defining space-use patterns as was assumed by Stears et al. (2019).

Data collection at the two sites within KNP did not overlap, and therefore statistical comparisons of overall 95% and core area home range sizes between the sites were not possible. However, anecdotally, across all estimation methods, the largest 95% home range was used by the hippo at the golf course which was also the largest (345 cm) and only dominant bull in the study.

The golf course system appears to have had a more sophisticated network of wading locations available as this hippo used and re-visited at least four wading locations found nearby. The golf course hippo was the only dominant individual in this study, and therefore an explanation for the revisitation of several wading sites may indicate that dominant individuals can hold dominion over several wading locations in close proximity at the same time; after all, this individual was the only adult male identified at the golf course dam for three weeks leading up to telemetry deployment. An alternative explanation may point towards the stochasticity of dominance within hippo pods. Smaller, potentially less fit males may opportunistically presume dominance at certain wading locations for short periods or periods outside of the mating season until they are expelled by more fit individuals when dominance at wading sites is more heavily contested for mating rights. This was reinforced by observations made of a different male mating with females at the Golf Course Dam during the data collection period, when the collared individual was not present (pers. obs.) and may bring the short-term observations of social status included in this study into question.

In comparison, wading locations in the Olifants system were virtually exclusively found within the riverbed (pers. obs.), as may also be true for other river systems like the Ruaha River in Stears et al. (2019). Home range estimations for the individuals occupying the same social status in the Olifants River system were highly consistent in size and shape, even though individuals differed in size and age class. Therefore, these findings show variations in home range size in response to system type as has been inferred in previous studies (Lewison and Carter, 2004) and potentially social status as well.

The results of our study support that hippos do not venture far from their wading localities. This is in contrast to previous suggestions (Lewison and Carter, 2004). Hippo livelihoods are

strongly tied to their aquatic requirements, and the position of their wading habitat within the landscape is fundamental in determining what grazing and other resources they have access to (Chapter 3). Previous studies have shown that hippo distribution is first determined by wading habitat availability; however secondary determinants like grazing resource availability are less well-studied (Viljoen, 1980; Smuts and Whyte, 1981; Prinsloo et al., 2020). Spatial and temporal availabilities of wading resources are determined stochastically by environmental drivers. Therefore hippos would require an understanding of their environment before ranging long distances through habitats with uncertain aquatic wading habitat availability. We would argue that social cues like territoriality and competition also play an important and understudied role in determining hippo space use.

The results of our study show that hippos spend a significant portion of their day wading (~18 h/day) and much less time foraging (~6 h/night) as well than was previously documented (Lewison and Carter, 2004). Unlike other large African mammals like the African elephant, hippos are not able to spend the majority of their day foraging and in part, points towards their bulk grazing feeding strategy (Boettiger et al., 2011; Codron et al., 2011; Woolley et al., 2011). Hippo home ranges were relatively small compared with other large African mammalian herbivores and showed a preference for grazing areas immediately surrounding wading locations (Shadrack et al., 2017; le Roex et al., 2019). Bulk grazing by hippos along water sources will have serious impacts on other grazing dependent species that also require ready access to water, especially in hot and dry seasons (Lock, 1972). This also shows that the large majority of allochthonous contributions by hippos tend not to be sourced from vegetation closer to water sources, and therefore energy transfers may not be as significant as previously assumed. The amount of time hippos spend

wading in aquatic habit determines the degree of allochthonous inputs they contribute. Hippos in this study spent a significant amount of time wading, regardless of season, justifying the substantiality of inputs recorded in systems with hippos across Africa (McCarthy et al., 1998; Grey and Harper, 2002; Bengis et al., 2016).

All hippos in our study likely occupied larger home ranges than are depicted in this study. This is because GPS monitoring was only possible for a portion of the proposed study period, and it is assumed that hippos did not lose their collars in the study area but instead vacated the areas they were using for the period they were successfully tracked and went missing before all data could be collected and downloaded. Issues with monitoring late in the study were because of a lack of access to research sites and restricted movement of researchers during the COVID-19 pandemic.

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Conflict of interest

The authors declare they have no conflict of interest.

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CHAPTER 6

An exploration of helicopter-based hippo capture methods and a comparison of success, cost, and effort required for current methods

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Running header: Comparison of hippo capture methods

6.1 Abstract

Conservationists are sometimes required to capture and immobilise a representative sample of a wildlife population to answer certain behavioural or ecological questions. The common hippopotamus (*Hippopotamus amphibius*, hereafter hippo) is widely regarded amongst conservation, veterinary, and game capture professionals as being one of the most difficult and dangerous animals to capture and immobilise in Africa. For this reason, hippo capture and immobilisation techniques are understudied and rarely used. We used three different hippo capture methods in Kruger National Park, South Africa, from July-November 2019. Here we make comparisons of capture success, cost, and effort of the three methods. A total of 15 hippo capture attempts were conducted using active capture at bait stations (A-BS), active capture from a helicopter (A-H), and passive baited boma captures (P-B). A-H methods were the cheapest, most time and effort efficient method attempted in this study but resulted in 3 capture related mortalities that were attributed to unfamiliarity with immobilisation drugs and techniques rather than to the capture methodology. P-B based capture methods are probably the most widely accessible methodology for conservation entities in Africa. Therefore, a guide, based on average cost values experienced in periods of this study, is presented to help determine what capture attempt rate is most appropriate when using P-B based capture once the project timeline is established.

Keywords: hippo capture; game capture; immobilisation

6.2 Introduction

Conservationists are sometimes required to capture and immobilise a representative sample of a wildlife population to answer certain behavioural or ecological questions (Ferreira et al. 2013, Breed et al. 2019, Hampton et al. 2019). Reasons for which these practices may be required are wildlife translocations, telemetry deployment, veterinary interventions, or sample collection (Jessup and Mazet 1999, Ryser-Degiorgis 2013, Batson et al. 2015, Hennig et al. 2020). Once capture methodologies are shown to be successful, they can be reproduced widely; within the means of the entities that utilise them, and safely; for both the people and animals involved (Burroughs et al. 2012). Therefore, overcoming initial steep learning curves, in respect to capture methodologies, lead to effective and implementable methods and aid in the understanding and ultimately the conservation of the targeted species (Karesh and Cook 1995, Deem 2007).

The common hippopotamus (*Hippopotamus amphibius*; hereafter referred to as hippo) is listed as vulnerable according to the IUCN Red List of Endangered Species (Lewison and Pluhacek 2017). Hippos once occupied the majority of the inland lakes, rivers and wetlands in Sub-Saharan Africa; however, over-hunting and habitat loss have caused global declines and have left the majority of the remaining populations confined to protected conservation areas (Lewison and Pluhacek 2017). Compared to the other large African herbivores, hippos are relatively understudied (Lewison and Carter 2004, Lewison and Pluhacek 2017, Prinsloo et al. 2020). Hippos are drivers of ecological processes in both terrestrial and aquatic systems, although their ecological contributions have been shown to have both facilitative and adverse effects depending on the system in which they occur (Subalusky et al. 2014, McCauley et al. 2018, Schoelynck et al. 2019). In natural systems, hippos create grazing lawns that promote grassland species diversity and

facilitate access to grazing resources for other grazing herbivores (Field 1970, Lock 1972, Lewison and Carter 2004, Kanga et al. 2013, Zoeller and Bond 2013). In addition, hippos contribute allochthonous nutrients that support populations of micro-and macroinvertebrates as well as fish in aquatic systems (Subalusky et al. 2014, McCauley et al. 2015). Altered or unnatural systems like rivers with altered flow regimes, man-made impoundments/dams, and fenced conservation areas with hippos are less equipped to mediate these ecological effects and dense populations can result in overgrazing of grazing resources and eutrophication of aquatic habitats (Field 1970, Lock 1972, Stommel et al. 2016, Dutton et al. 2018, Stears and McCauley 2018). For this reason, management entities in Africa require appropriate hippo capture methods for when management related interventions are required.

Hippos are widely regarded amongst conservation, veterinary, and game capture professionals as being one of the most difficult and dangerous animals to capture and immobilise in Africa. For this reason, hippo capture and immobilisation techniques are understudied and rarely used (Pienaar 1967, Miller et al. 2014). This is mainly because of their evolved semi-aquatic nature and physiology, shared habitat with Nile crocodiles (*Crocodylus niloticus*), gregarious wading strategies (pods of up to ~100 hippos), and their tendency towards aggression (Pienaar 1967, Harthoorn 1973, Walzer and Stalder 2015). Because of their high volume to surface area ratio, hippos have evolved a relatively thin epidermal skin layer and a thick dermis containing high concentrations of blood vessels to permit effective thermoregulation in aquatic habitats (Luck 1959, Luck and Wright 1964, Miller et al. 2014). Outside of aquatic refugia, these same physiological characteristics lead to significant water loss and over-heating, especially in terrestrial

environments with elevated ambient temperatures (Luck 1959, Luck and Wright 1964, Miller et al. 2014).

Several capture techniques for hippo have been employed in the past in both aquatic and terrestrial settings, although these methods take place as part of conservation and management and are scantly reported in the scientific literature (Pienaar 1967, Miller et al. 2014). The most common and widely used methods make use of passive capture bomas (Burroughs et al. 2012, Miller et al. 2014). These methods present the least danger to all parties involved but require extensive time and effort. Other, more experimental methods that were adapted to fit unique scenarios have also been used in the past (Pienaar 1967, Burroughs et al. 2012). These typically make use of active capture in aquatic habitats or active capture on the land of more docile animals.

Attempted immobilisations of hippos must either use drug combinations that allow hippos to retain their breathing reflex and permit processing of hippos in shallow water. Alternatively, the use of capture methods that enable the processing of hippo individuals terrestrially by either coaxing individual hippos out of aquatic refugia, or capturing hippos as they forage on land nocturnally is required (Pienaar 1969). A variety of immobilisation drug combinations have been used, however, even in favourable settings, hippo immobilisation outcomes are inconsistent, and the search continues for the 'silver bullet' drug combination (Miller et al. 2014, Walzer and Stalder 2015).

Conservation management requires adaptable methodologies that can be applied widely for veterinary, scientific, or conservation-based interventions; however, there remains little evidence that any particular capture methodology can fulfil these requirements for hippos. Therefore, our study explored the applications of novel helicopter-based capture techniques for

hippos and compared the success, cost, and effort required with two more traditional capture techniques.

6.3 Methods

6.3.1 Study area

Our study took place in Kruger National Park (KNP), managed by South African National Parks (SANParks), located in the Limpopo and Mpumalanga Provinces, South Africa. The KNP encompasses 19,485 km^2 of low-lying savannah with rainfall ranging from 300-500 mm and 500-700 mm in the northern and southern regions of the park, respectively, most of which falls in the wet, summer months between November-March (MacFadyen et al. 2018). The Olifants River more or less splits KNP into the northern and southern regions and is the largest of the six major perennial river systems that flow through the park, including the Sabie River in the south. These rivers and their associated impoundment/dam systems are aquatic habitats for more than 8,000 hippos inside KNP. They account for the majority of the national population of hippos in South Africa (Eksteen et al. 2016, Lewison and Pluhacek 2017).

Within KNP, the Olifants River passes through Mopane bioregion characterised predominantly by Lowveld Rugged Mopaneveld and Mopane Basalt Shrubland and Lebombo Uplands ecoregion characterised by Tshokwane-Hlane Basalt Lowveld and Northern Lebombo Bushveld (South African National Biodiversity Institute 2006). The majority of our study took place during the driest six months when discharge levels in the Olifants River are lowest. The Olifants River is predominantly bedrock with sandy banks, and the surrounding environment is very dry and rugged (Fig. 6.1a). Reduced in-stream flow formed pools of various sizes and depths

(1-10 m) in the exposed bedrock that were used as wading habitat by hippo pods of different sizes (1-60 individuals). Hippos and other grazing species are dependent on the Olifants River's broad riparian zone, where moderate amounts of grazing can be found (pers. obs.). When grazing resources are limiting, nutrient-poor grazing also remains available on the crests of the small hills that run along the Olifants River (pers. obs.).

Anthropogenic structures in KNP exist predominantly in the tourist rest camps, of which Skukuza (450 ha) is the largest. In addition to being the hub of KNP in terms of tourist visitation, Skukuza has ~1600 permanent residents comprised of scientific, management and general staff, a nine-hole golf course (25-30 ha), and a small commercial airport (South African Census Community Profiles 2011). Skukuza is situated overlooking the Sabie River at its confluence with the N'waswitshaka River, a smaller seasonal river that runs entirely within KNP. Also in the vicinity are two human-made impoundments/dams, of which one is located on the Skukuza Golf Course. These impoundments are less than 500 m away from one another, and both had hippo pods with ~30 individuals during our study (Fritsch unpublished data).

6.3.2 Data collection

Our study was conducted as part of a registered project with KNP and SANParks Scientific Services and, although it included some explorative aspects, followed strict protocols for capture and immobilisation of hippos. All African game species present distinct challenges in terms of capture and immobilisation (Burroughs et al. 2012). However, methods for capturing hippos, because of their aquatic nature, aggressive tendencies, and uniquely thick skin physiology, are unreliable and lack field testing. Therefore, elements of this research required SANParks KNP

Veterinary Wildlife Services (VWS) staff to learn through application and to be exposed to unfamiliar immobilisation drug combinations and novel applications of capture procedures routinely used on other species like African elephant (*Loxodonta africana*) and black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*). Hippos were captured in order to deploy telemetry bracelets for the collection of hippo space use data. Ethics committee approvals were obtained from both the University of KwaZulu-Natal and SANParks. All captures and immobilisations were conducted by and under the supervision of SANParks KNP VWS, and only people with the required skillsets were involved in capture operations. An external specialist researcher and research assistant were also involved in all captures.

Three different capture methods were attempted, i.e. active capture at bait stations (A-BS), active capture from a helicopter (A-H), and passive baited boma capture (P-B) from July-November 2019. All attempted A-BS captures ($n = 2$ attempted capture events) occurred at a single site (24°59'12.6"S, 31°34'43.9"E) on the Skukuza Golf Course at a small impoundment associated with the Sabie River system in July 2019. All A-H captures ($n = 7$ attempted capture events) took place over 3 days from the 8-10 October 2019 within the Olifants River between (24°04'28.9"S, 31°14'58.6"E; 24°03'29.6"S, 31°42'43.9"E). Passive boma captures ($n = 7$ attempted capture events) occurred along the Olifants River at a single location (24°03'24.6"S, 31°43'19.0"E).

6.3.3 Methods for active capture from a helicopter

Active capture methods from a helicopter were subject to SANParks Air Services (AS) and VWS equipment and staff availability as well as dependent on clear weather and mild early morning temperatures in particular. Because of limited space in the aircraft, these methods only involved

five professionals; a pilot, a marksman armed with either a bolt action or self-loading carbine rifle, the lead veterinarian, a veterinary assistant, and the researcher involved. Captures were conducted with the assistance of SANParks AS from a SANParks Airbus H125 (AS350B3) helicopter equipped with external sling load provisions. This method permitted a team to perform a string of sequential captures during the day and over the course of a few hours. The objective was to capture ten total individuals with this method.

Mild early mornings were targeted for captures as hippos dehydrate quickly in warm ambient temperatures outside of their aquatic environment. Captures were called off once temperatures rose above 30 °C. For safety reasons, SANParks helicopters did not operate before dawn. Therefore, taxiing from Skukuza Airport north 100 km to the eastern section of the Olifants River in KNP began at dawn, at roughly 6 am. After a ~45 min taxi, the helicopter and crew arrived at the Olifants River and flew west along the river.

Adult subdominant males often wade solitarily or in small bachelor pods (2-3 individuals) in shallow pools (< 1 m) on the periphery of larger family pods during the annual mating season. Because these pools were so shallow, hippos could not fully submerge themselves when disturbed, and they would instead vacate their pools in search of cover on land or in a deeper pool further away. This behaviour had been observed previously on foot and was crucial to the A-H methodology (pers. obs.). These hippos were targeted and coaxed out of the water by hovering above them (<1 min) and subsequently herded away from deeper pools and onto the riverbank or out of the river entirely, using the helicopter (Fig. 6.1b). Once the hippo moved away from the areas with deep water, the lead veterinarian darted the hippo in the hindquarter from above with a combination of Butorphanol, Medetomadine, and Azaperone (Wildlife Pharmaceuticals, White

River, South Africa and Kyron Laboratories, Johannesburg, South Africa), and the helicopter promptly manoeuvred away from the target. The hippo was given time to settle and to permit the immobilisation drugs to take effect and was monitored from a distance (~200 m) by the team whilst hovering. If required, the pilot periodically manoeuvred the hippo away from deep pools and guided them towards shaded areas close to a satisfactory landing location. This process lasted ~20 min. and required immense skill from the SANParks AS pilot. Additional doses were administered from the helicopter when deemed necessary by the VWS team members. As soon as the hippo showed symptoms of immobilisation, the team landed the helicopter within eyesight of the now recumbent hippo.

Post capture processing and transmitter deployment began once the hippo was darted and appeared recumbent. The armed marksman and the lead veterinarian approached and ensured the hippo was fully immobilised before others joined them and began processing (Fig. 6.1c). The team was limited in size, and therefore, post-capture processing had to be efficient to ensure the safety of all parties involved. A specially designed cloth with ear holes was velcroed over the hippo's eyes, and a heavy-duty cargo tiedown with a ratchet was passed under the head and tightened over both jaws (Fig. 6.1d). A rope was tied around two of the hippo's legs so that it could not run if it regained consciousness during processing activities. The hippo was rolled to its side so that the telemetry bracelet could be attached to one of its front legs. Morphological measurements, individual sex and body condition, and blood, hair, and tissue samples were taken and recorded for each individual. The reversal antidote containing Alphanil and Naltrexone was administered as soon as the telemetry bracelet was attached, all data was collected, and all equipment and restraints were removed from the hippo. The hippo was monitored from a distance or while

hovering in the helicopter for a total period of at least 20 min. or once the hippo was seen erecting itself before continuing. Sometimes a second hippo could be darted while monitoring the now recovering hippo. Helicopter time was limiting for financial and logistical reasons, and therefore multiple (n = 2 or 3) attempted captures were required each day before 09h00 when ambient temperatures became too high to continue.

6.3.4 Methods for active capture using a bait station

Hippos on the Skukuza Golf Course are exposed to golfers and vehicles on a daily basis and have therefore become semi-habituated to their presence and movements. We expected these hippos to be less sensitive to SANParks VWS personnel and vehicles during captures and presented an opportunity to experiment with A-BS based capture methods. Following a failed active capture attempt from a vehicle without a bait station, the first step for A-BS methodologies was to introduce and habituate hippos to lucerne hay which would later be used as bait. Lucerne, also referred to as "candy grass", is commercially available as it is used as cattle feed. It was assumed that once hippos were exposed to lucerne hay, they would seek it out during their nightly foraging boughts. Two pre-baiting locations were identified; the first was the proposed capture location on the golf course, the second was chosen based on apparent hippo 'foot traffic' and had been used successfully in the past as a passive capture location by SANParks VWS. Both locations were within 500 m of the dial wading habitat of the target hippo pod. Two camera-traps (Moultrie M-888, Calera, AL) were mounted to trees or metal steaks at .5-1 m heights near each bait site and were used to monitor the timing, number, age-class, and sex of hippos visiting. Once ~5 hippos

were visiting the bait site on a daily basis, it was determined that baiting would continue but exclusively at the proposed capture location and now in larger quantities.

The capture location was situated in the middle of the golf course and roughly 100 m away from the dam. Hippos, in general, are skittish, and if disturbed, hastily seek refuge in their aquatic wading habitat. Therefore, the capture location was chosen based on the need for open terrain that, if necessary, could easily and safely be navigated by game capture personnel and vehicles at night. Following a total of 12 days baiting, a gap in SANParks VWS staff availability permitted attempted captures. A total of 12-15 personnel were present for captures, including SANParks Scientific Services and VWS staff, as well as the lead researcher. Camera trap images revealed that hippos were visiting the bait station starting from 20h00; therefore, all vehicles and people involved arrived on site an hour before (19h00) and waited far enough away (100 m) to avoid disturbing the baiting site. All personnel involved were split across three teams; two teams in two 4x4 Toyota Landcruiser vehicles; one with the veterinarian responsible for immobilisation standing in the back, and precautionarily, the other with a well-trained marksman with a .458 calibre bolt action rifle, and the third team on standby for processing once the animal was darted. Both vehicles used a spotlight (Gamepro Ninox rechargeable spotlight) equipped with red light filter and periodically drove slowly to and around the bait site until a candidate for capture was identified (Fig. 6.2d). Hippos were darted in the hindquarters using a combination of Butorphanol, Medetomidine, and Azaperone (Wildlife Pharmaceuticals, White River, South Africa and Kyron Laboratories, Johannesburg, South Africa) either from the back of one of the vehicles or on foot. Hippos responded differently to being darted, where some were startled, and others were happy to continue feeding on the bait. After being darted, hippos were corralled using the Landcruisers into open

areas on the golf course and away from the nearby dam and, if necessary, were topped up with additional doses. The armed marksman was in charge, the lead veterinarian delegated tasks and ensured the safety of all parties, two veterinary assistants assisted the lead veterinarian and scribed, three-game capture professionals, prepared restraints, the researcher prepared their equipment, and all other personnel awaited processing.

Once the hippo became recumbent, the lead veterinarian confirmed the hippo was fully immobilised before the team approached. Three VWS game capture professionals exercised a number of safety measures before the commencement of processing. A towel was thrown over and fastened over the recumbent hippo's eyes, and a heavy-duty cargo tiedown with a ratchet was wrapped tightly around the hippo's mouth to prevent it from opening. The hippo was then pushed onto its side, and a rope was tied around the hind legs to prevent the hippo from running if it were to wake mid-way through processing. Once the hippo was secured, the first step was to attach the transmitter on one of the front legs. While this took place, VWS staff took blood, hair, tissue, and faecal samples. The researcher then took morphological measurements, including total body length (nose to base of tail), ½ chest girth, and a number of head measurements. Once processing was complete, all restraints and safety equipment were removed, and the VWS lead veterinarian remained to administer an antidote containing Antisedan and Naltrexone via the sublingual vein in the tongue. The hippo was monitored for 20 min. following recovery and eventually returned to the impoundment.

6.3.5 Methods for passive capture using a capture boma

Passive hippo boma-based capture methods are different from previous active capture methods as any number of individuals can be captured in a single capture attempt, depending on how many individuals are commensally feeding on the bait inside the capture boma at the time of capture. These methods took place on the Olifants River and targeted a pod of hippos (~30 hippos) that consistently used a large pool below a gauging weir (Fig. 6.2a). The pool provided favourable wading habitat, even through periods of reduced flow, and therefore, offered an optimal location for constructing the semi-permanent boma structure. Good road access, a hard bank 3 m above the Olifants River high water line with a clearing where the boma could be constructed, and the presence of permanent gauging weir maintenance staff also contributed to the decision of capture boma placement.

The boma was erected early on in the baiting process (1 week after baiting commenced) to ensure hippos became habituated to the presence of the structure. The capture boma, which was provided by SANParks VWS, was specifically designed for hippo capture and used 3 m tall sheets of 3 mm steel to construct 3 x 3 m sections that were assembled in the field to form two 8 m diameter circular compartments, each with their own entry door, separated by a shared sliding door (Fig. 6.2a-b). All doors, which were also constructed of thick steel, were mounted on small wheels that ran on sets of guide rails and had to be opened manually. Two compartments meant that, if necessary, VWS staff could process different animals simultaneously in each compartment. One compartment entry door and the shared sliding door were left open for the entirety of the capture process so that hippos would eventually walk through the first compartment and into the second, deep into the boma to access the feed, allowing time for VWS staff to slide the boma doors closed

manually. A shipping container (2.5 m x 2.5 m x 6 m) was transported on-site and filled with six large bales of lucerne hay to be used while baiting. A small pump house (2 m x 2 m) on-site would eventually be used as cover for VWS staff during captures.

Hippos were introduced to lucerne hay in August 2019, mid-way through the dry/winter season (June-November), as the availability of existing grazing pastures in the area diminished. It was expected that the lucerne hay would provide welcomed satiation as it was presented in large quantities, had high nutrient content, and was within easy access to the riverine wading site. Feeding took place every 2-3 days and was done by the lead researcher, a research assistant and an armed guard. The bait was placed in 1-3 piles (2 m circumference x .5 m height) depending on bait site visitation. Piles were first placed directly next to the river, as close to the in-stream pod as possible, and gradually moved away from the river and closer to the capture boma site (~50 m away) as the hippos visited the feed. Five baiting sites were used, each roughly doubling in the distance from the previous away from the river (1 m, 5 m, 10 m, 20 m, 50 m away from the river) until the final site (50 m away from the river) was at the entrance of the open capture boma door. All feeding sites were monitored with either one or two camera-traps. Images from the camera traps were used to identify the age, sex, social status and, if possible, individuals (based on size, markings, and if they visited with other hippos) of the hippos visiting the bait site. Periodic point counts were used for monitoring the numbers and age classes of the individuals within the target hippo pod.

As the visitation at bait sites close to the capture boma took place more consistently, it became time to attempt to get hippos to seek out bait inside. Bait was first placed inside the boma after 16 days. At this stage, it was found to be most effective to use a continuous narrow line of

bait, rather than separate piles (pers. obs.) trailing from the boma entrance into the second compartment, where a relatively large pile of bait was left (Fig. 6.2b). Camera-traps were set at the entrance of the boma and above the large bait pile in the second compartment for monitoring purposes. After 39 days since the start of baiting, hippos were confidently feeding inside the boma on a nightly basis. An elevated rope (2 m off the ground) was attached to the outward-facing first compartment door. When pulled hard by a single individual, the rope quickly drew the boma door closed. A VWS Toyota Landcruiser 4x4 vehicle was parked 8 m away with the driver-side door facing the boma and the windshield facing the hippo wading pool. The rope connected to the boma door was drawn taught through the open window of the driver-side Landcruiser door where VWS sat during attempted captures.

Attempted captures went forward on nights when hippos were consistently visiting the bait inside the capture boma, and SANParks VWS staff had overlapping availability. Preparation for each attempted capture began at 17h00, and sets of captures took place over 3-4 nights. Two teams of two individuals were split into two vehicles parked 8 m away from the capture boma and behind a small pump house. The teams hid the two vehicles under a 5 m x 5 m sheet of camouflage netting and used a set of night vision goggles (AGM NVG40 NWi Dual Tube Night Vision Goggle/Binocular) to monitor the entrance of the capture boma. By 19h00, everyone hid inside the vehicles and monitored the boma. Over seven nights of attempted capture, no hippos were observed entering the boma, and therefore no attempts were made to trap individuals inside. However, if a hippo had been captured, the idea would have been to secure all individuals inside the boma, notify VWS professional staff. Early in the morning the following day, the hippos would have been separated in different compartments and immobilised and processed.

6.4 Results

A total of 15 capture attempts took place over two seasons in 5 months from July-November 2019. Across the three capture methodologies attempted, a total of 6 hippos were captured. Drug dosages were dependent on the size of the animal, the response of the animal to the drugs (uptake), and the location of the dart (where muscle tissue eased uptake of drugs. Overall, increased dosages of antidote, and capture during cooler temperatures, permitted hippos to return to aquatic refuges more quickly, decreasing recovery time and mortality risk.

Table 6.1 A summary of the success, cost and effort required for three hippo capture methods (active capture methods using a bait station: A-BS, Active capture methods from a helicopter: A-H, and passive capture methods using a passive capture boma: P-B) based on average values gathered during the capture of 15 hippos in the Kruger National Park, South Africa in the present study.

Capture method	Time of day of attempted captures	Capture sampling area (km of aquatic habitat)	Number of hippos that can be captured in a single effort	Hippo population habituated to people	Maximum processing team size	Mean person-hours required/attempt (hours)	Days required/attempt	Successful captures/ total attempts	Mean elapsed "handling" time for successful captures (min)	Capture related mortality	Mean capture related cost per capture attempt (excl. transport costs)	Mean personnel costs per capture attempt	Mean veterinary and immobilisation costs per capture attempt	Mean total cost per capture attempt (excl. vet costs)
A-BS	Night	<1	1	Yes	15	26	12	**1**/1	150.00	None	$212.12	$739.39	$247.50	$951.52
A-H	Day	>30	1	No	5	6.56	0.3	**5**/7	87.20	3	$783.17	$54.30	$113.36	$837.47
P-B	Night	<3	>1	No	N/A	47	14	**0**/7	N/A	N/A	$329.56	$963.64	N/A	$1,293.20

6.4.1 Active capture from a helicopter

Each capture methodology was characteristically unique. A total of five hippos were captured in seven total attempts utilising A-H methods. Active helicopter-based methods were the only method that took place during light hours and could be conducted adaptively without extensive planning and preparation. These methods could also be conducted across a much larger sampling area (more than 30 km of river in each attempt) than the other methods, but capture opportunities were limited to isolated individuals or those that could be separated from groups. Successful coaxing of hippos out of wading areas was only realised in groups that were three individuals or smaller in pools less than 1½ m in depth (per. obs.). Because of the structure of the hippo population on the Olifants River during the low flow season, this limited captures to secluded males or males that were successfully separated from small bachelor herds (Fig. 6.1a). A few attempts were made to split up larger pods or family groups as well as pods occupying deeper pools, but all attempts were unsuccessful. Hippos were mostly processed one at a time, but some overlap in the recovery of the previous individual and capture of the subsequent individual could take place if capture sites were close enough in proximity. Overall, these methods resulted in the shortest time between the administration of the first dart and the recovery antidote. The number of personnel and involved in captures was limited by the seating arrangement (6 seats) and storage capacity of the helicopter. It was also necessary to consider the weight of the personnel and equipment taken on the aircraft as these impacted helicopter fuel costs and manoeuvrability in flight. For these reasons, A-H methods used a smaller team of highly trained individuals, which also meant that only a fraction of the person-hours were required for each capture attempt (Table 6.1). Unlike the other capture methods, A-H methods took place in remote and rugged terrain, necessitating increased vigilance around immobilised hippos, consideration of other dangerous wildlife, and in general, increased

adaptability across capture processes. Processing captured hippos often took place in thick bush and required some level of bush clearing or site preparation before processing could commence (Fig. 6.1c-d). At $ 837.41 (incl. helicopter fuel and maintenance, wages, and overnight accommodation and subsistence but excl. veterinary and immobilisation costs), total costs for A-H methods were the least expensive per capture attempt of all methods as well as the most time and effort efficient (Table 6.1).

Unfortunately, a total of three hippos died during this study. Although all capture related mortality was experienced while employing A-H capture methods, not all deaths were attributed solely to the capture methodology but were also related to the steep learning curve associated with the novelty of hippo capture. Of the five successfully captured hippos using A-H methods, two expired unexpectedly following processing and were later determined to have died because of a combination of reasons 1) immobilisation drugs took longer to affect hippos that were actively manoeuvred by the helicopter and hippos were not allowed enough time to succumb to immobilisation drugs before additional doses were administered, 2) in addition to already somewhat deteriorated body condition attributed to dry-season-induced wading and feeding resource scarcities and interspecific competition from the concurrent mating season, persistent individuals that required more 'handling time' prior to recumbency carried elevated levels of exhaustion, stress, and associated body heat into capture procedures, 3) hippos were insufficiently monitored following processing and although they appeared to be stable or had recovered and walked away from the processing location, were either too deeply immobilised and subsequently overheated in ambient temperatures above 30 °C or were not administered enough antidote and recovered only for a short period before becoming recumbent again and overheating in ambient temperatures above 30 °C. A third hippo died after it was darted, and the capture team failed to

keep it away from a deep pool where it became deeply immobilised (lost its breathing reflex) and inaccessible and subsequently drowned. It is worth mentioning that the personnel involved in the study navigated a steep learning curve at the start of the project and that these three deaths occurred in the first three attempts employing A-H capture methodologies, one of which was only discovered retrospectively. No additional capture related mortality was encountered following subsequent adaptations in methodology. It was determined that the most important aspects to consider to avoid capture related mortality using A-H methods were to 1) take time to find a target that is more than 300-500 m away from deep pools that would render the individual inaccessible if it was immobilised and sought refuge inside, 2) that ambient temperatures are low and that, where possible, 'hippo handling time' is limited to decrease capture related stress, 3) that appropriate immobilisation and recovery drug dosages are administered, 4) that 30-60 min. of post-capture monitoring time is afforded per individual and if possible, that individuals are herded back into shallow aquatic wading habitat away from other hippos to permit appropriate thermoregulation and accelerate recovery.

Figure 6.1. A selection of photographs taken while implementing active helicopter-based capture methodologies a) the Olifants River in dry season reduced flow b) a hippo coaxed out of a shallow pool and now being manoeuvred by the helicopter c) SANParks VWS putting a towel over a recently recumbent hippo's eyes and a marksman surveying the process in the rugged terrain in which capture methods occurred d) a heavy-duty cargo tiedown with a ratchet wrapped around a captured hippo's mouth.

6.4.2 Active capture using a bait station

Following a failed exploratory capture attempt without a bait station, A-BS methods were attempted on one occasion and resulted in the successful capture of one individual. These methods

required that potential targets visited the bait station on the night of the proposed captures. The sampling area was comparatively small to A-H methods, and only hippos from the nearby dam (< 200 m away) visited the bait. Therefore, to increase the likelihood of capture success, capture attempts only took place once several ($n \geq 3$) hippos consistently visited the bait site. Camera-trap imagery showed that all visits to the bait site took place between 17h00 and 05h00 the following day, roughly 90 min. after sunset and before sunrise, respectively. Therefore, capture attempts were only exercised at night and required prior planning to ensure the availability of all involved parties (Fig. 6.2d). After 12 days of baiting, more than five hippos visited the bait site at predictable times on sequential nights. Captures took place in a predetermined location in a 'controlled environment' with the assistance of a large team of 15 people comprised of highly experienced game capture and veterinary professionals. This also meant that the person-hours required for each attempted capture were four times the amount required for helicopter-based captures (Table 6.1). Only one hippo was captured in each capture effort, and no attempts were made to overlap the processing of more than one individual. These methods benefited from the fact that the subpopulation was semi-habituated to people and allowed SANParks VWS vehicles and personnel to come within 20 m during attempted darting. Because hippos are naturally very skittish, these methods may not work in populations that do not have some level of habituation to vehicles and people. Once darted, the hippos were successfully corralled away from the impoundment using the game capture vehicles. The total time from the first dart to the antidote was 150 min. and was the longest of all methods (Table 6.1). This is mostly because of the novelty of the capture and processing as it was the first hippo capture performed by SANParks in this way and the first hippo capture in the living memory of many of the VWS personnel using any methodology (pers. comm.). The capture related costs using A-BS methods were the cheapest of all methods ($

212.12); however, the personnel costs ($ 783.17) brought the total costs up significantly ($ 951.52), and therefore A-BS methods were the median method in terms of the total cost (Table 6.1).

6.4.3 Passive capture using a capture boma

A total of seven capture attempts were made using P-B methods of which none were successful. Because successful captures were not realised using this method, some of the resulting evaluative data were not collected. Two sets of capture efforts (three attempts in October and four attempts in November) took place over 99 days from August - November 2019. This was the longest period demanded by any of the methods attempted in this study (Table 6.1). These methods required habituating the hippos in the vicinity of the capture boma to lucerne hay that would later be used as the attractant in the capture boma. Boma based capture methods were the only methodology in the study that presented the opportunity to capture multiple individuals in a single capture effort. The sampling area of the P-B method is limited to the individuals that are in the direct vicinity of the capture site and were therefore mostly limited to the hippos present in the pool adjacent to the capture site. A series of point counts were conducted of the hippos in the nearby river pool throughout the study period. The highest counts were obtained in August and numbered 31 hippos, 17 hippos were counted in mid-September closer to the first set of capture attempts, and between 3-8 hippos were counted in November before and during the second set of capture attempts. The reduction in hippos detected in November was attributed to a major flooding event that occurred before and during the second set of attempted captures where hippos were either voluntarily or forcefully dispersed downstream. Attempted captures took place at night and were subject to some level of human error where on three occasions, across three attempts, hippos entered the boma but were not detected by capture team personnel and evaded capture (Fig. 6.2b). Both sets of attempts

took place in the ‘wetting’ season from September to November, although average rainfall in the region in November was three times that in September and 25% more than October (SANParks unpublished data). Before the first set of attempted captures, lucerne hay was replenished on 21 occasions so that bait was present at the capture location for 48 consecutive nights. Hippos first entered the boma after 26 days of baiting, and after 42 days, numerous individuals in groups as large as three were entering the boma on multiple occasions during the night. Due to the availability of the researcher and staff, the capture site could only be supplemented with feed on ten occasions in the 44 days between the first and second set of captures, although the amount of bait left at the site was double the normal amount. Hippos fed inside the boma on ten occasions in this period and readily entered the capture boma to access the bait. Capture related costs were calculated based on an average cost for each capture attempt and included the average bait cost per capture attempt ($ 181.82) and the average cost of the initial boma erection and rental per capture attempt ($ 147.74) (Table 6.1). These amounted to less than the capture-related costs for A-H methods but more than A-BS methods. The person-hours and days required per capture attempt for the P-B based capture were the highest of all methods. So when personnel costs including wages, accommodation and subsistence costs ($ 963.64) were added to the capture-related costs, the P-B based methods ($ 1,293.20) were at least 25% more expensive than all other methods per capture attempt. The timeline of these methods is unpredictable as they are primarily dictated by the timeline of visitation of the capture site by hippos, and therefore, the costs associated with the P-B method will differ in different scenarios (Fig. 6.3a-b).

No attempted captures were successful using the P-B method; however, this was later attributed to some shortfalls in the passive capture methodology 1) VWS staff availability was limited and dictated the timing of capture efforts resulting in insufficient capture attempts when

hippos were most frequently visiting the capture site in the appropriate season; 2) disturbance at capture sites and human error induced lapses in the detection of hippos inside the capture boma during capture attempts could have been mediated with the implementation of relevant low-cost technology, and 3) although costs would have increased, pre-baiting could have taken place at more than one location to permit attempted captures at multiple locations. The timing of captures is first determined by the visitation of hippos inside the capture boma, and depending on that, the rate at which captures are implemented should be considered to permit budget savings (Fig. 6.3a-b). Hippo capture programs that are able to realise viable capture opportunities early-on in their timeline are able to employ high rates of capture attempts and will realise the best cost savings per capture attempt (Fig. 6.3a). Alternatively, capture programs that are only able to identify capture opportunities later in the program will generally be more expensive per capture attempt and will also need to concentrate their effort on fewer capture attempts, potentially having consequences on the number of successful captures.

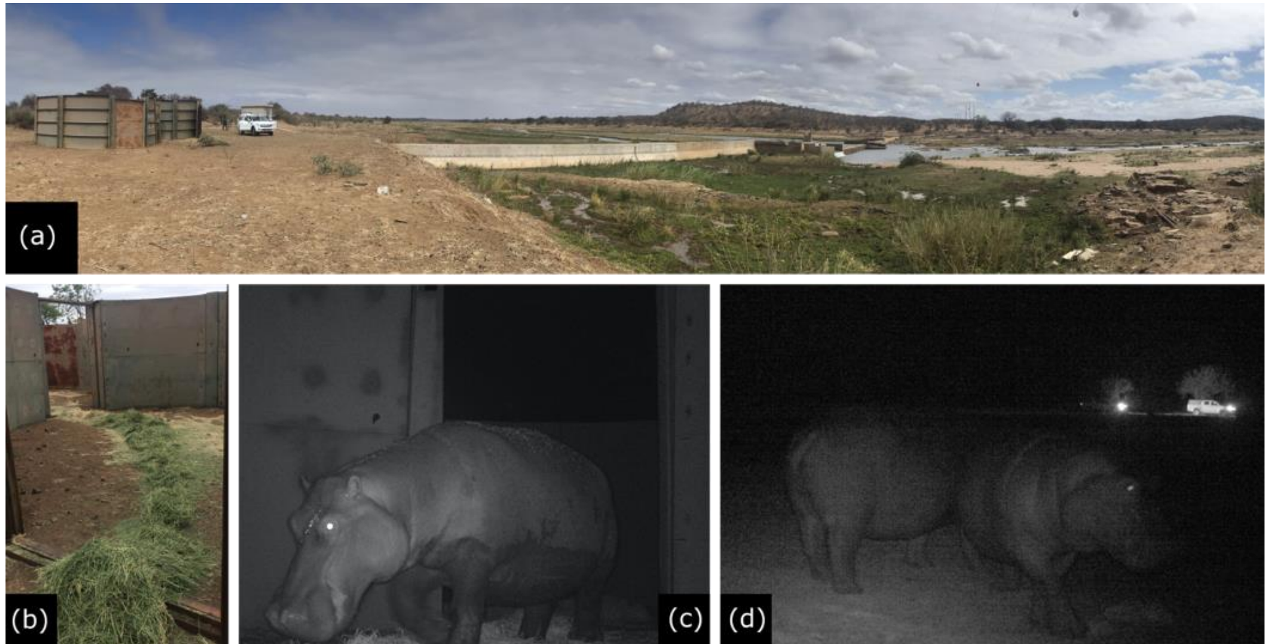

Figure 6.2. A selection of photographs taken during passive boma based captures (a-c) and active capture with a bait station (d) methods a) the placement of the passive capture boma on top of the hard bank overlooking a pod of ~25 hippos below the gauging weir b) drawing a line of lucerne from the entrance of the boma to the second compartment encouraged hippos to go further into the boma when eating the bait c) a missed capture opportunity of an adult hippo inside the boma d) 3 hippos (one out of the picture) feeding on the bait in the foreground as, in the background, the A-BS capture team approaches the bait site to identify a target.

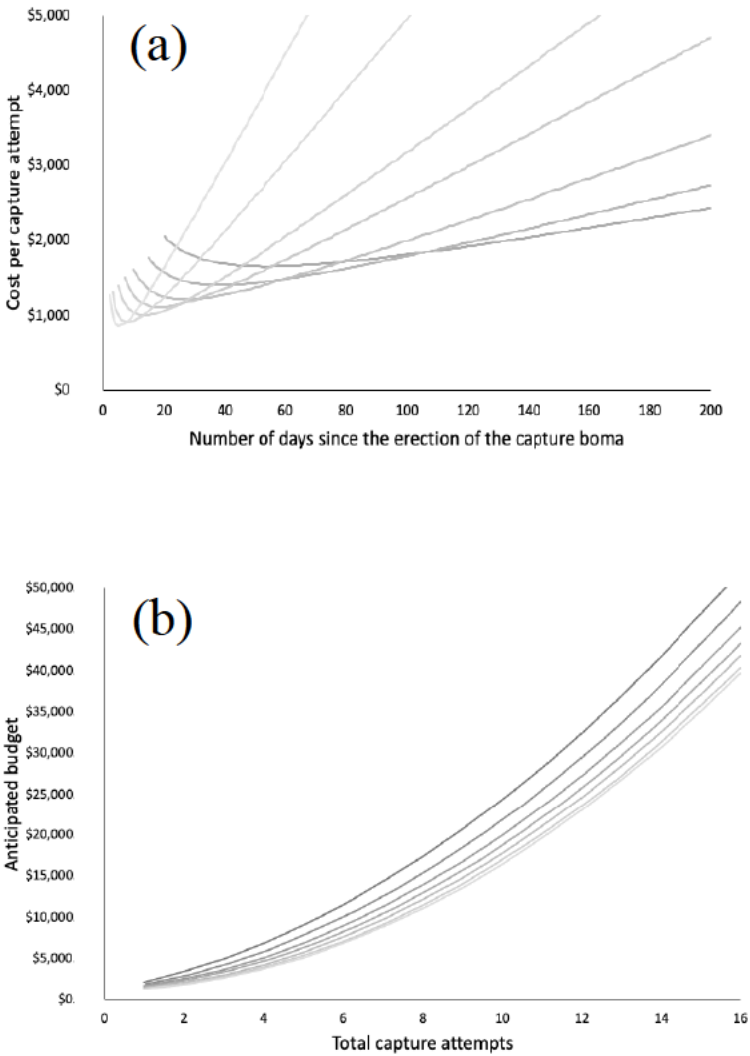

Figure 6.3. Hippo capture costs where a) is the predicted cost per capture attempt for various possible capture attempt rates (capture attempts/total days the boma has been erected), and b) the total budget required for the first 15 capture attempts using different capture attempt rates. This guide is based on average cost values experienced in periods of this study and can be used to help determine which capture attempt rate is most appropriate once the project timeline is established (once hippos are entering the capture boma, rendering capture attempts viable). These figures do not include veterinary and immobilisation costs. The capture rates shown from light to dark are 0.50, 0.33, 0.20, 0.15, 0.10, 0.07, 0.05.

6.5 Discussion

Modern capture methodologies for hippos require amelioration as they are dangerous, costly in terms of time and budget, and generally ineffective when compared with capture methods for other large African mammals. Before this study, there was no evidence of the possible application of A-H capture methods for hippos. Helicopter based capture methods were the cheapest and the most time and effort efficient method attempted in this study. These methods also present an adaptable strategy that can be used in dynamic conservation scenarios. Unlike other large African mammals of conservation importance like African elephants and black and white rhinoceros, there are no current, reliable capture methods for hippos that permit the targeting of individuals of interest, for instance, snared or injured animals to allow veterinary interventions. Currently, hippos requiring veterinary assistance are often culled because of the cost and dangers associated with the capture and immobilisation of the species. Although these methods resulted in the highest levels of capture related mortality, it is believed that these deaths were attributed to a combination of the capture team's unfamiliarity with the immobilisation drugs and lack of experience utilising A-H methods and therefore are believed to be avoidable going forward if the necessary recommended adaptations to the capture methods are enacted. It is also acknowledged that the success of A-H based captures may be dependent on the characteristics of the system and the structure and distribution of the hippo population on which they are implemented. These methods were only proven to be effective when attempted on isolated individuals and small pods in systems that are either seasonally or perpetually deprived of deep and expansive aquatic habitat, as was present in the shallow pools in reduced flow in the Olifants system, and will be less effective or ineffective in systems with sprawling, deep bodies of water, i.e. lake or large impoundment systems where it

is unlikely that hippos will be coaxed out of aquatic refugia. There may be potential for application in small impoundment systems, shallow ephemeral wetlands, shallow expansive lake systems, and particularly in systems with few hippos and those without crocodiles that could permit capture and processing in aquatic habitat. In addition, these methods were limited in the demographic of the hippos that we captured, where no opportunities to capture females or dominant male hippos were realised.

Active capture methods using a bait station were only attempted once but were also efficient and successful. Future experimentation using A-BS methods to permit captures on hippo populations that are less habituated to people may permit more widespread acceptance of the viability of A-BS capture-based methods. These methods may be applicable if bait sites are situated far from wading locations, and captures take place late at night when hippos visit secluded baited areas. This will also require that bait sites are in open areas that permit vehicles to access and subsequently herd targeted hippos.

Passive capture methods are the most common and universally used method for hippo capture, although capture attempts are generally limited. These methods offer the opportunity to capture several individuals simultaneously but are subject to high levels of uncertainty as they are dependent on the habituation and subsequent timing (within the project timeline) of the visitation of hippos at the capture sites. Although the effectiveness of these methods was not realised as part of this study, evidence of the success of P-B methods exists from game capture and veterinary professionals that make part of highly respected and knowledgeable conservation organisations like SANParks and Ezemvelo KwaZulu-Natal Wildlife (EKZNW). In addition, different adaptations of hippo capture boma structure, as is seen in spring trap versions or large wooden bomas, would yield different rates of capture success. Boma based capture methods are more

accessible to African conservation entities that do not have access to helicopters. This study has produced a guideline to determine the best possible capture attempt rate to be used, depending on the budget available, once hippos are feeding at capture sites and opportunities for capture are presented. In light of budgetary limitations of conservation efforts across sub-Saharan Africa, these guidelines should present cost savings for entities that employ passive capture methodologies. Future studies that utilise P-B methods should ensure they are adequately equipped with available technology that would curb issues of capture site disturbance and efficient and error-proof detection of capture opportunities. These would include remote detection of hippos inside the boma with infrared camera traps with Wi-Fi capabilities or a Wi-Fi or cell phone network-based surveillance system. In addition to these, the ability to quickly and remotely close the capture boma with a remotely deployed guillotine door would also be very valuable.

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Conflict of interest

The authors declare they have no conflict of interest.

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CHAPTER 7

Various neighbouring community impacts on the Phongolo Floodplain at Ndumo Game Reserve, South Africa

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Running header: Human-wildlife conflict at a Ramsar site

7.1 Abstract

In the last 200 years following severe depletion of wildlife populations because of hunting, the vast majority of large mammal species remaining in South Africa are restricted to fenced protected areas and game farms. By 2060, sub-Saharan Africa is predicted to experience the largest increases in human population numbers of any other region globally. If these increases are realised, the species in the region will incur the greatest increases in extinction risk of any other species in any other region in the world, of which large- and medium-sized mammals are the most susceptible. Ndumo Game Reserve (NGR) is an Ezemvelo KZN Wildlife (EKZNW) managed protected area with target species for conservation like hippopotamus *Hippopotamus amphibius* (hereafter hippo), and until recently, white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceros. Land claim issues between EKZNW and neighbouring communities have instigated the removal of NGR's eastern boundary fence by community members in 2008 and again in 2011. Community encroachment issues have followed along with increased instances of illegal activity, including poaching and deforestation. During a 1-year monthly survey of the hippo population at NGR, our camera-trap data and unmanned aerial vehicle (UAV) footage opportunistically documented illegal activity in NGR. We collated and summarised these data here, along with encountered snares and run-ins with poachers while walking in NGR. We found repeated instances of hippo and other wildlife snaring and poaching, thus impacting NGR as a conservation area. Post-apartheid government initiatives have failed to reconcile differences between South Africa's internationally renowned protected areas and neighbouring impoverished black rural communities. This has ultimately caused negative impacts on and mismanagement of, in this case, a Ramsar site and one of South Africa's most biodiverse wetlands areas in NGR.

Keywords: human-wildlife conflict, habitat loss, illegal hunting, large mammal conservation, conservation in developing countries in Africa

7.2 Introduction

Unprecedented human expansion across the globe has created increased competition for space between people and wildlife (Cardillo et al. 2004; Jetz et al. 2007; Steffen et al. 2007; Mawdsley 2009; Tilman et al. 2017). Today, the global human population is estimated at over seven billion and projected to increase by almost three billion by 2060 (Tilman et al. 2017). Sub-Saharan countries in Africa are anticipated to experience the greatest population increases of any other region globally (1.7 billion by 2060) (Tilman et al. 2017). Human population expansions correlate with increases in overall land consumption and transformation (Krummel et al. 1987; Foley et al. 2005; Tilman et al. 2017). If human population growth projections in sub-Saharan countries are realised, an estimated 430 million ha of additional land will be transformed to sustain the human population (Tilman et al. 2017). Decreases in size, patching, and overall declines in natural habitat are projected to cause widespread threats to biodiversity in the region (Tilman et al., 2017; Fahrig, 2019). These effects are disproportionately real for large- and medium-sized mammals that because of their increased size and subsequent elevated resource requirements, are more susceptible to accelerated change and are predicted to rise 1.5-2 Red List Categories on average by 2060 (Tilman et al. 2017).

Conservation of natural systems is important for the persistence of all taxa including humans (Bolund & Hunhammar, 1999; Chan et al., 2006; Worm et al., 2006; Costanza et al., 2014). Humans grow increasingly distant from the sources of their consumption, yet remain entirely dependent on natural resources for subsistence (Butchart et al. 2010; Nyaki et al. 2014).

The impacts of localised natural resource dependence are particularly apparent around disadvantaged communities in Africa that, because of their impoverished status, are reliant on informal economies built the localised resource utilisation in the form of subsistence agriculture and livestock farming, hunting, and foraging (Gandiwa et al., 2013; Barnes et al., 2016; Diouf et al., 2020). Conservation entities in Africa are tasked with managing and monitoring the ecological components of protected natural systems and are increasingly required to highlight their socio-ecological value to mitigate increased human and climactically induced resource threats (Sinclair and Walker, 2003; Rogers et al., 2016; Nel et al., 2017). Along with low GDP per capita and political instability across the majority of Africa, widespread natural system deterioration outside of protected areas has intensified the close association between natural resources in protected areas and disadvantaged communities, increasing the risk of unsustainable natural resource exploitation in the form of illegal activities (i.e. illegal hunting and harvesting, poaching, and deforestation) inside protected areas (Meer and Schnurr 2013; Nyaki et al. 2014; Tilman et al. 2017).

Human-wildlife conflict impacts are expanding in many parts of the world, especially in impoverished areas (van Velden et al., 2018). However, the effects of wildlife consumption and trade are understudied. Protected areas in South Africa and the species occurring within them have become particularly susceptible to human and wildlife conflict since the intervention of colonialisation and the recent degeneration of apartheid (Tapela & Omara-Ojungu, 1999; Picard, 2003; Warchol & Johnson, 2009; Meer & Schnurr, 2013). Therefore, additional research detailing the depth of the dependence of people on wildlife and wild areas will contribute to a greater understanding of how to mediate and present alternatives to illegal wildlife and natural resources consumption. In addition, more research on the extent of anthropogenic impacts on different species will contribute to the future management of human impacts on wild populations.

Ndumo Game Reserve (NGR), South Africa, was founded as a common hippopotamus *Hippopotamus amphibius* (hereafter hippo) sanctuary in 1924. It is one of South Africa's oldest game reserves (Meer and Schnurr 2013; Calverley and Downs 2017). Continued disagreement over land rights has had severe implications for the present success and continued future value of NGR as a conservation area (Meer and Schnurr 2013, Calverley and Downs 2017). The aim of this study was to recount the types and distribution of human impacts encountered during Aug 2016 - July 2017 in NGR, and to use these data to understand the drivers of human encroachment in NGR to inform future mitigation of threats to hippos and other wildlife.

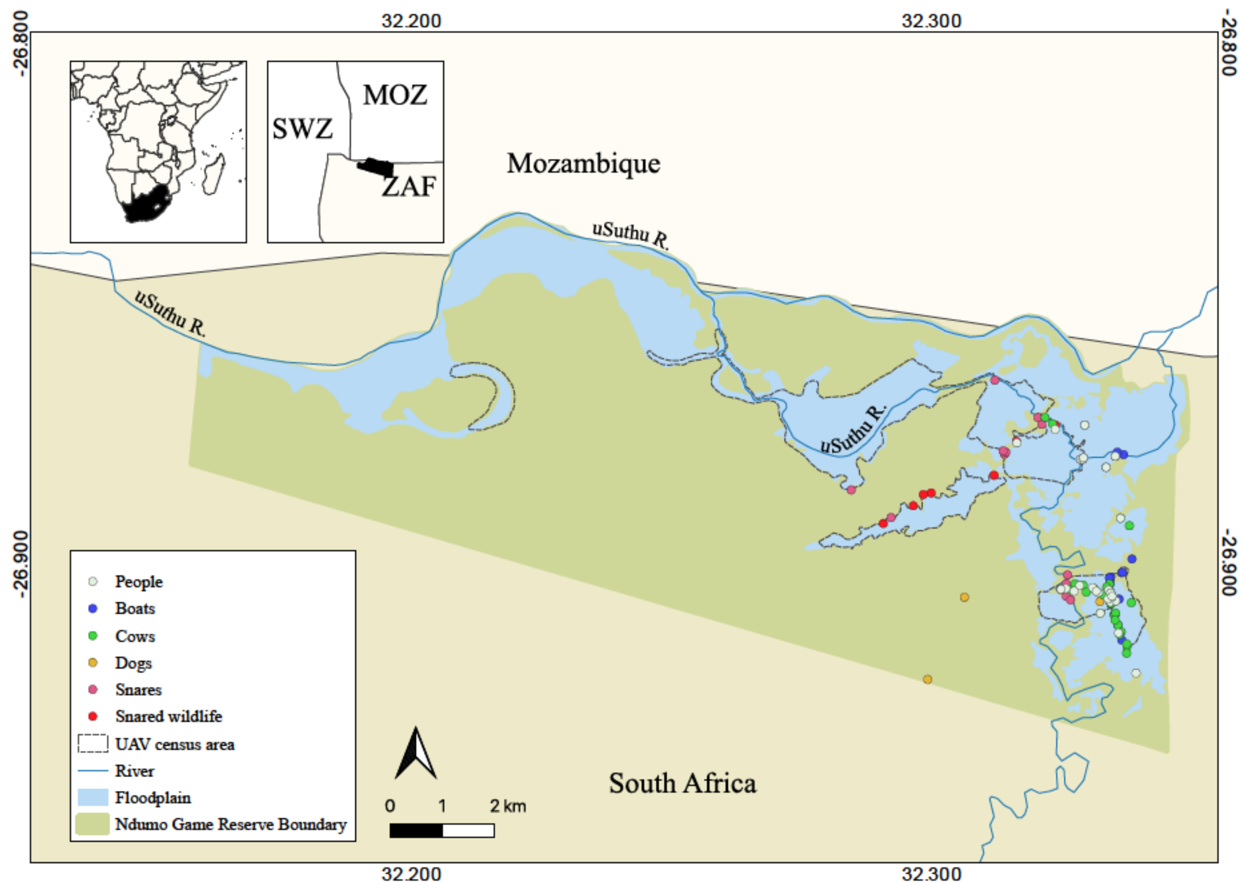

Figure 7.1 A map of Ndumo Game Reserve (NGR), South Africa, showing the locations of all encountered evidence of community encroachment and poaching seen during yearlong survey from 2016-2017. (Red dots depict the locations where camera-trap footage of poachers and snared hippo were taken; purple dots depict the locations of snares and poachers encountered while on foot; blue dots depict UAV footage taken of farming, deforestation, people, boats, fishing nets, and livestock in the NGR).

7.3 Methods

7.3.1 Study site description

NGR is a Ramsar site (Ramsar site No. 887) situated along South Africa's northern border with Mozambique in a predominantly rural region of Maputaland, South Africa (Fig. 7.1). The reserve covers approximately 10,000 ha and contains biologically rich wetlands. These wetlands host South Africa's third-largest hippopotamus population, the densest Nile crocodile *Crocodylus niloticus* population in South Africa and South Africa's densest avifaunal diversity (Pooley 1982; Meer and Schnurr 2013; Calverley and Downs 2014, 2017). NGR has two major river systems in the Phongolo and uSuthu Rivers, as well as 12 associated pans and lakes (Calverley & Downs, 2014a). The old uSuthu River channel runs from west to east forming NGR's unfenced northern boundary with Mozambique. However, damming of the river upstream has caused an alteration of flow and created the new uSuthu River channel (2000), which runs through NGR and eventually joins the Phongolo River in the north-eastern corner of NGR (Calverley & Downs, 2014a, 2014b). The Phongolo River, one of South Africa's most species-rich river systems, runs from south to north in the eastern half of NGR. Outside of the wet season, 15% of NGR's surface area is covered by water; however, flooding of the river systems and their associated floodplains can inundate approximately 40% of the reserve (Fig. 7.1). The wetland areas are concentrated in the north-eastern corner of NGR where the old uSuthu River channel no longer suffices as a boundary, and people and fauna can move in and out of NGR (Meer & Schnurr, 2013; Calverley & Downs, 2014a, 2014b, 2017). No additional fencing has been put in place although altered flows have exhausted the uSuthu River's role as a reserve boundary (pers. obs.). In addition, NGR's eastern boundary was removed in 2008 by neighbouring communities who wanted access to the Phongolo floodplain in the eastern half of NGR. In 2011 an attempt was made to reinstate the border fence; however, it was removed again within three days (Meer & Schnurr, 2013; pers. comm. C. Hanekom)

7.3.2 Political and social history of NGR

Following the establishment of NGR in 1924 the reserve was still accessible to local community members who relied on its resources like water, fish, game, medicinal plants, wild fruit, and reeds (Hanekom, 2016). However, in the 1950's, all community residents within NGR were forcefully evicted, and severe fines were imposed to discourage further hunting and resource collection within NGR (Meer & Schnurr, 2013). The majority of the evicted residents settled along the periphery of NGR where they built houses and prepared fields for cultivation, although the sandy soils outside of the floodplain were far less productive (Hanekom, 2016; pers. obs.). Following the dissipation of apartheid in 1994, the first community members began to seek restitution in 1995 with the Department of Land Affairs (Meer & Schnurr, 2013; Hanekom, 2016). In 2000 the local communities around NGR and the government reached an agreement. This allowed access to part of the north-eastern corner of NGR to community members and provided compensation in the form of ZAR10,000 (~$1 000) per household. However, this agreement was soon discarded, and compensation halved (R5,000 or ~$500) after both national and international furore caused a reconsideration of the claim as it threatened the Ramsar status that NGR was proclaimed 1997 (Meer & Schnurr, 2013; Hanekom, 2016). An additional land claim was made in 1995 by a different community, which ended in the joint venture between the claiming community and an international safari company called Wilderness Safaris (Meer & Schnurr, 2013; Hanekom, 2016). This venture intended to create a profit-making safari lodge along the uSuthu River within NGR whose profits would provide monetary compensation to the claiming community without relinquishing any land. The community did not support the venture and instead wanted access to plots of land to cultivate and hunting rights within NGR. The venture ultimately lasted from 1995-2004 and failed to turn a profit in any single year, ultimately costing Wilderness Safaris at least

ZAR5 million ($500,000). No further compensation was made to the claiming community even after the venture failed. In 2008 the local communities removed the NGR eastern boundary fence to bring attention to their claims. In 2011 they again removed the fence when management attempted to reinstate the boundary (Meer & Schnurr, 2013; Hanekom, 2016). EKZNW now have to mediate issues with the rural communities and have hired representatives from Peace Parks to try and identify alternative cultivation areas and alternative cultivation practices that would allow the communities to continue subsistence farming while limiting their impacts on NGR (Meer & Schnurr, 2013; Hanekom, 2016). These findings have not yet been published (Meer & Schnurr, 2013; Hanekom, 2016).

Following the destruction of the NGR eastern boundary in 2008, community members gained access to the floodplains inside (Meer & Schnurr, 2013; Hanekom, 2016). In 2009, 3.5 ha of the floodplain had been cultivated, by 2015, approximately 640 ha were cultivated, and cultivation and deforestation continue in NGR to the present (Hanekom, 2016; CF pers. obs.). In 2015, a total of 716 head of cattle and 39 goats were counted along the Phongolo floodplain inside NGR during the annual helicopter-based census (Hanekom, 2016). Livestock grazing has facilitated bush encroachment of the grazing area on the Phongolo flood plain (Hanekom, 2016). Hardwood collection has spread west of the Phongolo River, and cultivation and snaring continue to spread west inside NGR (CF pers. obs.). Hunting of antelope is an ongoing issue; however, the focus of EKZNW has been to eliminate the poaching risk of target species for conservation like hippo and white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceros (hereafter rhino). The black rhino population in NGR was 57 individuals in 1989; however, presently, none remain in NGR after the last solitary black rhino, and five white rhino were removed from the reserve in 2017 because of high poaching risk (Hanekom, 2016; pers. obs.).

7.3.3 UAV data collection

We conducted a yearlong UAV survey estimating hippo population numbers at NGR, beginning in August 2016 and concluding in July 2017. We conducted surveys four times each month for the entire year with the exception of May, when only three surveys were conducted. Eight survey locations were covered across the predominant water bodies in NGR (Fritsch & Downs, 2020); Chapters 2 and 3). A DJI Phantom 3 Standard Drone (2.7 K Camera; 3-Axis Gimbal; capacity for shooting 12 megapixel JPEG files; a 1/2.3" sensor, fast f/2.8 prime lens; a preset focus optimised for aerial images; and battery life of up to 22 min was used as part of the UAV surveys (Fritsch & Downs, 2020; Chapters 2 and 3). We made an effort to photograph any evidence of community encroachment or poaching while conducting aerial surveys. We separated images containing evidence of community encroachment, geo-location of each such image and then mapped the locations in QGIS 2.8 (QGIS Geographic Information System. Open Source Geospatial Foundation Project, www.qgis.osgeo.org). We provided the images and their exact locations to the NGR management staff for management purposes. Additional details on the UAV census methods used in this study can be found in Fritsch and Downs (2020).

7.3.4 Camera trap data collection

We placed single camera-traps (n = 13; Moultrie M-888, Calera, AL) along hippo paths at five different locations in NGR to identify seasonal changes in hippo wading and grazing times. We identified camera-trap locations based on their proximity to frequented hippo wading areas and based on evidence of freshness of the paths, e.g. freshness of dung and spore (CF pers. obs.). We also took into account the risk of equipment being broken or stolen by local poachers. Camera-

traps were attached to nearby trees at various heights between 0.5-2 m to capture imagery of hippos that could be used to identify individuals. We set camera-traps on ‘motion detect’ at ‘low’ sensitivity to capture only relevant imagery. Camera-traps collected both photographs and video footage. We separated camera-trap images containing evidence of poaching, e.g. poachers or snared wildlife, or community encroachment, with the associated date, time and global position system (GPS) locations recorded. We provided copies of these to the NGR management staff.

7.3.5 Other methods of collection of evidence of poaching and community encroachment

We took photographs of evidence of poaching and community encroachment when encountered while driving or walking through NGR during the one-year survey period between August 2016 and July 2017 for hippo research (Chapters 2 and 3). We usually took photographs using an iPhone 6-camera phone with the primary 8 MP (f/2.2, 29mm, 1/3", 1.5µm) camera. When necessary, photographs were taken from a distance using a Canon 1300D digital camera. We then geolocated the photographs taken using either camera type. All date, time and location information were recorded, and copies given to NGR management staff.

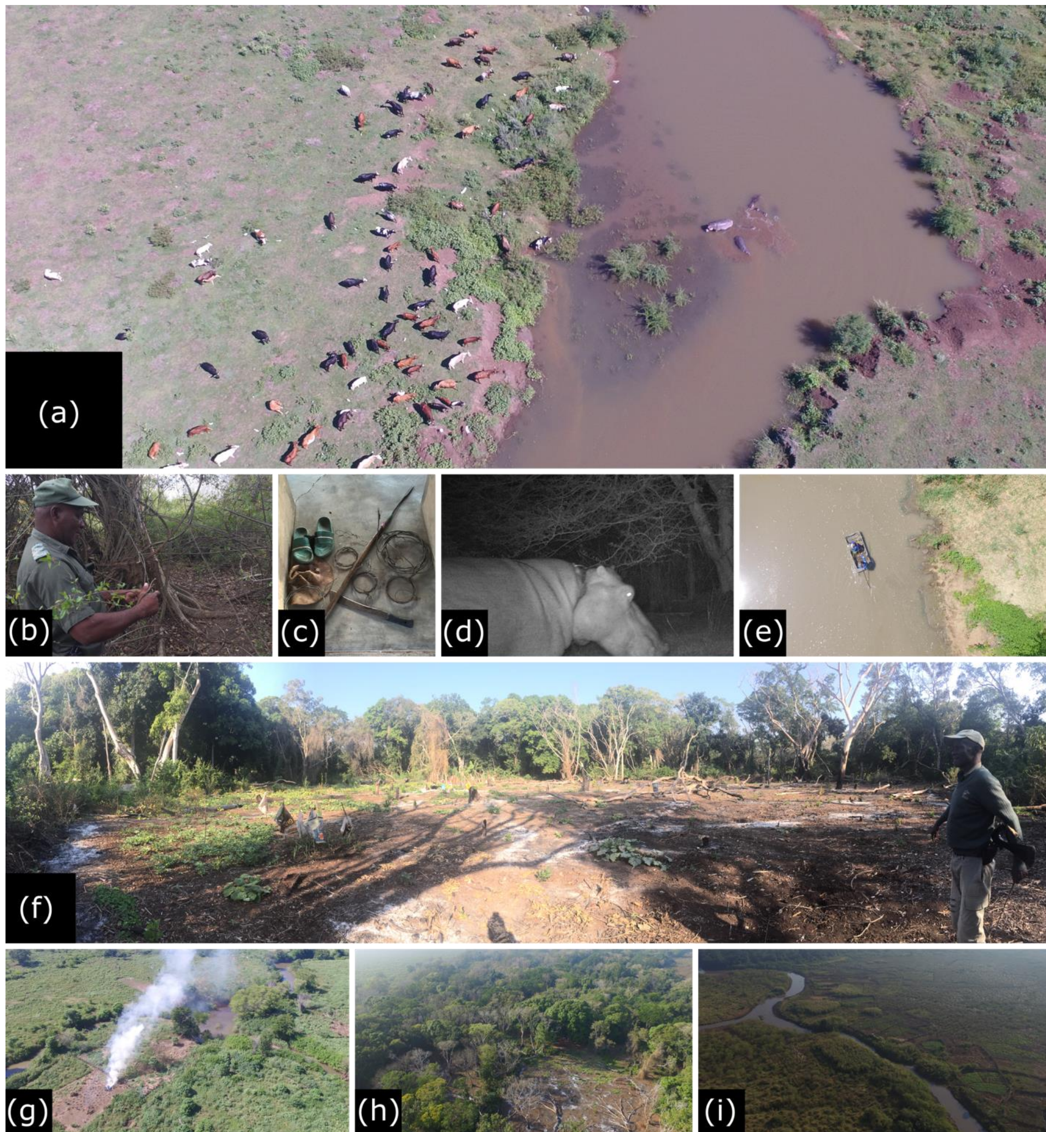

Figure 7.2 A selection of photographs obtained during the present study showing the impact of the neighbouring human communities on NGR where a) is a camera-trap photograph of a snared hippo at Nyamithi; b) confiscated gear from an encountered poacher; c) a poached male Nyala *Tragelaphus angasii* found inland of Pholwe; d) hippos competing for space with grazing cattle at Pholwe; and e) exemplified deforestation near Pholwe in NGR.

7.4 Results

From August 2016 – July 2017, we conducted a total of 362 UAV flights, accounting for 1,367 km of total flight distance and over 53 h of total flight time (excluding four censuses conducted in January 2017 as these flight records were lost). Camera-traps were set for a total of 2,311 camera trap nights during the same period.

Using the UAV, a total of 66 photographs were captured of encounters with people (n = 20; 49 people), livestock (n = 32; 1197 cows), fishing boats (n = 37), and dogs (n = 1; 4 dogs) within the boundaries of NGR. Additional photographs were captured of permanent structures like forest and bush burning and clearing, farmland, and cattle corrals. Across the camera-trap imagery, a total of five encounters were recorded including people (n = 2; 3 people) and snared hippos (n = 3). An additional 27 encounters took place on foot (n = 8; 10 people), cattle (n = 5; 73 cows), dogs (n = 2; 2 dogs), snared wildlife (n = 4), and snares (n = 16). All encounters occurred in the eastern side of NGR and were concentrated along the Phongolo River and associated floodplain, although additional impacts likely took place in other parts of NGR, particularly poaching, as at least eight rhino were poached during the study period, many of which were known to use the Sand and Matakini clay forests in the central and western portions of NGR (Fig. 7.1).

Fishers were observed predominantly using gill nets, which they set from a boat; however, instances of seine-netting and line-fishing were also recorded (Fig. 7.2e). A maximum of six different boats was observed in a single UAV census. These were either docked on the side of the river or were being used by the fishers. Boats also appeared to be used to ferry across the river or the floodplain when there was increased inundation. Cattle were seen on 53% of the 47 UAV surveys conducted and were encountered at least once in 11 of the 12 survey months (Fig. 7.2a). The total number of cows detected in a single UAV survey ranged from 1-172 cows. Cattle were

concentrated in the floodplain grasslands along the Phongolo River where they used the grazing resources. The most apparent and widespread human impacts in NGR were the clearing and burning of floodplain grasslands and peripheral forests and their subsequent transformation into agricultural plots (Fig. 7.2f-i). The Phongolo River was depended on as the sole source of crop irrigation, and therefore agrarian plots were densely grouped together along the river with the largest plots covering ~5,000 m^2. Some plot groupings accounted for more than 700,000 m^2 of transformed land area inside NGR. Most of these areas became inundated when the Phongolo River swelled and flooded the floodplain in the wet summer months (November 2016-February 2017). The anthropogenically transformed land area in NGR was observed to be expanding through the study period.

People were observed taking part in various activities in NGR during the study period including hunting ($n = 4$; 5 people), poaching ($n = 1$; 2 people), fishing ($n = 8$; 11 people), livestock herding ($n = 5$; 8 people), farming ($n = 2$; 4 people), burning and clearing ($n = 2$; 5 people), and washing laundry ($n = 2$; 8 people). Active hunting methods encountered during the day included using dogs, small calibre rifles, and spears and generally targeted bird and antelope species. Passive capture methods (snares) appeared to target antelope and included thicker wire snares fastened to large trees designed to capture hippos (Fig. 7.2b-d). We found snares were mostly set in forested habitats on the periphery of the floodplain. However, some were also set in reed-thickets on the floodplain. Poaching activities documented by the camera-traps only took place at night. Armed poachers were identified based on the high calibre rifles they carried, which they used to kill black and white rhinos to collect their horns.

7.5 Discussion

Various anthropogenic ecosystem impacts, including landscape transformation, the erection of semi-permanent structures, and human and livestock activities, were documented inside NGR during the study period. The people using these areas appeared to be gathering resources required for their subsistence; however, these activities were also observed to impede conservation efforts inside NGR significantly. The observed impacts were mainly concentrated along the Phongolo River's floodplain grasslands and peripheral forests inside the protected area boundary, where they impacted the biodiversity and brought into question the future of NGR's distinction as an internationally important wetland area and Ramsar site.

The root of the human use of NGR's wetland areas by the disadvantaged communities on the periphery of the park appears to extend from the community members needs to fulfil their basic human resource requirements like gaining access to food and water. Economic hardship has previously been linked to increased illegal and unsustainable use of natural resources in protected areas globally, with many studies already conducted in African savanna and forest ecosystems types (Gandiwa et al., 2013; Rija et al., 2020). Of the communities surrounding NGR, more than 70% of the population survives on less than R800/month (~$80) provided by government grants and a small informal economy (Meer and Schnurr 2013). Community members have access to minimal infrastructure: 80% of the population is without electricity, 76% are without piped water, and 92% without municipal waste removal (Meer and Schnurr 2013). The population within the communities is predominately young as ~70% of its members are under the age of 18 (Meer and Schnurr 2013). Land demand associated with a growing human population, a high unemployment rate and political insecurity form the foundation of a broader spectrum of issues outside of protected areas that are affecting the management of conservation areas in South Africa today

(Tapela and Omara-Ojungu 1999; Picard 2003; Warchol and Johnson 2009; Meer and Schnurr 2013). However, the majority of these issues are rooted in the wake of South Africa's recovery from the apartheid regime (1948-1994)(Meer and Schnurr 2013). Many protected areas in South Africa were created to protect species prized by colonial hunters and historically focused on the exclusion of black South Africans (Meer and Schnurr 2013). These protected areas have since become national or provincial parks attracting international tourists. The associative disdain left in the collapse of apartheid, along with the continued alienation of neighbouring communities from the monetary benefits generated by the protected areas, has caused continued disagreements between conservation area managers and the communities neighbouring these protected areas (Picard, 2003; Meer & Schnurr, 2013; Dell et al., 2020). The perspective of the overwhelming rural black majority in South Africa is changing because of changes made by the national parks through the abolition of 'protect and conserve' and the adoption of 'stewardship and sustainable use' conservation strategies and increased conservation education. However, the reality is that the overwhelming majority remain undernourished and without work, and therefore do not consider the importance of the conservation of biodiversity in the short-term (Picard 2003; Warchol and Johnson 2009; Meer and Schnurr 2013).

Anthropogenic activities in NGR present several threats to wildlife. Direct exploitation of the wildlife for bushmeat or as a result of poaching activities decreases wildlife population size, particularly if harvested at unmonitored, unsustainable yields. Growing industries like the bushmeat trade, hunting industry, and black-market poaching industry are having potentially the largest impact on wildlife species in Africa (Carpaneto et al., 2007; Tilman et al., 2017; van Velden et al., 2018). The majority of these issues are particularly difficult to address as they are related directly to extreme poverty where bushmeat is a source of protein and the trade of animal parts

provides a source of income (van Velden et al., 2018). Hunting and use of wild game sometimes form part of cultural ceremonies and beliefs that have been passed down for generations, and therefore controlling the ceremonious use of wildlife is relatively difficult, especially as human populations spread and impacts expand (van Velden et al., 2018). The exploitation and consumption of wild game have only recently become a subject of extensive research with 92% of research taking place since 2000 (van Velden et al., 2018). The recent increase in research showing the extent of human consumption of wild game and the impact it has on wildlife populations highlights the need for additional research on the subject, especially in impoverished areas with high biodiversity and species of conservation focus.

The clearing, transformation and exclusion of wildlife from natural habitat for the purposes of farming has significantly reduced the habitat and resources available to wildlife in NGR. An increase of 636.5 ha of transformed land between 2009 and 2017, accounting for nearly 1% (.07%) of NGR (Hanekom, 2016). In addition, the burning and clearing of riverine forest habitats have likely reduced localised bushmeat yields and lead to increased disturbance further into NGR where the forest habitat remains intact. Farming practices involve the use of banned pesticides and other chemicals out of a need to increase crop yields which impact aquatic biodiversity and ecological processes (Acosta et al., 2020). In addition, the abstraction of water from the river affects the flow and discharge of the river, impacting river connectivity (Arnell & Gosling, 2016; Vezi et al., 2020; Acosta et al., 2020). The impacts of agriculture farming are more apparent upstream of NGR along the Phongolo River in the Jozini area, where subsistence farming practices expanded to industrial crop and sugarcane farming before a demand reduction has caused these communities to struggle financially (CF pers. obs.). These farms developed high water demand and used petrol-powered water pumps with outputs of 600 l/min (CF pers. obs.). Hippo, crocodile, and fish populations

along these stretches of the river have reduced or gone locally extinct and may provide indications of future wildlife and fisheries trends within NGR with increased reliance on agriculture in the floodplains (Calverley & Downs, 2014b, 2017; Acosta et al., 2020).

Increases in the number of livestock using the grazing areas in the Phongolo floodplain creates grazing resource pressure for wildlife in NGR. In addition to the direct consumptive-derived competition, pastoral pastures are structurally homogenous and are less grass species rich, and therefore can be used by a decreased number of species. The Phongolo River in NGR hosts the densest numbers of hippo in NGR, largely because of the favourable grazing available in the floodplain alluvial soils (Chapter 3 and 4). Wildlife population die-off events are often caused by cyclical fluctuations in resource availability (Young, 1994; Smit et al., 2020). Therefore, seasonal, annual, or decadal changes in the availability of grazing resources will have detrimental impacts on wildlife carrying capacity in NGR. Hippo population numbers in NGR have recently declined, and although hunting has played a role, the dramatic decline of over 60% in the last 5 years is likely because of wading and grazing resource depletion (Chapter 3 and 4).

The anthropogenic transformative impacts inside NGR are exacerbated by others upstream and outside NGR. Ndumo Game Reserve is a small protected area in an otherwise anthropogenically modified landscape. Unsustainable clearing of forest for wood, the transformation of the landscape for agriculture, overgrazing by domestic livestock, and consumption of bushmeat directly outside of NGR has increased the value of natural resources inside the protected area for people and wildlife (CF pers. obs.). Alterations in the timing, quality, and quantity of river flow following the damming of the Phongolo River at Jozini (Phongoloport Dam) in 1973 has altered the spatio-temporal heterogeneity of floodplain communities, impacting ecosystem services. These anthropogenic induced impacts, in combination with climatic effects

like alterations in rainfall patterns and increases in temperature, put increased pressure on fragmented natural systems (Shekede et al., 2016; Fahrig, 2019).

The future management and protection of NGR are jeopardised without compensation allocated to neighbouring communities or alternative livelihoods developed. Ultimately, the dependence of the growing human population surrounding NGR on farming practices in the floodplain is unsustainable. There are several needs that need to be addressed, including involving communities in conservation; highlighting the ecosystem services provided by natural systems to these communities; establishing sustainable yields; decrease reliance on economically driven unsustainable resource abstraction, and develop an understanding of the drivers of human population increases around NGR. All these require mitigation with, at the very least, access to basic human needs like food, freshwater, ablutions, and electricity and possibly further through increased access to education and employment to improve overall livelihoods. Community-based natural resource management (CBNRM) programs have been adopted across the world in an effort to minimise the damage to protected and conservation areas while also alleviating gaps in compensation incurred by communities (Dressler et al. 2010; Cornelissen 2017). Serious considerations need to be made for quality compensation for the neighbouring communities around NGR before further negative impacts on its biodiversity are incurred, and its status as a protected area of international importance is reduced.

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CHAPTER 8

CONCLUSIONS

8.1 Background

The unprecedented accelerated effects of climate change and the direct and indirect associative impacts of the expansion of anthropogenic landscape modification threaten conservation efforts globally (Butchart et al. 2010; Rands et al. 2010; Tilman et al. 2017). Projected human population increases in sub-Saharan Africa (1.7 billion people by 2060) in the context of current political instability and a low global GDP per capita in the region will create exceptional challenges for conservation (Tilman et al. 2017). Freshwater systems are amongst the most threatened as increasing human populations will also come increasing water-resource dependency, particularly because of recent shifts in the spatiotemporal distribution of freshwater resources (Moss 2015, Rodell et al. 2018, Grantham et al. 2019).

The common hippopotamus (*Hippopotamus amphibius*) (hereafter hippo) is one of Africa's most iconic and socio-ecologically influential large mammal species. Historically hippos occupied many of the lentic and lotic habitats across Africa (Eksteen et al. 2016, Lewison & Pluhacek 2017). Today, habitat loss (aquatic habitat in particular), unsustainable hunting practices, human-wildlife conflict, and a lack of management and monitoring data have more or less confined hippo populations to patchily distributed remote and protected areas (Eksteen et al. 2016, Lewison & Pluhacek 2017). Recent global population estimates of hippo are between 125,000-148,000 individuals (Eksteen et al. 2016, Lewison & Pluhacek 2017). The largest hippo populations in South Africa occur in Kruger National Park (KNP; 3,500-5,000), iSimangaliso Wetland Park

(iSWP; 800-1,000) and Ndumo Game Reserve (NGR; 200-300) (Eksteen et al. 2016, Lewison & Pluhacek 2017).

Hippos bring value to the hunting and tourism industries and are ecological engineers on land and in freshwater. However, historically, research on hippo behavioural ecology has been limited, particularly in comparison to other African large mammal species (Eksteen et al. 2016, Lewison & Pluhacek 2017; Chapter 1, Supplementary information Table 1.1). Hippos facilitate foraging for other grazing species by creating functionally diverse grazing lawns, and their allochthonous inputs in aquatic systems are used by micro-and macroinvertebrates and fish (Field 1970, Subalusky et al. 2014, McCauley et al. 2015, Schoelynck et al. 2019, Voysey et al. 2020). However, hippo ecology shines in a different light in the context of anthropogenically driven environmental change. Landscape fragmentation and the concentration of hippo populations in patchy conservation areas has led to inter- and intra-species grazing competition and overgrazing of grazing pastures (Field 1970, Smuts & Whyte 1981, Payne 2004, Kanga et al. 2013, McCauley et al. 2018, Voysey et al. 2020). In addition, hippo inputs in aquatic systems that are unable to dilute hippo inputs because of reduced water quality and quantity can cause shifts in aquatic food webs; reducing biodiversity, and catalyse eutrophication of freshwater resources that cause fish population die-offs (Dawson et al. 2016, 2020a, b, Stears et al. 2018, Dutton et al. 2018). Freshwater resources and fish play a pivotal role in the subsistence of impoverished communities; therefore balancing the socio-economic needs of people and the ecological requirements of nature will be the next great challenge for the conservation of hippos in the developing world in Africa (Dube et al. 2015, Acosta et al. 2020).

8.2 Research findings

8.2.1 Hippo behavioural ecology

Over the past 5 years, we have investigated a number of aspects of hippo behaviour across populations in NGR and KNP to elucidate the drivers of population trends and to understand how individual behaviour and population structure shape the hippo's role as an ecological engineer (Chapters 3-4,6). In addition, we explored alternative methods for collecting management and monitoring data, including the use of unmanned aerial vehicles (UAVs) in population censuses, compared the cost, effort, and success of several hippo capture methods, and built on novel GPS telemetry methods for hippos (Chapters 2, 5-6). These methods were explored with the aim of increasing access of resource-deprived conservation organisations in Africa to management tools that would permit the collection of additional hippo population monitoring data. Lastly, our aim was to understand aspects of human-hippo conflict and the threats they pose to natural systems with hippos within the modern climate and anthropogenic impacts (Chapter 7).

Recent research from the Ruaha River in Tanzania provided a first look into hippo space use in a seasonal river system (Stears et al. 2019). We built on these findings in a perennial river system in the Olifants River in KNP, South Africa (Chapter 6). Compared with other large mammals like African elephant (*Loxodonta africana*) that occupy much larger home ranges ($n > 3000\ km^2$), our findings suggest that hippos occupy mean home ranges sizes of $6\ km^2$. From the data we collected, we can see that hippo space use is almost entirely limited to aquatic systems and closely associated grazing pastures ($n < 5km$). Our data also revealed that, on average, hippos spend roughly 18/24 hours wading. We can also see that space use patterns between individuals occupying different levels of social status (dominant males vs sub-dominant males), and between individuals inhabiting different system types (seasonal rivers, perennial rivers, and impoundment

systems) differ. In addition, our findings showed that individual space use changes seasonally in response to the spatiotemporal distribution of wading and grazing resources and mating cues. These findings support previous research on the reliance of hippos suitable aquatic wading habitat and undisturbed associated grazing areas (Lewison & Carter 2004, Chansa et al. 2011, Stears et al. 2019).

Building on our findings of individual space-use, we used monthly population census data (Aug 2016- July 2017) to identify population-level changes in distribution in response to inundation area in the Phongolo and uSuthu Rivers and associated seasonal floodplains in NGR (Chapter 3). Through the study period, we identified different pod structures present within the population, including solitary males, small family groups, and large nursery pods. During periods of low inundation, hippos congregated in perennial wading areas, forming amalgamations of several smaller groups creating nursery pods, increasing overall individual and pod density and increasing pod size (Chapter 3). Previous studies have detailed the added direct and indirect inter- and intraspecies stress associated with these seasonal population concentrations and their role in regulating hippo population numbers (Pienaar et al. 1966, Sayer & Rakha 1974, Marshall & Sayer 1976, Smuts & Whyte 1981). As the inundation area increased, we saw hippos disseminate across the landscape into smaller pods. Because NGR is an open system, we also saw a decrease in abundance as hippos distributed to areas on the floodplain outside NGR. These expansions in dispersal coincided with aspects of hippo biology, like reproduction, where females were able to find solitude when giving birth to their young. As a result of our findings, we can see that the availability of wading habitat determines the monthly distribution of hippos and that aspects of hippo reproductive biology coincide with cyclical changes in river flow and ultimately play a role in determining population dynamics. These seasonal inundation-area driven changes in population

distribution and structure also determined the distribution of hippo ecology across the landscape where dense groupings of hippos in the dry season concentrated their ecological impacts in terrestrial and aquatic environments.

To understand the drivers of hippo population trends across NGR and to understand the historical importance of various wading areas within NGR, we compared our year-long study data to historical annual dry-season census data collected by NGR management; Ezemvelo KZN Wildlife (EKZNW), from 1951-2017 (Chapter 4). Overall population trends revealed a substantial decrease from a maximum of 448 individuals in 1979 to between 250-300 in 2016-2017. The population was observed to have nearly doubled over a 10-15 year period between in 1968-1980 when the Pongolopoort Dam upstream of NGR on the Phongolo River followed a biannual release pattern and flooded NGR twice each year. Previous studies have shown that hippo populations do not have a strict mating season and that populations that endure two major rainy seasons like on the Luangwa River, Zambia see two peaks in reproductive behaviour annually (Sayer & Rakha 1974, Norton 1988, Chomba 2013, Chomba & Chabwela 2016). Historical trends in NGR also revealed the drastic population decreases during drought periods in the 1980's, 1990's, and 2015's following the abolishment of the biannual release pattern (Chapter 4). Studies conducted in other systems in Africa have also shown the dramatic population die-offs attributed to drought (Viljoen 1995, Smit et al. 2020, Utete 2020). Historical data reinforced currently observed patterns of wading area utilisation where, on average, over 60% preferentially used the Phongolo River and associated floodplain over other areas (Chapter 4). This was attributed to preferential wading habitat available and ready access to substantial grazing in the productive alluvial floodplain soils (Chapter 4). The preferential use of the Phongolo floodplain continued even through increased

anthropogenic disturbance on the floodplain following the removal of the eastern boundary fence by communities on the periphery of NGR and highlighted its importance as a hippo habitat.

The second objective of this research was to compare a yearlong UAV survey of the hippo population at NGR to historical population counts of the hippo population in NGR that dated back to 1951 (Chapter 3). The UAV survey was comprised of four monthly surveys every month for a year from August 2016 to July 2017. Eight predominant wading areas were surveyed during each survey to get a minimum number of hippos within the reserve as well as identify changes in different populations of hippo in different locations within NGR. Historical counts of hippo fluctuated between ~150-395 individuals. Fluctuations in the NGR hippo population over the past 70 years correlated with major drought events as well as invasions of NGR by neighbouring communities, which facilitated increases in poaching of hippo within NGR. Changes in the hippo populations in NGR at each of the eight survey locations were identified (Chapter 3). Pholwe and Bhakabhaka were the most important wading areas within NGR as they accounted for the largest portions of the hippo population throughout the yearlong survey period. In addition, correlations between water level, constructed as a categorical variable, and the number of hippos detected using the UAV were identified where increased water levels decreased overall detection.

8.2.2 Methods in conservation

Stemming from a lack of resources available to conservation entities, several African countries have unknown hippo population statuses because of a lack of population monitoring data in those regions (Barnes et al. 2016, Lewison & Pluhacek 2017, Lindsey et al. 2018). Therefore, we explored the application of low-cost consumer-grade UAV’s for conducting population censuses of hippos in NGR. We conducted 47 censuses from August 2016-July 2017 and used these data as

part of our analyses of monthly and annual hippo population trends in NGR (Chapter 2). Census data collected using the UAV was comparable to data collected using traditional methods but incurred substantially lower costs and could be repeated with much less effort over sub-annual timescales (Chapter 2). A growing number of studies are including UAV's as part of research and management of species like Nile crocodiles (*Crocodylus niloticus*) and African elephants (Vermeulen et al. 2013, Ezat et al. 2018), and previous studies have highlighted the possibility of their implementation specifically for hippos but lacked application in the field (Lhoest et al. 2015, Linchant et al. 2018, Inman et al. 2019). Our research has shown that UAV's have a place in the conservation management toolkit and are particularly applicable in regions and protected areas with restricted budgets.

Hippos are widely regarded by African wildlife game capture and veterinary professionals as one of the most difficult and dangerous animals to capture. In addition, current capture methods are costly and time and effort consuming (Burroughs et al. 2012, Miller et al. 2014, Walzer & Stalder 2015). Until recently, no data had been collected on hippo space use because of the complications they pose and conservation research lacked a fundamental understanding of the drivers of hippo space use and activity (Lewison & Pluhacek 2017, Stears et al. 2019; Chapter 5-6). We experimented with three different capture methodologies in an attempt to increase hippo capture success (Chapter 5). We found that traditional methods using a passive capture boma were costly in time, effort, and budget, particularly when hippos take a long time ($n > 40$ days) to enter the boma and present capture opportunities. However, these methods have been shown to be successful outside of our case study, particularly in capturing several hippos in a single effort, and therefore using the data we collected, we were able to present a model to help future capture programs using capture boma methods to predict and manage their budget according to the effort

and time they are investing (Chapter 5). Our use of experimental helicopter-based active capture methods was cost, effort, and time-efficient than the other methods attempted in the study (Chapter 5). These methods were also adaptable and catered to the needs of wildlife veterinary professionals that require adaptive immobilisation techniques to deal with problem animals or those injured with snares. Sadly, these methods also resulted in instances of capture-related mortality (Chapter 5). However, future ameliorations of these methods based on our findings will expand on the knowledge on these capture techniques, adding to the wildlife professional's capture toolkit and ultimately aiding in conserving hippos across Africa.

8.2.3 Human-hippo conflict

Our final research objective was to describe the type and distribution of anthropogenic impacts encountered during our yearlong hippo survey in NGR. We found that illegal use of NGR's floodplain area stemmed from the need of members of the peripheral communities to fulfil their most basic subsistence resource needs like access to water, subsistence farming, and subsistence hunting (Chapter 7). However, we found that these activities were having a significant impact on the Phongolo floodplain, particularly through landscape modification resulting in habitat loss, wildlife grazing competition with livestock, and poaching of target species for conservation, including hippos (Chapter 7). These impacts were also focused on the most important habitat for hippos and along the floodplains, for which NGR was distinguished internationally as a Ramsar site (Chapter 7). Based on our findings, it is clear that continued modification at the current rate in NGR will have catastrophic impacts on wildlife and the natural resources in NGR. Similar impacts have been recorded across the globe where economically disadvantaged communities turn to unmanaged resource use, often in protected or conservation areas, to fulfil their basic subsistence

needs (Noss 1998, Gandiwa 2011, Gandiwa et al. 2013, Ripple et al. 2016, Manqele et al. 2018). However, because this resource utilisation is unmanaged, it is often also unsustainable, resulting in decreases in natural habitat and wildlife (Noss 1998, Gandiwa et al. 2013, Ripple et al. 2016, Fahrig 2019). Our findings show that this is not as much a conservation issue, as it has often been perceived in regard to NGR, but is a social issue that stems from South Africa's history of apartheid. Our findings will highlight the need for local and international social and political intervention to ensure continued management of NGR for its conservation importance of which its status as a refuge for hippos is paramount.

8.3 Discussion and future research

As part of our study, we were able to contribute to multiple aspects of the conservation of hippos in Africa (Chapters 2-7). Future conservation of hippos in Africa will need to be adaptable in the context of changes in climate and expanding anthropogenic impacts (Capon et al. 2013, Foden et al. 2019, Grantham et al. 2019, Malherbe et al. 2020). Challenges on political and social fronts will present additional obstacles for conservation, particularly in the developing world (Beinart 1989, Myers et al. 2000, Tilman et al. 2017, Lindsey et al. 2018).

A basic understanding of individual and population behavioural ecology is fundamental for conservation research and management of hippos (Lewison & Pluhacek 2017). Our research provides novel insights into male hippo space use in perennial river and impoundment systems (Chapter 6). Our research on hippo population structure and distribution provides novel detail on population social behaviour and brings additional context to the drivers of hippo population dynamics (Chapters 3 & 4). Future research on hippo female and pod space use in various systems, including floodplains, lakes, and anthropogenically modified landscapes will further benefit

conservation management of hippos in various system types. Additional research linking hippo behaviour to their ecology in the context of system management will benefit the conservation of hippos and the systems within which they occur.

We explored the application of different management and monitoring methods with the intention that they would be applied practically in conservation. Future published work detailing ameliorations of these methods as part of management programs will further aid in mainstreaming their application. Furthermore, additional research on the potential contributions of automation and using satellite imagery will continue to reduce conservation costs and permit the collection of important population and system-level monitoring data.

Current conservation initiatives fail to identify the economic importance of natural areas (Bruner et al. 2004, Lindsey et al. 2018). Future studies outlining the ecosystem services provided by wild areas will benefit their future management (Chan et al. 2006, Bennett et al. 2015, Nel et al. 2017). In addition, increased anthropogenic pressures in the future are unavoidable (Cohen 2003, McKee et al. 2004, Tilman et al. 2017). Therefore, conservation managers need to use risk models that account for social, political, and economic pressures to inform adaptive conservation management programs (O'Brien et al. 2019, Powers & Jetz 2019, Vezi et al. 2020). This highlights the need to bridge gaps between conservationists, technology, policy, social science, and economics. Embracing these relationships will bring more context to conservation initiatives, provide conservation with the appropriate tools to be successful, and give conservation the stage it deserves, ultimately ensuring sustainable management of our systems and natural resources.

8.4 References

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