Aspects of the spatial and behavioural ecology of *Hippopotamus amphibius* in the Saint Lucia Estuary, KwaZulu-Natal, South Africa.

By Alexa Simone Prinsloo

Dissertation presented for the degree of Master of Science in the Department of Biological Sciences
University of Cape Town
January 2016

Supervisor: Dr Deena Pillay
Co-supervisor: Prof M. Justin O'Riain

Plagiarism Declaration

"I know the meaning of plagiarism and declare that all of the work in the dissertation, save for that which is properly acknowledged, is my own."

Signed by candidate

Alexa Simone Prinsloo

Acknowledgements

I would like to take this opportunity to thank the multitude of organisations and individuals that have made this dissertation a reality. Firstly, I acknowledge the financial support provided for this endeavour, both in a project and personal capacity, by the National Research Foundation. Secondly, it is with my deepest gratitude that I acknowledge the support, supervision and guidance that my supervisors, Dr. Deena Pillay and Prof. Justin O'Riain provided throughout this experience.

A sincere thank you to the iSimangaliso Wetland Park Authority and KZN Wildlife for allowing me access and providing logistical and field support where they could, during my fieldwork in the St Lucia Estuary. A special thanks to Nerosha Govender for her logistical support in arranging permits and access passes. Caroline Fox for her constant support during this experience, from organising safe storage for our boat, to sharing available data and knowledge of the system at every turn, and for always being no more than an email or phone call away. To the multitude of skippers; Steven Hart, Mark Robertson, Nick, Fred, Oom Piet and Christiaan Bennett, thank you for your time, skill and patience. For shuttling me up and down the estuary in the often unreliable boat yet always ensuring I made it ashore in one piece. I realise that watching a single group of hippos for hours a day is certainly not everyone's idea of fun. My thanks to Frikkie for towing the boat and always waiting to haul us out at day's end.

A warm thank you to the Bateleurs for providing the means of obtaining a bird's eye view of this spectacular system and an opportunity to grapple with the difficulties associated with aerial surveys of an amphibious species. Specifically, I would like to thank my pilots, Chris Rattray and Clive van der Spuy, for flying my hippo mission. Furthermore, a big thank you to Lawrence Beith and Adam Robinowitz for acting as spotters and photographers.

I acknowledge the impeccable service and support of the GIS specialists (in the UCT GIS Lab), Nicholas Lindenberg and Thomas Slingsby. I thank them for their patience, good humour and willingness to share their expertise. Also, to Katya Mauff, for her guidance and advice with the statistical components of this project.

On a more personal note, I would like to thank my friends, for their willingness to listen to hours of hippo talk, for the moments shared, compassion, comfort, laughter and especially

their enthusiasm for joining me in a rant and rave session when either the literal, or figurative engine wouldn't start. Particularly, I would like to thank Kirsty Robertson and Kelly Cowell for their part in the emotional journey that this experience proved to be. To Chantel Williams, Babette de Jong, Janice Southey, Fabian von Hase and Shaun Irwin for being epic friends, no matter how far apart we are.

My teary-eyed, heart-over-flowing thanks to my family for their unwavering love and support. Pappa (Alex (J.M.) Prinsloo), thank you for supporting me financially and emotionally through it all. Mamma (Matilda Prinsloo), for always being there when I needed you most. For the hours spent talking on the phone about everything and nothing. To my wonderfully inspiring sister, Brigid Prinsloo, thank you for being the person I can turn to when things are at their best or worst. Your love, mixed with your can-do attitude and your belief that our dreams are there for our own making, inspires me daily. Last, but by no means the least, thank you to my love, Nico van der Merwe. For being the brilliantly practical man that you are, able to fix anything and always willing to help (whether it's fixing boat engines, car radiators, all in an endeavour to keep my dream alive). Thank you for encouraging me and supporting me emotionally and financially to ensure that I could continue with my studies. For always being on my side, even when I wasn't. For enriching my life and teaching me that there is so much more enjoyment to be had when you have someone to share it with.

The past few years have certainly been a challenge and an adventure. Thank you to all who have made this project a possibility, a reality and an experience of a life-time.

Table of Contents

Abstract

The common hippopotamus (*Hippopotamus amphibius*) is endemic to Africa but threatened by range restriction, exploitation and competition with humans and domestic livestock for access to critical resources such as fresh water and grazing. Collectively these impacts have resulted in population declines throughout most of their range with the consequence that hippos are classified as *Vulnerable* on the IUCN Red list. Despite these threats to their persistence and their important ecological role as ecosystem engineers there have been surprisingly few studies concerning factors that influence their current distribution and habitat use. Such research is important for developing effective conservation and management plans to improve the protection of vulnerable and ecologically important species such as hippo. South Africa is home to one of a few growing hippo populations and one of the last persisting in an estuarine habitat. The St Lucia Estuary, one of three Ramsar Wetlands of International Importance located in the iSimangaliso Wetland Park (itself a UNESCO World Heritage site), in northern KwaZulu-Natal is not only the largest estuarine system in Africa, but is also home to one of South Africa's largest hippo populations.

In this study I explore aspects of the spatial and behavioural ecology of hippo within the St Lucia Estuary. More specifically, I investigate select abiotic and biotic predictors of hippo presence and the frequency with which they return to their diurnal lie-up sites. I used binary logistic regression models to evaluate the effects of the selected habitat features on hippo occurrence at two spatial scales (broad and fine). I used a negative binomial with log-link model to evaluate the effects of the selected habitat features on the frequency of use of sites (hippo persistence) in the fine-scale study. In addition, I employed both instantaneous scan sampling and continuous sampling methods in an attempt to determine the diurnal activity budgets and social interactions of a single group near the mouth of the St Lucia Estuary. I used non-parametric tests to evaluate differences in behaviour with daytime and across sampling days with a view to an improved understanding of how the environment influences the behaviour of hippo in an environment subject to ongoing human modification.

The resultant broad-scale model indicated that hippos preferentially select diurnal lie-up sites in the Narrows and rivers that are closer to river inlets and further from human settlements. The fine-scale occurrence model suggested that hippos preferentially settle in sites that had water depths between 0.5 - 1.49m deep that are further from human settlements. Hippo also appeared to be more likely to select a site in close proximity to neighbouring groups. The fine-scale frequency of use model suggested that hippos most frequently settled in sites with a water depth between 1.0 – 1.49m, closest to natural wetland vegetation and in close proximity to neighbouring groups. The behavioural component of the study highlights the fact that hippos utilise their diurnal lie-up sites predominantly as resting sites (spending 79.39% of the day resting), however a high degree of variability existed between observation days, suggesting that hippo activity budgets are subject to other variables (e.g., behavioural thermoregulation, social events). Social behaviours such as dung showering, tail paddling and vocalising exhibited significant variability between days, with no distinct diurnal patterns. Only yawning showed a clear diurnal pattern increasing in frequency in the late afternoon (15:00 to 17:00).

As an initial study into the spatial ecology and behaviour of the St Lucia hippo population, this study distinguishes the key habitat variables that influence hippo distribution on two landscape scales, illustrating that hippo presence and hippo persistence within the St Lucia estuary are governed by a combination of hippo behavioural thermoregulation, habitat and social requirements. It also highlights aspects of hippo ecology and behaviour that are yet to be analysed and incorporated into future studies and management plans.

Chapter 1: Introduction

As global climate change and the expansion of rural and urban development threaten species worldwide, so the importance of understanding species landscape requirements for conservation purposes is increasing (Bennet & Saunders, 2010; Guisan & Zimmermann, 2000; Austin, 2007). Our understanding of species landscape requirements hinges on our ability to link species distribution patterns to biological and social requirements. Thus, it requires knowledge of the physiology, spatial and behavioural ecology of the species concerned (i.e. addressing both the where and the why animals utilise certain areas) (Sims, 2003). This approach has been used to elucidate the landscape requirements of diverse species including badgers (Feore & Montgomery, 1999), otters (Ottaviani *et al.*, 2009), roe deer (Börger *et al.*, 2006), horses (van Beest, *et al.*, 2014), dolphins (Karczmarski *et al.*,2000; Lusseau *et al.*, 2004), baboons (Hoffman & O'Riain, 2012) and elephants (Blake, 2002; Chamaillé-Jammes *et al.*, 2007; de Beer & van Aarde, 2008).

Many wildlife species utilise resources across the landscape or are affected locally by changes occurring elsewhere in the landscape (Orians & Wittenberger, 1991; Fausch *et al.*, 2002; Bennet & Saunders, 2010). Thus, landscape requirements need to be assessed at multiple spatial scales, which together with geographic information systems (GIS) and multivariate statistical techniques enable us to model and predict species distributions, movements and behaviours at different spatio-temporal scales. These findings enable us to make the links between population dynamics and biological processes in order to better inform conservation planning (Guisan & Zimmermann, 2000; Laidre *et al.*, 2004; Marker & Dickman, 2005; Austin, 2007). Each species 'perceives' the landscape differently and thus responds differently to changes to the environment (Bennet & Saunders, 2010). One animal that has received scant attention in the scientific literature, but has experienced substantial range reduction and thus could greatly benefit from a better understanding of its landscape requirements and behaviour, is the common hippopotamus (*Hippopotamus amphibius*).

Listed as a *Vulnerable* species on the IUCN Red list of Threatened Species in 2006 (Lewison & Oliver, 2008), hippos are endemic to Africa and currently have a fragmented distribution throughout sub-Saharan Africa (Fig. 1.1). Declines in population numbers in recent decades have occurred due to substantial range restriction, (habitat loss and fragmentation) exploitation (for meat and ivory) and human-hippo conflict (Oliver, 1993; Lewison & Oliver, 2008; Kendall, 2011; Klingel, 2013).

Historically hippos were widespread throughout the eastern parts of South Africa, the lower Orange River, ranging all the way to the Cape (Kingdon, 1979 in Klingel, 2013; Taylor, 2013). However, hunting and both habitat loss and fragmentation (Klingel, 2013) resulted in their range being greatly restricted with populations being eradicated from most of their historical range (except for the Kruger National Park) by the early 1960s (Sidney, 1965 in Eltringham, 1993). However, an increase in the number of protected areas within South Africa has seen hippos return in isolated patches to parts of their former range (Taylor, 2013). One of South Africa's largest hippo populations now resides in the St Lucia Estuary in KwaZulu-Natal, which is not only the largest estuary in Africa, but also one of the last to support hippos (CITES Scientific Authority of South Africa, 2011; Whitfield, 2013; Fig. 1.2). Being one of the few populations in Africa reporting an increase in numbers it is important to understand their spatial ecology and behaviour with a view to the long term management of the hippo population as competition for limiting resources (e.g. fresh water and grazing) are likely to increase (CITES Scientific Authority of South Africa, 2011; Taylor, 2013).

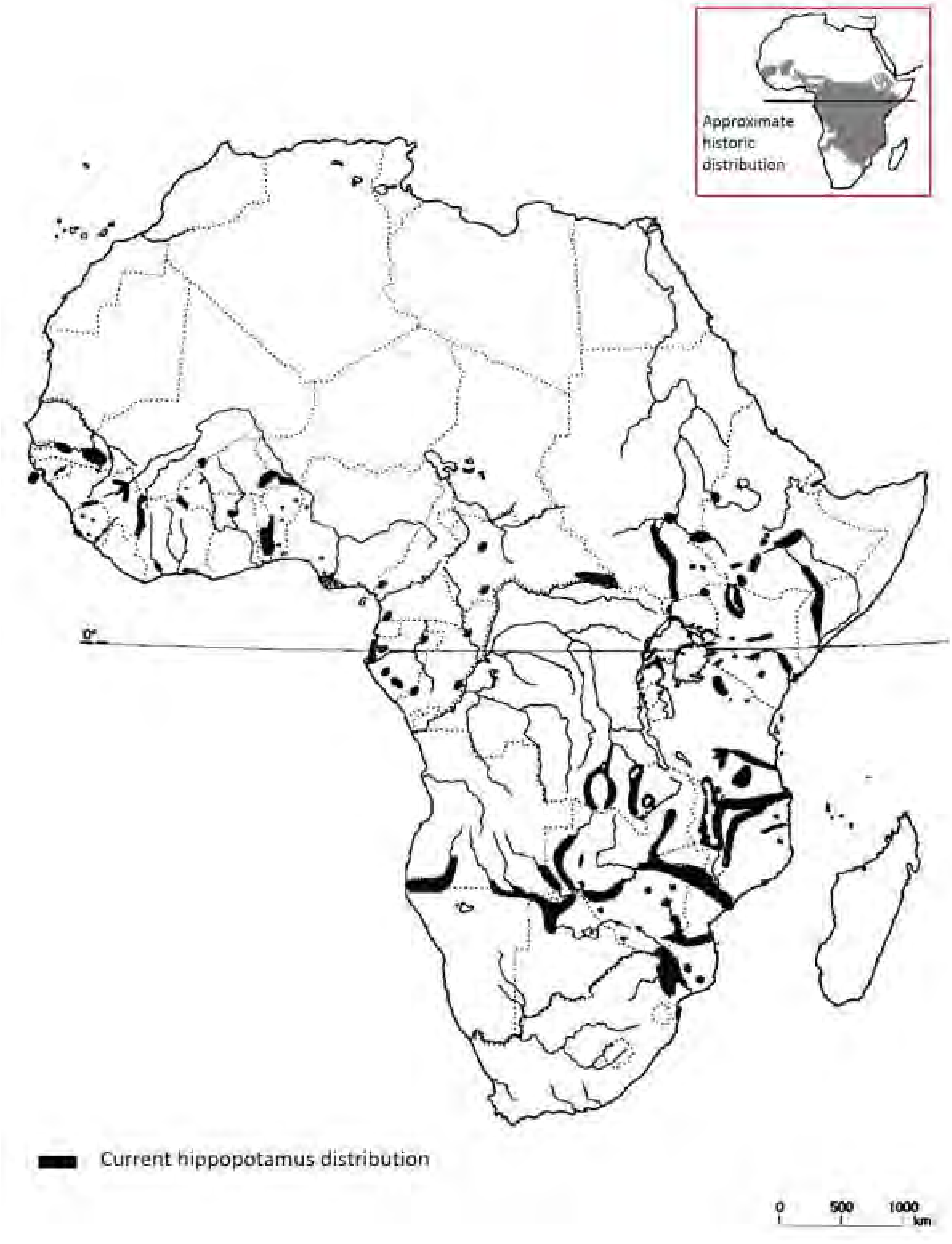


Figure 1.1: Past and present hippopotamus population distribution throughout sub-Saharan Africa (adapted from Oliver, 1993 and Lewison, 2007).

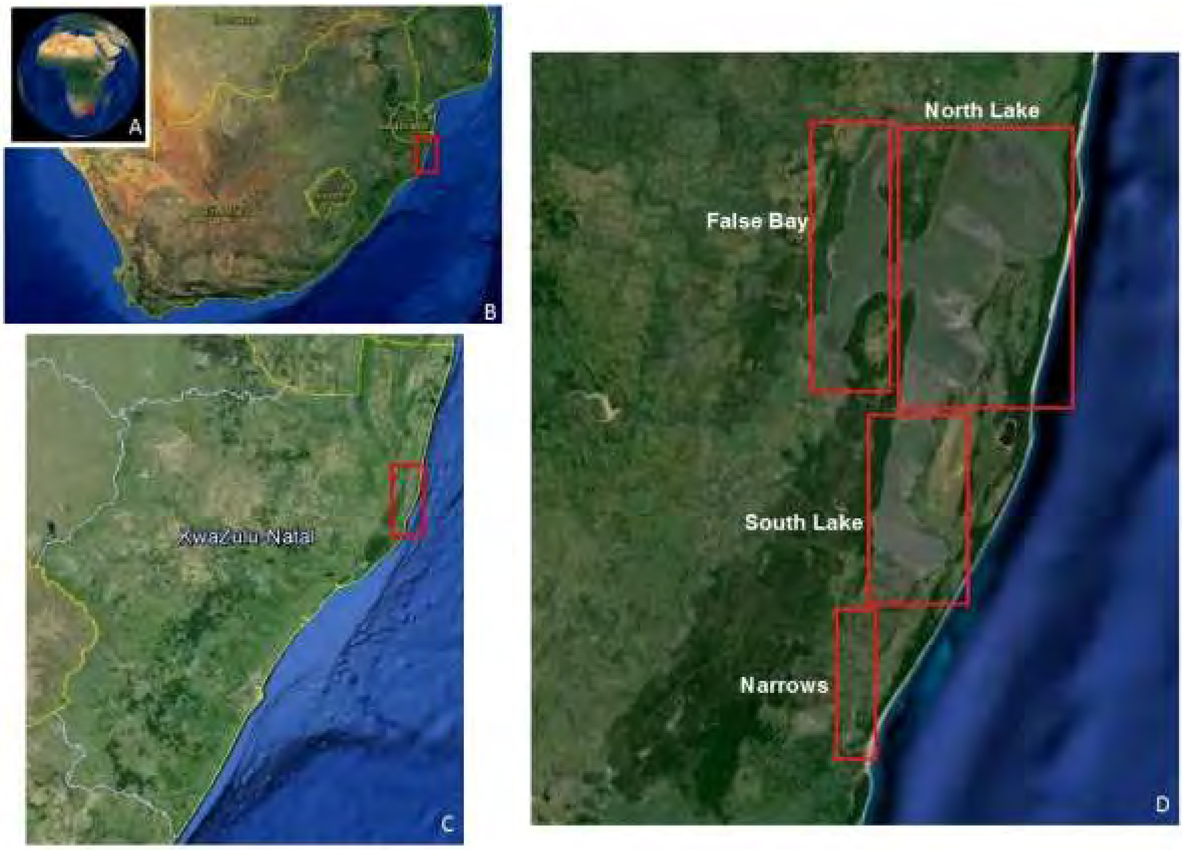


Figure 1.2: The location of the St Lucia Estuary within Africa (A), South Africa (B), KwaZulu-Natal Province (C) and a map illustrating the St Lucia Estuary with associated components (D) (Images adapted from Google Earth).

Phylogeny and current taxonomic status

Recent genetic studies (Ursing & Arnason, 1998; Gatesy, 2009 in Boisserie *et al.*, 2011) suggest that approximately 54Mya, the hippopotamus-whale clade diverged, giving rise to the extant families of Hippopotamidae and Cetacea. While the precise origins of hippopotamids remain unclear, hippopotamid evolution is firmly rooted in the Neogene, with the earliest fossil records dating back to the Early Miocene (21.0Ma) (Boisserie *et al.* 2011; Seiffert & Kingdon, 2013).

The family Hippopotamidae is divided into two extant genera, *Choeropsis* and *Hippopotamus*, both of which have only one extant species viz. *C. liberiensis* (Pygmy Hippo) and *H. amphibius* (Common Hippo), respectively (Boisserie & Eltringham, 2013; Eltringham *et al.*, 2013; Gent, 2013; see also Kingdon & Hoffmann, 2013 for a detailed review of the evolutionary history of the Hippopotamidae). Members of the genus are thought to have thrived during the late Neogene due to a suite of morphological and physiological traits, including a tolerance to lower temperatures, ability to cross seas and higher crowned teeth allowing them to feed on more abrasive C4 grasses. Together these adaptations enabled *Hippopotamus* to out-compete other hippopotamids and expand their range during this time of climatic change (Boisserie *et al.* 2011).

Recent genetic studies suggest that hippo populations exhibit no continent-scale phylogeographic structuring (Okello, *et al.*, 2005; Stoffel, *et al.*, 2015). This lack of genetic structuring is potentially a remnant of the previously mentioned range expansion which may be linked to the Late-Pleistocene drainage overflow event, which connected numerous drainage basins and allowed hippo populations to increase and disperse easily across the entire continent (Boisserie *et al.* 2011; Stoffel *et al.*, 2015).

Hippopotamus amphibius was thought to include five subspecies (viz., *H. a. tschadensis, H. a. constrictus, H. a. amphibius, H. a. capensis and H. a. kiboko)* grouped primarily on morphological variation and geographical distribution (Eltringham, 1993; Okello, *et al.*, 2005). A genetic study, by Okello *et al.*, (2005), on the latter three subspecies provided support for their classification based on phenotypic variation. However, a more recent study by Stoffel *et al.*, (2015) of all five subspecies, found no genetic evidence to distinguish between the subspecies. Rather the study by Stoffel *et al.* (2015) highlighted eastern Africa as a diversity hotspot with a high degree of genetic differentiation among hippo populations. Hippo populations are currently fragmented leaving populations genetically disconnected, and resulting in high levels of genetic endemism (Stoffel, *et al.*, 2015). Both

Okello *et al.*, (2005) and Stoffel, *et al.*, (2015) urge management and conservation authorities to recognise the importance of conserving maximum genetic and phenotypic diversity by managing hippos at regional instead of continental scales.

In keeping with the majority of the literature on this group (*H. amphibius*), as well as the most recent findings by Stoffel, *et al.* (2015), I have identified my study animals to the level of species only.

Morphology and adaptations to an amphibious lifestyle

Hippopotamus amphibius (hereafter referred to as Hippos) is a semi-aquatic, nocturnal, mega-herbivore. Hippos have a barrel-shaped body with short, stout legs and four toes per foot, protected by broad, robust nails (Klingel, 2013). Much like their sister group, the Cetacea, hippos have no sebaceous glands, little to no hair, vocalise under water and mate, birth and nurse their young in water (Klingel, 2013; Seiffert & Kingdon, 2013). These amphibious ungulates exhibit a unique assemblage of adaptations to life at the interface between land and water; not only are their ears, nose and eyes positioned high up on their heads, allowing them to perceive their surroundings whilst most of their bodies remain entirely submerged (Klingel, 2013), but each of these organs are adapted to function at this interface. For example, hippo eyes have an iridocorneal angle (the angle between the cornea and iris, the site of aqueous humour outflow) intermediate between that of land artiodactyls and marine cetaceans (Hatfield *et al.,* 2003), while hippo ears and slit-like nostrils close by reflex on contact with water in a manner similar to cetaceans (Klingel, 2013). Hippo skin has a surprisingly thin epidermis (which dries out easily), a thick dermis, little subcutaneous fat and no true sweat glands, yet they are able to maintain a core body temperature of 36°C (Luck & Wright, 1964; Klingel, 2013). This is partly due to the insulating properties of their dermis in combination with behavioural thermoregulation through habitat selection (Eltringham, 1993; Klingel, 2013).

Hippo skin exhibits very high evaporative water loss, especially when wet with the viscous secretion from the subdermal glands (Luck & Wright, 1964; Hashimoto, *et al.*, 2007). This alkaline secretion, often referred to as “hippo sweat”, undergoes a colour change (from colourless to red to brown) when secreted from the skin (either in or out of water), due to the polymerization of two key pigments, hipposudoric acid (red pigment) and norhipposurdoric acid (orange pigment) (Saikawa, *et al.*, 2006; Hashimoto, *et al.*, 2007; Galasso & Pichierri, 2009; Roberts, *et al.*, 2015). Both pigments exhibit UV protective and antibacterial properties (Luck & Wright, 1964, Eltringham, 1993; Hashimoto, *et al.*, 2007; Galasso & Pichierri, 2009). Eltringham (1993) suggested that hippos are unable to control water loss, thus their skin dries out quickly when exposed to air for long periods of time, which explains both their diurnal aquatic life-style and their nocturnal terrestrial foraging behaviour.

Habitat and feeding ecology

Hippo’s dependency on water for thermoregulation and sun protective purposes limits both their temporal and spatial foraging range, effectively restricting hippos to nocturnal foraging bouts within 10km of their diurnal resting sites (Eltringham, 1993; Wright, 1964 in Noraird, *et al.*, 2008; Klingel, 2013;). Hippos are restricted to lakes, rivers, swamps and estuaries within 10km of grasslands or grassland-bushland mosaics that they rely on for foraging (Chansa *et al.,* 2011a; Klingel, 2013). Hippos appear to adhere to the central place foraging strategy, adjusting their foraging behaviour (bite rate, a measure of intake; step rate, a measure of time spent searching) in response to both the distance from a central place (in their case, water refuges) and vegetation quality (Lewison & Carter, 2004).

They are pseudo-ruminants, with a four-chambered stomach in which the first three chambers allow for the fermentation of low quality foods and grasses and the fourth chamber is responsible for gastric digestion (Eltringham, 1993; Cerling, *et al.*, 2008; Klingel, 2013). Hippos prefer short grasses that they graze by plucking the blades with their horny lips (Eltringham, 1993; Klingel, 2013). With repeated foraging in an irregular pattern they create and maintain extensive areas of shortly cropped grass which are commonly referred to as “hippo lawns” (Olivier & Laurie, 1974 in McCarthy *et al.*, 1998; Verweij, *et al.*, 2006; Klingel, 2013). Through the maintenance of these lawns, hippos manipulate the quality of available forage (higher energy per unit mass; kJ/kg) (Verweij *et al.*, 2006). Hippo lawns are characterised by short grasses; with an increased leaf to stem ratio, younger shoots, which are both more digestible and nutritious (higher levels of phosphorous, sodium and protein) than neighbouring un-grazed stands (Lewison & Carter, 2004; Verweij, *et al.*, 2006).

Hippos weigh, on average, 1500kg (Luck & Wright, 1964; Marshall & Sayer, 1976) with ranges from 1000 – 4500kg reported by Nowak (1999, in Coughlin & Fish, 2009), 1100 – 2600kg reported by Grubb (1993) and 995 – 1999kg reported by Klingel (2013). Given their large body mass, it is surprising that hippos only eat an estimated 50kg of grass per night and spend only 30% of their total day foraging, which is considerably less than any other mega-herbivores (Lewison & Carter, 2004; Clauss *et al.*, 2007; Chansa *et al.*, 2011a). Clauss *et al.* (2007) suggest that this low volume of food consumed represents an adaptation to increasing gut throughput time and improved digestive efficiency (increased consumption accelerates ingesta passage through the gut, decreasing gut throughput time; Clauss *et al.*, 2007). In this way hippos are able to consume less forage than other herbivores of similar size (elephants, rhinos), or lower quality forage whilst still obtaining sufficient nutrients (Eltringham, 1993; Clauss, *et al.*, 2007). Numerous studies have illustrated that hippos are not obligate grazers (Boisserie *et al.*, 2005, 2011; Cerling *et al.*, 2008). Hippo diets are adaptable, varying from nearly pure grazing material (C4 grasses) to a substantial amount of browsing material (C3 plants; Cerling *et al.*, 2008; Boisserie *et al.*, 2011), and even some rare cases of carnivory and cannibalism during severe droughts (Dudley, 1997). In order to capitalise on increased gut retention time, hippos spend most of their daylight hours resting in water refuges, digesting food consumed the night before (Clauss, *et al.*, 2007; Harrison, *et al.,* 2007; Klingel, 2013).

Hippos prefer slow-flowing, shallower waters to rest in and this explains their preference for river bends (Olivier & Laurie, 1974; Harrison, *et al.,* 2007; Viljoen & Biggs, 1998 in Coughlin & Fish, 2009; Blowers, *et al.*, 2010; Attwell, 1964 in Chomba, *et al.*, 2013; Chomba, 2013; Klingel, 2013). Water slows on the lee side (inside) of a river bend which results in the deposition of sand and silt and ultimately the formation of sloping sand bars which are favoured basking sites (Chansa, *et al.,* 2011b). Furthermore, studies by both Bennett *et al.* (2000) and Chansa *et al.* (2011b) reported increased hippo abundance at river confluences. Confluence points such as these are often sites of sediment deposition and may provide shallower waters for rafting or basking sites for hippos (Chansa *et al.*, 2011b). The preferred water depth for resting during the day is disputed in the literature, with Blowers *et al.* (2010) reporting that captive hippos preferred water depths of 0.6 – 1.0m, whilst hippos in St Lucia Estuary, South Africa appear to prefer depths of approximately 1.4m (Taylor, 1980). There is however, consensus on the generality that hippos avoid resting in deep water, as they do not float nor swim, and would thus have to expend energy to maintain a breathing position at the water surface by punting (using their limbs to push off the substrate in an aquatic pedestrian locomotion; Coughlin & Fish, 2009).

Together these findings suggest that hippos are restricted to habitats that offer a combination of both terrestrial and aquatic features essential to nocturnal and diurnal activities (Olivier & Laurie 1974; Lewison & Carter, 2004; Harrison*, et al.*, 2007; Blowers, *et al.*, 2010; Chansa, *et al.,* 2011b; Chomba, 2013; Klingel, 2013). Potentially, the limited daytime habitat has resulted in this predominantly solitary nocturnal grazer adopting a gregarious diurnal lifestyle. In support of this suggestion is the finding that group size is dependent on population density and environmental variables rather than any sociobiological parameters (Karstad & Hudson, 1986; Barklow, 1997; McCarthy, *et al.,* 1998; Klingel, 2013).

Reproductive and social behaviour

Hippos conform to *K*-selected species strategies, combining a low rate of reproduction with high survival. Thus, population size is typically closely aligned to long-term environmental carrying capacity (Smuts & Whyte, 1981) and hippo populations are primarily limited by the availability of suitable habitat and forage rather than by diseases or predation (O'Connor & Campbell, 1986). Adverse environmental conditions are associated with reduced conception rates and increased survival rates of calves through both physiological and behavioural adjustments (Smuts & Whyte 1981; Eltringham, 1993). During favourable conditions hippos may mature earlier, as young as 2 years for males and 3-5 years for females (Marshall & Sayer, 1976; Smuts & Whyte, 1981), with the average age of sexual maturity being attained at 7-8 years for males and 7 years for female (Klingel, 2013).

Maximum longevity has been recorded as 61 years in captivity (Weisner & von den Driesch 1996, in Klingel, 2013) and up to 45 years in the wild (Chomba, 2013). Under favourable environmental conditions their relatively short gestation period of 8 months (given their large body size), short inter-birth interval of 21.8 months and limited predation (Laws & Clough 1966; Smuts & Whyte 1981), allow hippo populations to increase rapidly. For example, Kanga *et al.* (2011) reports an annual growth rate of 18.8% for the hippo population within the Massai Mara National Reserve in Kenya between 1971 and 1980 however, the same population experienced a -3.3 % annual growth rate between 1980 and 2006. Smuts and Whyte (1981) suggest that hippo density affects the age at which hippos reach full reproductive capacity, with overpopulated areas such as Uganda and Zambia reporting an average age of 20 years. By contrast, in the Kruger National Park, South Africa, where hippo numbers are lower per unit area, the average age of sexual maturity is 11 years (Smuts & Whyte, 1981).

Births occur year round, with a marked increase associated with the wet season (Laws & Clough, 1966; Marshall & Sayer, 1976; Smuts & Whyte, 1981). Shortly before the birth of her calf, a mother will seek isolation from the group and a safe place to birth and rest in close proximity to the water's edge (Laws & Clough, 1966; Field, 1970; Olivier & Laurie, 1974 in McCarthy *et al.* 1998). By fending off all conspecifics for up to 10 days after the birth, a mother is thought to ensure that no false imprinting can take place, whilst protecting her newborn calf from conspecific attacks (Klingel, 2013). Such attacks are however rare with only seven confirmed cases of infanticide reported over a 45 year monitoring period (Lewison, 1998). Lewison (1998) suggests that infanticide by male hippos is a post-mating competitive strategy in order to increase their own reproductive success following a territorial take over.

Female hippos may improve calf survival rates by extending their lactation periods, with calves weaned at a range of ages, from 6 to 15 months (Pluháček & Bartošová, 2011; Eltringham, 1999 in Klingel, 2013). Allosuckling (suckling from a non-maternal female) occurs in captivity (Pluháček & Bartošová, 2011) while in the wild, the presence of more lactating females than calves (Marshall & Sayer, 1976; Smuts & Whyte, 1981) suggests that it might occur outside of captivity too. Klingel (2013) reports that young remain in close proximity to their mothers until they are 6-8 years of age; a female may thus be observed with several offspring of different ages, exhibiting no disruption in the individual mother-calf relationships.

Little is known about hippo social organisation and communication, partly due to the fact that hippos are notoriously difficult to observe in the wild, given the aquatic and often inaccessible nature of their diurnal habitat (Barklow, 1997), nocturnal foraging behaviour, difficulties of individual identification (Blowers, *et al.*, 2010; Klingel, 2013) and their reputation for aggressive behaviour (Kingdon, 1979 in Klingel, 2013). Social organisation within hippo populations centres on mating territoriality (Klingel, 2013). Approximately 10% of adult bulls within a population occupy and defend territories within the water, along the shorelines of lakes and rivers (Klingel, 2013). These territories are of variable size, ranging from 250-500m along a single bank in a lake, to as little as 50-100m along both banks of a river (Klingel, 2013). Dominant bulls show strong site fidelity, with a maximum tenure encompassing a bull's entire adult lifespan (20-30 years). Such long tenures are the exception though, as adult bulls frequently challenge each other for dominance and the exclusive right to mate with all females within the territory is subject to frequent turnover (Karstad & Hudson, 1986; Klingel, 2013). Given their need to leave the water at night in order to feed, both male territoriality and female home range fidelity is intermittent

(Karstad & Hudson, 1986; Klingel, 2013). Following their nightly grazing, individuals preferentially return to the same site from which they departed the evening before, resulting in fairly consistent group composition over time (Klingel, 2013). According to Klingel (2013), changes in group composition may be observed throughout the day as each individual has its own home-range. Female home-ranges may extend across more than one male's territorial boundaries and females may thus mate with two or more dominant males (Klingel, 2013). However, it is the attractiveness of a site, not its dominant bull that is thought to attract females and other conspecifics (Klingel, 2013) and the favourability of a site may change as water levels, food availability and population density fluctuate (Klingel, 2013). Thus, it is favourable for males to maintain a territory, even if it is in a suboptimal area that does not attract females at any given time, as 'bad' territories may change to 'good' territories under different environmental states (Klingel, 2013). Following changes in water levels during severe drought conditions, multiple groups may coalesce, forming large groups numbering into the hundreds (Laws & Clough, 1966 in Blowers, *et al.*, 2010). If low water levels persist, the dominant bulls may even abandon sites (Karstad & Hudson, 1986; Klingel, 2013). Together these factors drive a fission—fusion society (Wittemyer *et al.*, 2005) with favoured sites being occupied by larger groups, the size and composition of which vary depending on environmental conditions (Karstad & Hudson, 1986; Viljoen, 1995; Barklow, 1997; Klingel, 2013).

Hippo social groupings can be divided into two main categories; nursery groups, which comprise females and their offspring that move between territories in response to changing water levels (Karstad & Hudson, 1986; Klingel, 1991 in Eltringham, 1993; Blowers *et al.,* 2010); and bachelor groups consisting of sub-adult males that have been evicted from their natal groups at 7-8 years of age (Dittrich, 1976; Skinner *et al.,* 1975, and Attwell 1963, in

Karstad & Hudson 1986; Klingel, 2013). Karstad & Hudson (1986), however, reported that bachelors remained solitary and showed little site fidelity. The animals within these groups are socially but anonymously attracted to one another, thus these groups are unstable social units based on a shared need for suitable resting places (Klingel, 2013).

Even though hippos have been equipped with formidable tusks and fight during territorial take-overs, they are remarkably tolerant of conspecifics, including neighbouring dominant bulls, as long as the latter behave subordinately (Klingel, 2013) when not in their own territory. Vocal and postural communication is vital to maintaining social structures within hippo groups whilst minimising the need for overt aggression (Karstad & Hudson, 1986). Social signals include dominant behaviours such as the animal holding its head up, dung spraying/showering (when a bull rapidly wags his tail, scattering faeces and urine in the vicinity) and gaping (open mouth exposing tusks – longer in duration than a 'yawn' which is thought to be an expression of excitement; Karstad & Hudson, 1986; Blowers, *et al.* 2010; Klingel, 2013). Submissive behaviours include holding the head low, lip smacking and tail wagging/paddling (lifting hindquarters clear of the water whilst rapidly wagging its tail) (Karstad & Hudson, 1986; Blowers, *et al.*, 2010; Klingel, 2013).

Hippos communicate vocally using a variety of calls, including aerial, underwater and uniquely amphibious calls, involving transmission of sound through air and water simultaneously (Barklow, 2004). The most common under water sounds include clicks, croaks and whines, with the most common amphibious call, often referred to as a wheeze-honk, consisting of a tonal element with a series of grunts (Barklow, 2004; Blowers, *et al.*, 2010; Klingel, 2013). This wheeze-honk call elicits a seemingly contagious response from all individuals within the group, even spreading to neighbouring groups, and is often given in response to a disturbance (e.g., hippo fights, predators, human presence) (Barklow, 2004; Blowers, *et al.*, 2010; Klingel, 2013). Calls are distinct and may serve as a means of individual identification (Klingel, 2013).

Klingel (2013) suggested that the only stable association, with individual recognition, is between mother and calf. The work of Blowers *et al.* (2010) on captive hippos, however, suggests that hippos are attracted to kin and individuals that are more familiar and that groups are thus non-random in composition. Unfortunately no genetic studies on relatedness within and between wild hippo groups have been conducted to support or refute this suggestion.

Distribution and abundance

The IUCN identified exploitation (unregulated hunting and poaching) and habitat loss (associated with water abstraction, diversion, land-use change and human population expansion) as the two greatest threats to hippo populations across sub-Saharan Africa (Lewison & Oliver, 2008). An overview of the IUCN (2014) red list on the state of hippos in Africa suggested a total population of 125000 – 148000 hippos; with 20 out of 35 countries reporting declining populations and eight countries including Chad, Ethiopia, Kenya, Malawi, South Africa, Tanzania, and Zimbabwe reporting stable populations. Only Zambia reports a growing population, with Uganda having a potentially increasing population. The remaining seven countries in which hippos occur do not have data on the status of the hippo population due to limited research often hindered by ongoing civil unrest (Lewison & Oliver, 2008).

Hippos are notoriously difficult to count as they spend most of the day submerged in water and seldom surface together (Klingel, 2013). Aerial or boat-based methods are the most common methods used for hippo population counts. However given that these censuses are costly, the data are generally poor with the most comprehensive data found in the IUCN Red List compiled from data collected in late 1980s and early 1990s (Lewison & Oliver, 2008). An update of which is certainly required, as Mackie *et al.* (2012) points out, with an estimated 3000 hippos currently in Mozambique instead of the 18000 hippos reported in the IUCN Red list (version 2012.1). Furthermore, the current South African hippo population is increasing (an estimated 6300 hippos; CITES Scientific Authority of South Africa, 2011), instead of being stable at 3000–5000 individuals as quoted in the IUCN (2014) red list derived from census records that commenced in the late 1980s.

The state of the South African hippo population

Even though the South African hippo population is growing and predominantly protected within national and private reserves, this species' reliance on fresh water (as both a refuge and a resource) is placing it at odds with a growing human population that consumes large quantities of water and transforms wetlands (Lewison & Oliver, 2008; CITES Scientific Authority of South Africa, 2011). The expansion of protected areas within South Africa has seen an increase in the total distribution of hippos, which are again present in small patches across much of their historic range (Taylor, 2013; CITES Scientific Authority of South Africa, 2011). However, these fragmented and isolated populations are invariably too small to be considered genetically viable and must thus be managed as a metapopulation (Taylor, 2013). The only viable independent populations remain in the Kruger National Park (3000 – 4000, CITES Scientific Authority of South Africa, 2011), adjacent areas in the Limpopo River, Ndumo Game Reserve and St Lucia Estuary (within iSimangaliso Wetland Park, in KwaZulu-Natal) (Taylor, 2013).

According to the CITES Scientific Authority of South Africa's (2011) most recent report on the status of the national hippo population, there is an increase in both human-hippo conflict (on communal and commercial farmland) and poaching in the KwaZulu-Natal province. For the moment, the KwaZulu-Natal population is still stable, mostly due to the large proportion of the population residing in well-managed and protected National reserves, such as the iSimangaliso Wetland Park, where hippo numbers are increasing annually.

The importance of the St Lucia Estuary

The St Lucia Estuary, within iSimangaliso Wetland Park, is not only one of Africa's largest and most productive estuaries, but it is also home to one South Africa's largest hippo population (Cyrus & Vivier, 2006; Whitfield, 2013). Both the study area and the hippo within it are thus of national significance (Taylor, 2013) and it is surprising that so little has been done (i.e., a Masters thesis by Taylor, 1980) to understand the ecology and behaviour of these mega-herbivores within the system.

Estuarine environments are highly dynamic and heavily impacted by human development, with a range of anthropogenic disturbances (e.g., abstraction of headwaters, land-use change, alien species invasion, pollution, increased climatic extremes) threatening their ability to support natural plant and animal communities (Perissinotto, *et al.*, 2014). Climate change predictions suggest that the KwaZulu-Natal coast may experience a 40cm rise in sea level with up to 10% increase in annual rainfall in the next 100 years (Været, 2008). The predicted changes may buffer the St Lucia estuarine system against droughts whilst increased water levels may compensate for the current 'shallowing' caused by sediment accumulation (Whitfield & Taylor, 2009; Whitfield *et al.*, 2013). In the short and long term, change is the only constant within the St Lucia Estuary.

Since Taylor's (1980) hippo land capability study, the St Lucia Estuary has undergone numerous changes including the removal of all pine plantations from the eastern shores and the reestablishment of grasslands (Taylor, 2013). This has potentially increased the available foraging area for hippos, and thus increased the system's capacity to support the growing hippo population (Taylor, 2013). With a near doubling of the number of hippos in the system in the past 25 years and uncertainty over the system's carrying capacity, there is an urgent need to understand the habitat requirements of hippo within this closed system (Taylor, 2013). However, the iSimangaliso Wetland Park, and the St Lucia Estuary within it, is not exempt from the threats facing hippos throughout Africa with both climate change and human encroachment posing long-term risks to the population.

The recent extended drought-phase (2002 –present) punctuated by a brief wet period in 2012-2013, has seen marked fluctuations in water levels, salinity and vegetation throughout the system (Taylor *et al.*, 2013c/d; Chrystal & Scharler, 2014). Water levels were at their lowest recorded level (water covering only 10% of lake surface area in July 2006 – Cyrus *et al.*, 2011), with salinity levels increasing up to twice that of sea water (Whitfield, 2013). This event forced the realisation that the future viability of the estuary and its ecosystem functioning requires active management. Groundwater flow to St Lucia has potentially been restored through a combination of pine plantation removal from the Eastern shores (the last of which was removed in 2006; Været *et al.*, 2009) together with indigenous vegetation restoration in the area (Whitfield & Taylor, 2009). However, Whitfield & Taylor (2009) suggested that this is not enough to ensure sufficient water levels throughout drought phases; instead, the reconnection of the Mfolozi River, with a recreated Mfolozi floodplain swamp filter (Fig. 1.3) is needed for the future viability of the estuary (Whitfield *et al.*, 2013). However, management needs to consider how changes to the system (e.g. relinking the Mfolozi River to the St Lucia Estuary in hopes of reopening the estuary mouth) may affect the hippo population. Hippos are dependent on water as a refuge and exhibit preferences for shallow waters (≤1.5m; Taylor, 1980; Blowers *et al.*, 2010; Klingel, 2013), thus changes to the water level may result in changes to hippo spatial distribution, which in turn may influence the ecosystem as a whole given hippos are considered to be ecosystem engineers.

Hippos are an ecologically important species both in the terrestrial and aquatic environments. On land they maintain hippo lawns that provide grazing for other mammalian grazers (Kanga, *et al.*, 2011) and by defecating in the water hippos transfer nutrients from the terrestrial - to the aquatic environment effectively fertilising lakes and rivers (Klingel, 2013; Taylor, 2013). Hippos shape swamplands by changing water flow patterns through the establishment of hippo paths (McCarthy *et al.*, 1998; Klingel, 2013). Hippos may therefore have played, and may again play, a vital role in the maintenance of the Mkhuze and Mfolozi swamps (Fig. 1.3), which act as sediment traps and are essential to maintaining sufficient water levels within the St Lucia estuary (Taylor, 1980; Whitfield & Taylor, 2009; Whitfield *et al.*, 2013).

The continued expansion of human settlements and associated land-use changes in the area surrounding the iSimangaliso Wetland Park have resulted in an increase in demand for water from an already heavily impacted catchment (Whitfield & Taylor, 2009; Chrystal & Scharler, 2014; Taylor *et al.*, 2015). River abstraction and diversion, and the increasing pressure being placed on groundwater resources combined with low rainfall, are leading to lower water levels and the onset of more permanent changes to the abiotic and biotic factors that define the current system (Whitfield & Taylor, 2009; Chrystal & Scharler, 2014; Taylor *et al.*, 2015).

Understanding hippo habitat selection and how changes to key determinants alter hippo distribution and persistence within the St Lucia Estuary is paramount to the successful management and conservation of not only the St Lucia estuarine hippo population but also the entire estuarine system and fringing habitats connected by hippo activities. This study aimed to contribute to our understanding of the resident hippo population by identifying the factors that influence hippo distribution and site preference within the St Lucia Estuary. Ultimately, these data may be used to measure the hippo responses to further anthropogenic changes and identify key habitat variables for management.

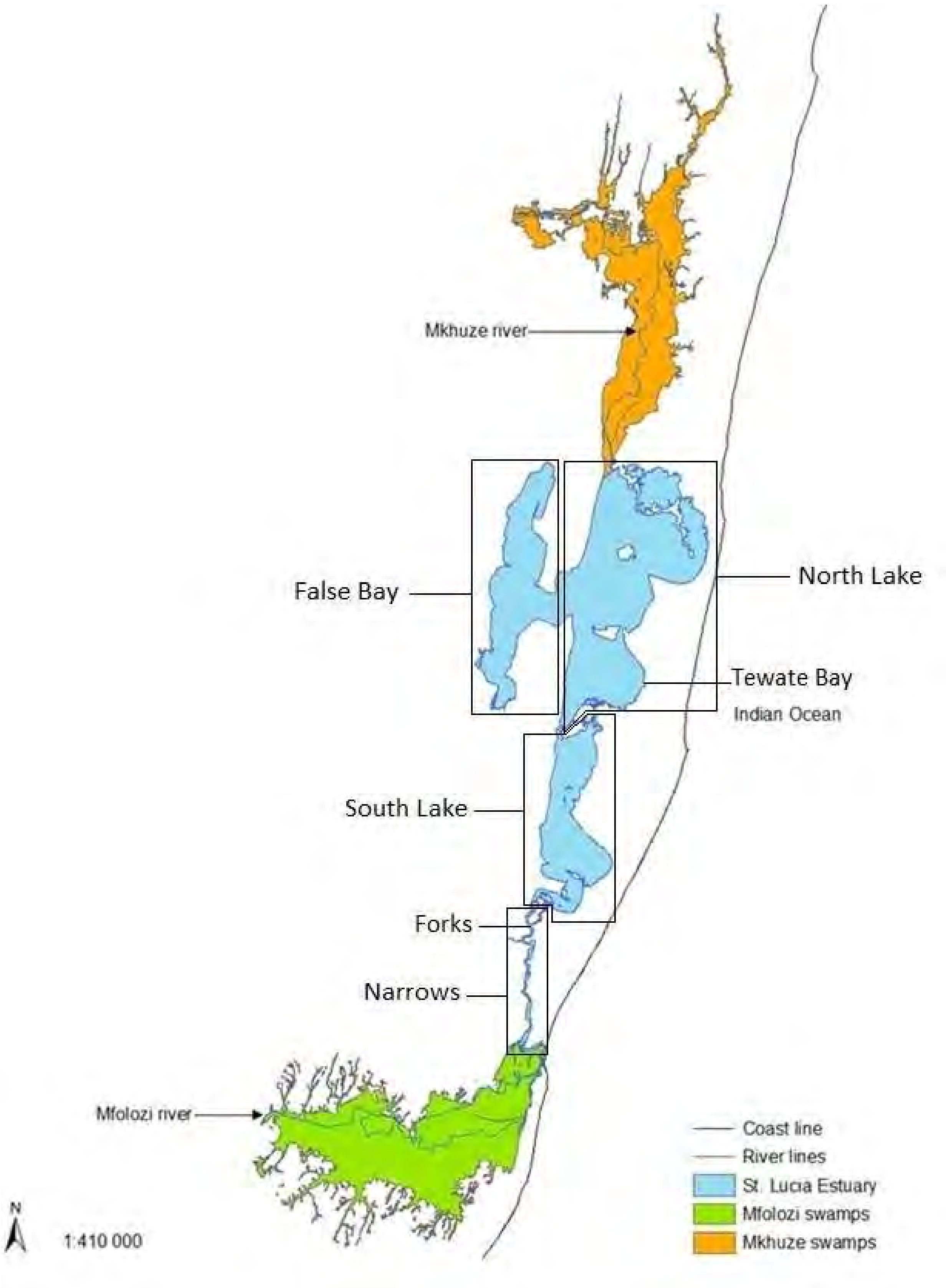


Figure 1.3: A map of the St Lucia Estuary with associated Mkhuze and Mfolozi swamps, the three lake components and the channel (Narrows) linking the lakes to the Indian Ocean.

The spatial ecology of hippos in the St Lucia Estuary

Population surveys, conducted nearly every year since 1957, have documented the spatial distribution of hippos within the St Lucia Estuary. Historically, hippos were distributed throughout the entire St Lucia Estuary, with the first survey recording a population of 189 hippos. Hippo were located in False Bay (especially in the southern sections near the Nyalazi and Hluhluwe river inlets), the northern parts of North Lake (where Mkhuze river enters), along the eastern shores of North Lake, and along the eastern- and western shores of South Lake, with a few hippo groups settling in the Narrows (predominantly at the Forks; Fig. 1.3) (Taylor, 2013). By 1979 the St Lucia hippo population had increased to 549 hippos, however, their distribution had shifted substantially. Human encroachment, water abstraction, land-use change and subsequent habitat loss contributed to the displacement of hippos from False Bay and the Mkhuze Mouth areas, with a greater density of hippos settling along the eastern shores of the Lakes and within the Narrows (Taylor, 2013).

Since the initial survey in 1957, this population has increased by 2-3% per annum, with a near doubling of numbers in the past 25 years (Lewison & Oliver, 2008; Taylor, 2013), resulting in a 2011 population count of 1137 hippos (Taylor, 2013). Following the onset of the recent drought and the associated shallowing of the entire system, hippos in North Lake have been compressed into Tewate Bay, where groundwater seepage maintains a small pond and provides access to fresh drinking water (Fig. 1.3), whilst others have moved south into the Narrows, potentially in search of lie-up sites of adequate water depth (Taylor, 2013). Without a known carrying capacity for the area, this near exponential growth in the hippo population, combined with the observed distributional shifts (higher hippo densities potentially increasing demands on natural resources) is of great concern to management as it could lead to overgrazing and increased human-hippo conflict (Taylor, 2013).

Numerous studies have indicated the importance of spatial analyses of abiotic, biotic and anthropogenic factors affecting the distribution of both aquatic and terrestrial species. Some examples include the influence of weather patterns on the behavioural ecology of baboons (Bronikowski & Altmann, 1996), the effect of landscape heterogeneity and surface water availability on the distribution and density of elephant populations (Chamaillé-Jammes *et al.*, 2007; de Beer & van Aarde, 2008) and the resultant changes in spatial distribution and densities of a variety of animals in response to anthropogenic disturbance (Averbeck *et al.*, 2012; Hoffman & O'Riain, 2011). Preferred water depths and habitat types (rocky reefs) have been identified as determinants of Indo-Pacific humpback dolphin distribution (Karczmarski *et al.,* 2000), whilst the influence of climate variation on prey availability have had indirect effects on the distribution and social organisation of bottlenose dolphin- and killer whale populations (Lusseau *et al.,* 2004). With an improved understanding of a species landscape requirements we are able to develop more effective conservation strategies, identify areas or resources that are of greatest importance to a species survival and potentially limit human-animal conflict.

The importance of behavioural ecology

Evaluating activity budgets (how much time animals allocate to different activities) and activity patterns (temporal distribution of activities during a 24-hour period) offers insights into the potential environmental, social and endogenous factors influencing survival and reproduction of wild animals (Fernandez-Duque, 2003; Aschoff, 1966 in Váczi, *et al.*, 2006). Activity budget and activity pattern studies have been used to gain a better understanding of the interactions and responses of a diverse group of terrestrial and aquatic animals including dolphins (Neumann, 2001), manatees (Miksis-Olds, *et al.*, 2007), ducks (Chettibi, *et al.*, 2013), greater rheas (de Azevedo, *et al.,* 2010), bats (Betts, 2010; Presley, *et al.,* 2009), elk (Green & Bear, 1990; Naylor, *et al.*, 2009), roe deer (Sönnichsen, *et al.*, 2013), hyenas (Kolowski, *et al.*, 2007) and numerous primate species (Fernandez-Duque, 2003; Guo, *et al.,* 2007; Kosheleff & Anderson, 2009; van Doorn *et al.,* 2010) to changing environmental or social conditions.

Observed differences in activity budget or activity patterns have been linked to differences in habitat structure, food availability, predation pressure, sex and age of individuals, time of day, weather, season, group size and anthropogenic disturbances (Neumann, 2001; Váczi, *e. al.*, 2006; Guo, *et al.*, 2007; de Azevedo, *et al.,* 2010; van Doorn, *e. al.*, 2010; Averbeck *et al.*, 2012). Thus, such studies allow us the opportunity to evaluate changes in behaviour that result from both natural and anthropogenic influences, making this type of study invaluable to management and conservation initiatives (Stock & Hofeditz, 1996 in Neumann, 2001; Miksis-Olds, *et al.,* 2007; Kosheleff & Anderson, 2009; Naylor, *et al.*, 2009; Presley, *et al.*, 2009; de Azevedo, *et al.*, 2010; Chettibi, *et al.*, 2013).

Animals alter their activity budget allocation in response to internal (digestive system, sex, age, physiological constraints) and environmental (forage quality/ quantity, predation risk, human activity and weather conditions) constraints (Green & Bear, 1990). Thus, understanding mammalian socioecology stems from a thorough understanding of how activity budgets and activity patterns are constrained by the ecological and demographic factors acting on an animal (Hill *et al.*, 2003). Once an animal has fed enough to meet its daily energetic requirements the remainder of its time may be allocated to the other activities, such as resting, moving or socialising (Doenier *et al.*, 1997 in Neumann, 2001). In this regard, hippos are a particularly interesting species to study as they exhibit a unique combination of physiological and behavioural adaptations to life at the interface between land and water (Boisserie *et al.*, 2011).

Aims, objectives and thesis outline

While hippo population numbers in St Lucia Estuary have been monitored since 1957 (Taylor, 2013), there has been no attempt to date to understand the factors influencing the distribution of hippos within the estuary or to improve understanding of hippo activity budgets or behaviour generally. In view of the above, the main aim of this dissertation is to provide information on the factors that affect the distribution of hippos within the St Lucia estuarine system and the frequency with which hippos utilise certain areas within the Narrows (the most densely populated biotope). Together these findings may provide information on the landscape requirements of hippos, highlighting the habitat variables of most concern to hippo conservation within this system. The secondary aim is to explore aspects of the behaviour of a single group, in order to generate baseline data on hippo diurnal activity budgets and social behaviours, in an attempt to improve our understanding of the behavioural ecology of hippos living in estuarine habitats that have and are being heavily impacted by anthropogenic factors (Perissinotto, *et al.*, 2014). Knowledge of changes in time allocation by hippos to specific activities (activity budgets) or changes in the frequency of certain social behaviours may function as bio-indicators of system health. Despite the limitations inherent in observing wild hippos, I considered it a worthy objective in the St Lucia Estuary as there is paucity of such data available in South Africa despite the potential of such data to inform both conservation and wildlife management decisions.

My dissertation is organized into four chapters: this chapter functions as an introduction to what is currently known about hippo taxonomy, morphology, habitat and feeding ecology, reproductive and social behaviour, conservation status and the national population distribution in the broader context. I also focus on the ecology and current status of the St Lucia Estuary and the hippo population residing within the system, setting out the main aims and objectives of the current study. Chapter 2 details the data collection, analysis and statistical methods used for both the spatial and the behavioural components of this study. The results are outlined in Chapter 3 and discussed in Chapter 4. I've elected to combine the spatial and behavioural components of the study in order to encourage a holistic approach to evaluating hippo spatial distribution and diurnal activity budgets and behaviour, given the degree to which behavior and ecology are interlinked.

Chapter 2: Methods

A: Spatial ecology of hippos

Study site

The iSimangaliso Wetland Park (between 27° 52′ S and 28° 24′ S and 32° 21′ E and 32° 34′ E), in northern KwaZulu-Natal, is classified as a UNESCO World Heritage site, and contains three Ramsar Wetlands of International Importance (Perissinotto, *et al.*, 2010) one of which is the largest estuarine system in Africa (Cyrus, 1989; Cyrus, *et al.*, 2011), the St Lucia Estuary (Fig. 1.2). The St Lucia estuarine system consists of three lakes (Fig. 1.2C; Fig. 1.3): False Bay, North Lake and South Lake, which flow into a narrow channel approximately 21km long, which connects to the Mouth, commonly referred to as the Narrows (Fig. 2.1; Perissinotto, *et al.*, 2010). The mouth connects through the Beach channel to the Mfolozi River, which feeds into the Indian Ocean at the Mfolozi Mouth (Fig. 2.1C). This link between the Mfolozi River and the St Lucia Estuary was re-established in July 2012 (Perissinotto, *et al.*, 2014), after having been severed in 1952 (Perissinotto, *et al.*, 2010). However, it is not a permanent link as it is affected by rainfall events and seasonal changes in water flow, resulting in an intermittent connection (Taylor *et al.*, 2013a; Taylor, *et al.*, 2015).

The St Lucia estuarine system includes a variety of vegetation types, including coastal forests, grassland, thicket, woodlands, wetlands and savannah (Scott-Shaw & Escott, 2011). Like many estuarine environments worldwide, it is threatened by land use change (e.g. forestry, cattle grazing, human settlement), water abstraction (Whitfield & Taylor, 2009) and poaching (Taylor *et al.*, 2013a).

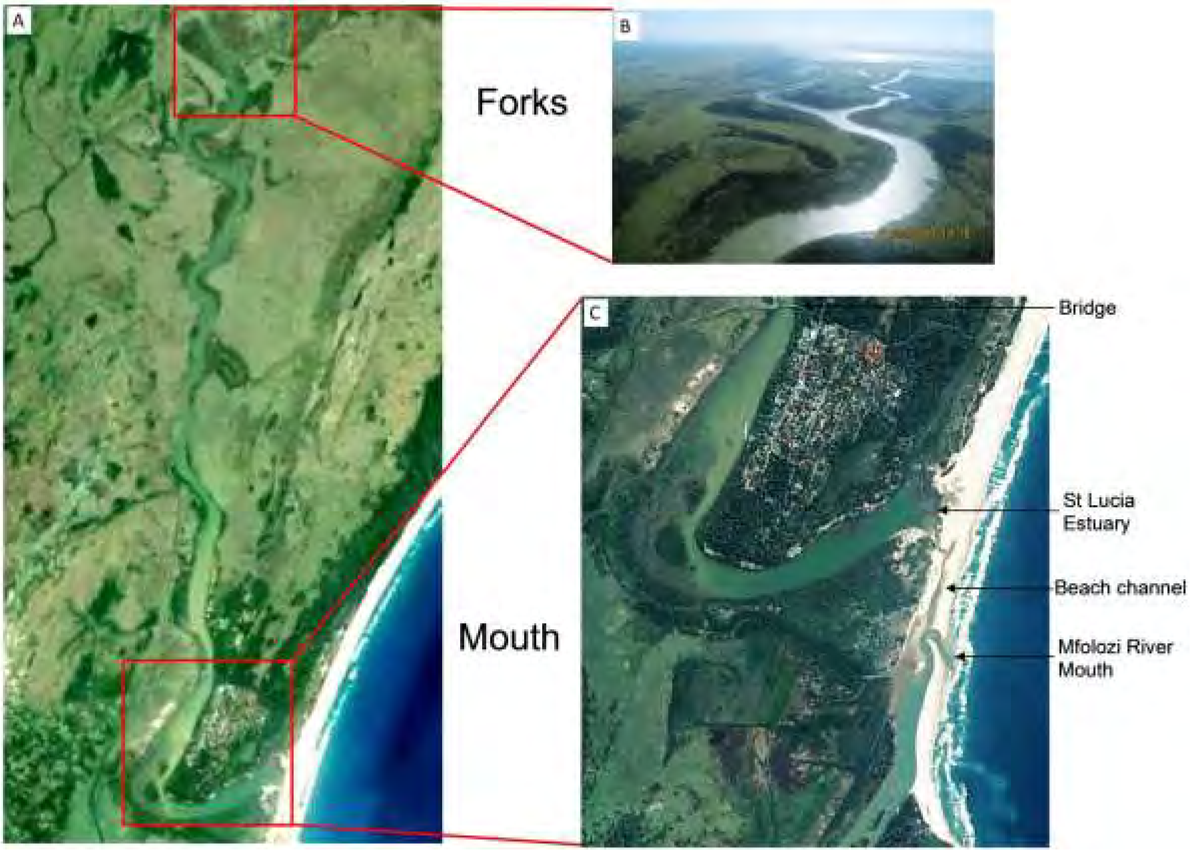


Figure 2.1: Google Earth imagery of the Narrows (A), focussing on the Forks (aerial photograph, B) and the Mouth (C) with its associated features.

The St Lucia Estuary experiences a subtropical climate, associated with hot, humid summers and mild winters, with an average minimum temperature of 16.90 ± 3.95 °C and an average maximum temperature of 26.97 ± 3.57 °C (AGRIC unpublished data provided by Ezemvelo KZN Wildlife). The climate is strongly influenced by the warm Agulhas current and has shown high inter-annual rainfall variability with quasi-periodic drought/ flood periods (Stretch & Maro, 2013). St Lucia experiences a wet- (October – March, 133 ± 91mm rainfall) and a dry season (April – September, 77 ± 65mm rainfall), with a mean annual rainfall of 1254 ± 330mm (unpublished data provided by Ezemvelo KZN Wildlife).

Spatial data collection

Broad-scale surveys

Two aerial surveys (26 November 2012 and 1 May 2013) were conducted by myself, volunteer spotters and two volunteer pilots (commissioned by the Bateleurs, a non-profit organisation flying for conservation). Volunteer pilots are assigned ‘missions’ as and when they are available to fly. I was therefore provided with a different pilot and plane for each survey. Community members volunteered as spotters to assist with hippo counts. Given the nature of volunteering and the weather dependence of flights, the number of available spotters differed between flights. On both occasions, a small fixed wing aircraft flew at low altitude (100m above sea level) along the periphery of the entire St Lucia estuarine system (Mouth, Narrows, South Lake, False Bay and North Lake; as seen in Figure 2.1C).

During the first survey, the pilot (experienced in aerial game counts) used the on-board navigation system to plot the GPS position (in decimal degrees) of hippo groups, whilst two spotters and I counted and recorded the total minimum number of hippos per group (Fig. 2.2A and 2.2B, examples of hippo groups).

During the second survey, we were unable to utilise the on board navigation system to record the GPS positions of hippo groups. Instead, I used a handheld Garmin GPS, recording the positions and total minimum count on a printed datasheet. A second spotter was responsible for photographing each hippo group in order to verify total minimum number of hippos per group.

Figure 2.2: Aerial photographs of hippopotamus groups taken during a census survey conducted on the 26th of November 2012. A total minimum count of 37 and 11 individuals were recorded from figures A and B respectively.

Ezemvelo KZN Wildlife's official annual hippo census was conducted on the 14th of June 2013, starting at 10:00 am. A small fixed wing aircraft flew at low altitude (100m above sea level) along the periphery of the entire St Lucia estuarine system (Mouth, Narrows, South Lake, False Bay and North Lake, Taylor *et al.*, 2013b). The approximate locations and a total minimum number of hippos observed were plotted on a handheld map during the flight, and subsequently plotted in Google Earth to obtain GPS coordinates of positions (Taylor *et al.*, 2013b). As such, the positional accuracy is coarse, and I thus opted to model hippo presence within a 1x1km grid, which does not assume the exact position of a group. During the aerial survey process individual groups were not plotted separately, instead, the data recorded are counts and locations in the system where any hippos were present. Thus, I was unable to use distance to nearest group as a predictor variable within the broad-scale data set. I entered the data obtained from this report, and each of the surveys conducted by myself and the Bateleurs, into an Excel spreadsheet, which I imported and transformed into a shape file in ArcMap 10.0.

According to the 2011 hippo census conducted by Ezemvelo KZN Wildlife, an estimated 1250 hippos reside within the St Lucia Estuary and adjacent wetlands (Taylor, 2013). When I compared the 2011 estimates to my two surveys (November 2012 and May 2013) and the June 2013 Ezemvelo KZN Wildlife hippo census (Table 2.1), it became evident that the inexperience of the spotters, the pilot and myself had resulted in a substantial underestimation of the total count. We thus decided to drop these data and to rely exclusively on the 2013 census data collected by Ezemvelo KZN Wildlife. Future counts will use the same methods as those used for this census and hence my findings will allow for comparisons over years and long term monitoring of the population.

Table 2.1: A comparison of the St Lucia Estuary hippo census results obtained during the three surveys conducted between November 2012 and June 2013.

Date	Survey conducted by	Total minimum number of hippos			
		Lakes	Narrows	Rivers	Other water bodies
26 November 2012	Myself, two spotters and a Bateleurs pilot	55	208	-	34
1 May 2013	Myself, one spotter and a Bateleurs pilot	124	397	-	-
14 June 2013	Ezemvelo KZN Wildlife	407	578	19	-

Fine-scale surveys

Using a small, shallow hulled boat with one 50 HP engine, a skipper and I traversed the Narrows on 10 occasions in the March – June 2013 period (dry season). Travelling at a steady speed (± 12km/h) up the Narrows, from the mouth to the Forks (Fig. 2.1A) both the skipper and I scanned the water for hippos. Upon sighting hippos, the boat slowed, approaching parallel to the bank and in line with the individual/group of hippos. After stopping 30-40 meters downstream of the hippos, the total minimum hippo count (using binoculars), GPS position in decimal degrees (using a Garmin handheld GPS device) and water depth in meters (using a 4m long aluminium pool pole, marked at 10cm intervals) were recorded on prepared data sheets. Ideally, water depths should also have been collected where hippos were absent to enable comparisons of water depths between sites where hippos were either present or absent. However, these data were not collected during the survey period, largely due to time constraints. To overcome this problem, water depth measurements were made in the St Lucia estuary in September 2013, at sites where hippos were absent. I divided the study area into 100X100m cells (n=362) and attempted to obtain a water depth for each of these cells for which hippos were absent during the March – June 2013 census period. Occasionally (n=140, out a total of 362) wind, water currents, encroachment of reed beds and the close proximity of hippos precluded a measurement. Given the extent of the estuary, these depth measurements required three days for completion (23, 27 and 30 September 2013).

To overcome temporal differences in water depths between the March-June and September sampling periods, water levels had to be corrected prior to analysing depth differences between sites with and without hippos. This was achieved by firstly averaging depth data that I collected during the March-June survey at a fixed water level gauge present on a bridge at the Narrows (n = 6, average water depth = 1.21m). I then compared this value to the depth data collected at the same water level gauge on each of the three sampling days in September (0.98m, 1.06m and 0.84m respectively). The difference in water levels between the two surveys was used as a correction factor and was added to each water depth measurement per site without hippos. With this adjustment, temporal changes in mean water depth between sampling periods (March-June and September) were accounted for in order to compare water depths between sites where hippos were present and absent.

Spatial data analysis

The spatial data analysis methods explained below have been modified from Hoffman and O'Riain (2011, 2012). I used ArcMAP (ESRI versions 10.0 and 10.1) for all spatial data analyses. I generated hippo distribution maps using overlays of habitat variables provided by Ezemvelo KZN Wildlife (Scott-Shaw & Escott 2011 vegetation maps; kznveg05v2_1_11_public_wll.shp), and the National Geo-spatial Information, located in Mowbray, Cape Town (NGI data 2013; river lines, human settlement, coastline). Maps were displayed in the geographic coordinate system WGS84, which I subsequently projected in

Transverse Mercator with central meridian 31, in order to facilitate distance and area calculations.

Habitat selection is scale-dependent thus the analysis of multiple spatial scales provides a more holistic understanding of underlying mechanisms driving landscape ecology (Orians & Wittenberger, 1991; Guisan & Zimmermann, 2000; Fausch, *et al.,* 2002). With this in mind, I set out to generate two separate data sets to understand drivers of hippo distribution at differing spatial scales (one broad-scale, spanning the entire estuary, including the three lakes and the Narrows; and a fine-scale data set, focussing on the Narrows where most hippos have traditionally been recorded (Taylor, 2013)). I selected and generated specific habitat variables for inclusion in the broad- and fine-scale analyses based on existing knowledge of hippos (see Chapter 1, e.g., water depth, position in relation to shoreline, nearest vegetation type).

Broad scale data

Using the ‘editing tool’, I first generated a St Lucia Estuary outline feature (Fig. 2.3A) and then using the ‘Geoprocessing tools’ I generated a 5000m buffer zone around the St Lucia Estuary outline feature (Fig. 2.3B). The buffer zone was set at 5000m to include the area that is theoretically available (Krausman, 1999) to hippos based on the average distance (ranging from >1km to 10km; Field & Laws, 1974; McCarthy *et al.*, 1998; Harrison *et al.*, 2007; Wengström, 2009; Chansa *et al.*, 2011a) that hippos are reported to travel in their nocturnal search for grazing. Given the fact that hippos do not utilise the marine environment, I then used the coastline feature provided by NGI to clip the buffer zone to ensure that it did not extend beyond the landmass into the Indian Ocean (Fig. 2.3C).

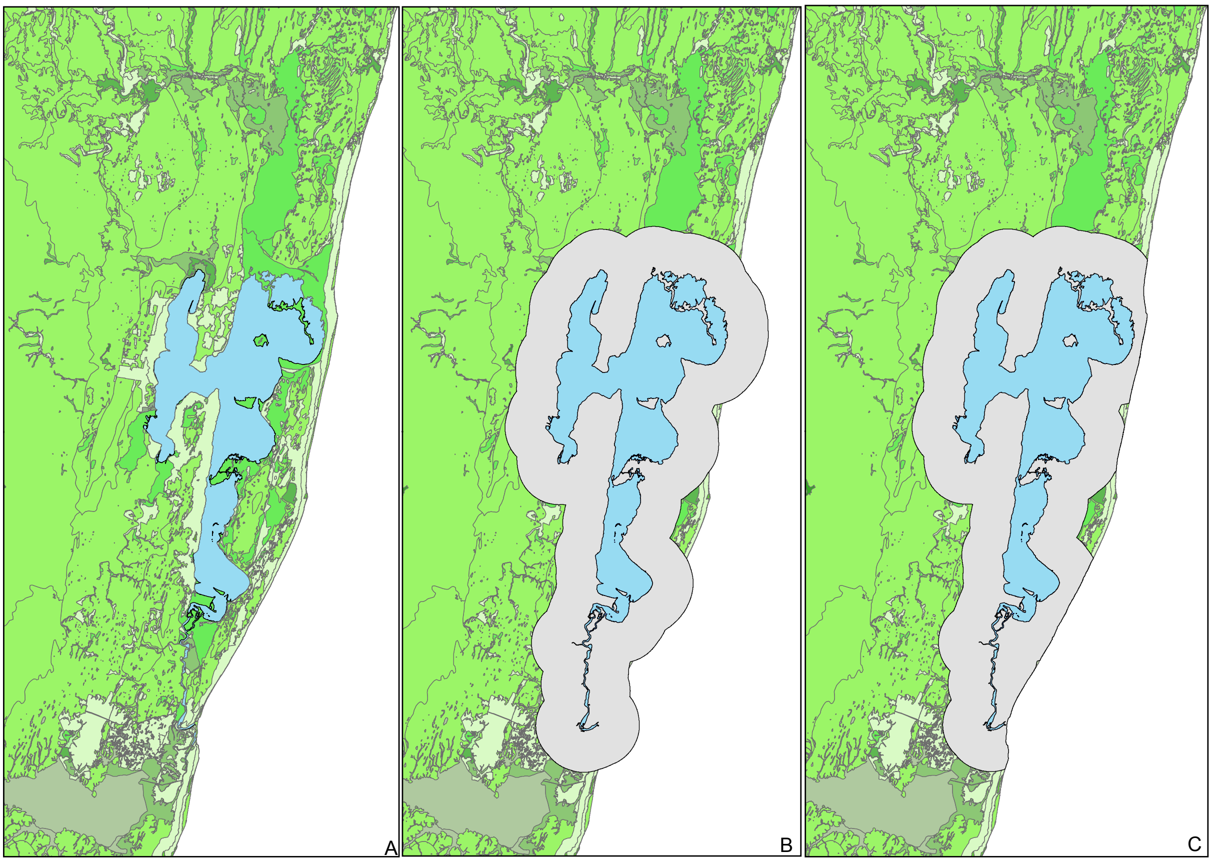


Figure 2.3: Vegetation maps showing the estuary (blue shading) outline (A) within the KZN vegetation map, the 5000m buffer zone (grey) established around the estuary outline (B) and the clipping of buffer zone the coastal outline (C) to provide the broad scale study area used for subsequent analyses.

Using the 'erase tool' I removed the estuary from the vegetation map as the estuary functions as a daytime refuge and is not a potential feeding site. Subsequent area and distance calculations for the dominant and nearest vegetation type did not therefore include water. I then used the 'Conversion Tool' in ArcToolbox 10.1 to generate a raster from the vegetation data at a resolution of 100m for my broad scale data (Fig. 2.4) set. This scale allowed me to explore the type of vegetation that dominates the area available to each hippo, not the precise area covered by each vegetation type. This broad-scale raster is used in all subsequent analyses that included vegetation data.

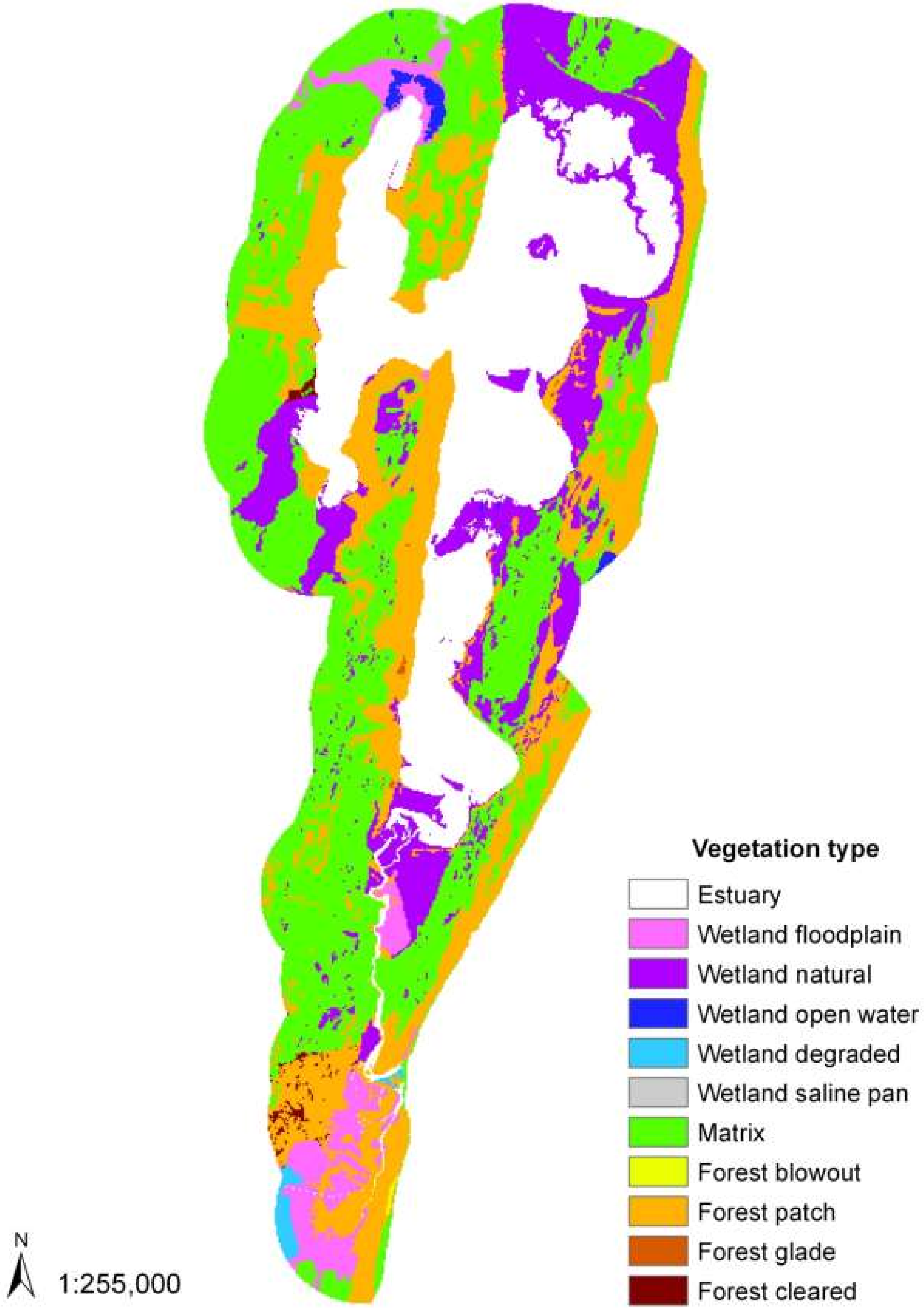


Figure 2.4: A map illustrating the different vegetation types within the study of the St Lucia Estuary.

Given the extent of St Lucia Estuary, and the low presence of hippo within the lakes biotope, I elected to examine the broad scale distribution of hippos on a 1X1km grid basis. Thereby minimising the high levels of zero-inflation, that are a consequence of low presence within the lakes biotope, and minimising the overlap in the generated habitat variable data. I generated the grid using the ‘fishnet tool’ (Fig. 2.5) and clipped the grid to fit the estuary outline, using the ‘Geoprocessing tools’. For cells that had been clipped (Fig. 2.6A), I used the ‘calculate geometry tool’ to determine the area of each clipped cell. Cells smaller than 250 000m^2 (i.e. 500X500m) were incorporated into an adjoining complete cell (Fig. 2.6B). To achieve this I used the ‘eliminate tool’, which merges selected polygons with neighbouring polygons that have the largest area. I did this in order to generate a broad scale data set representative of the landscape scale processes driving hippo distribution. Lastly, I converted each of these polygon features to points using the ‘feature to point’ tool. Here the centre of the cell viz., the centroid (Fig. 2.6C and Fig. 2.7) was used to derive a unique GPS point for each cell. These points were used for calculating distances from a given cell to a particular feature (e.g. distance to human settlement) in addition to serving as the reference point for inferring the biotope (aquatic habitat type) for each cell (e.g. river, lakes or Narrows).

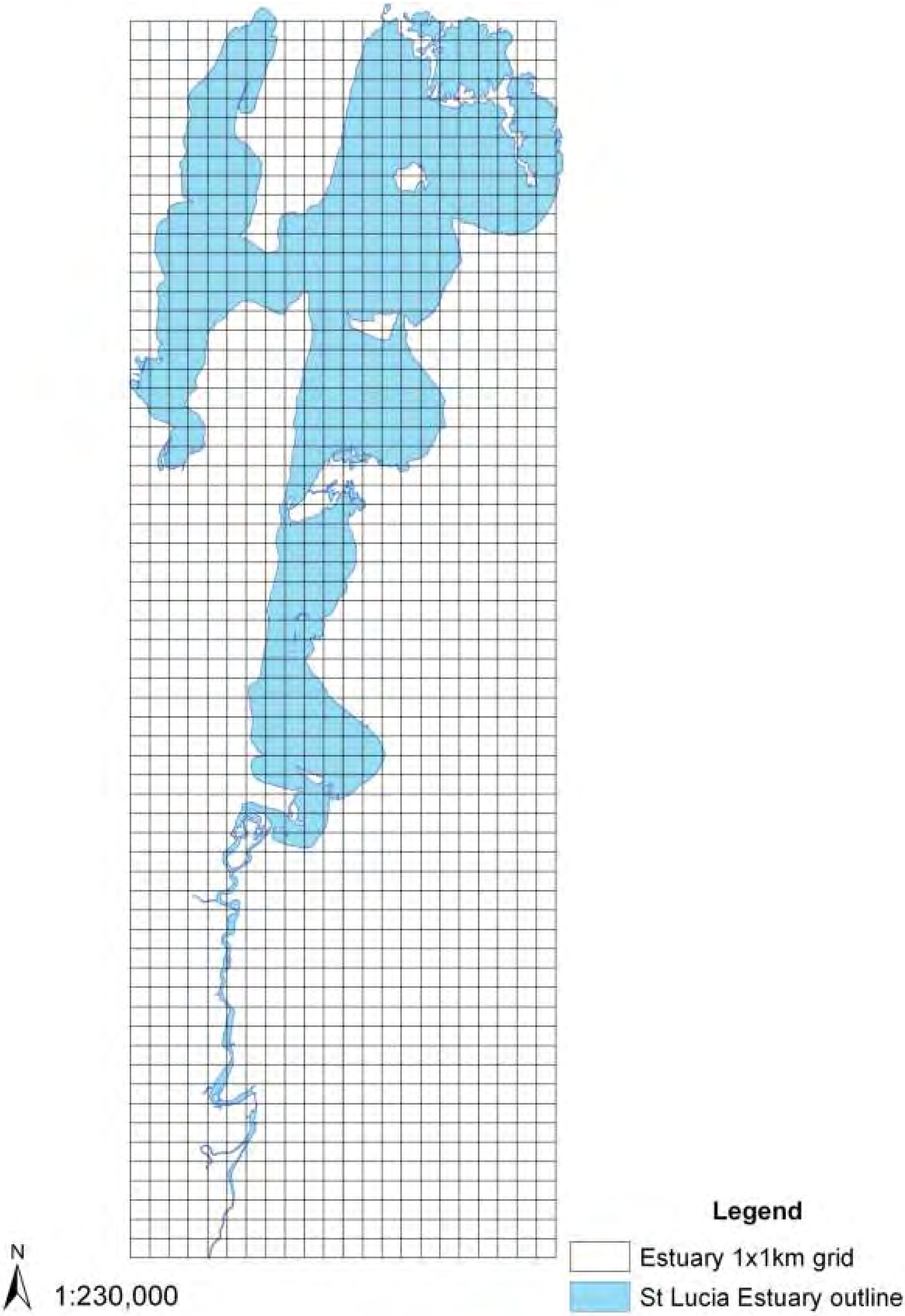


Figure 2.5: Map illustrating the ‘fishnet’ generated to create the 1X1km grid system over the St Lucia Estuary.

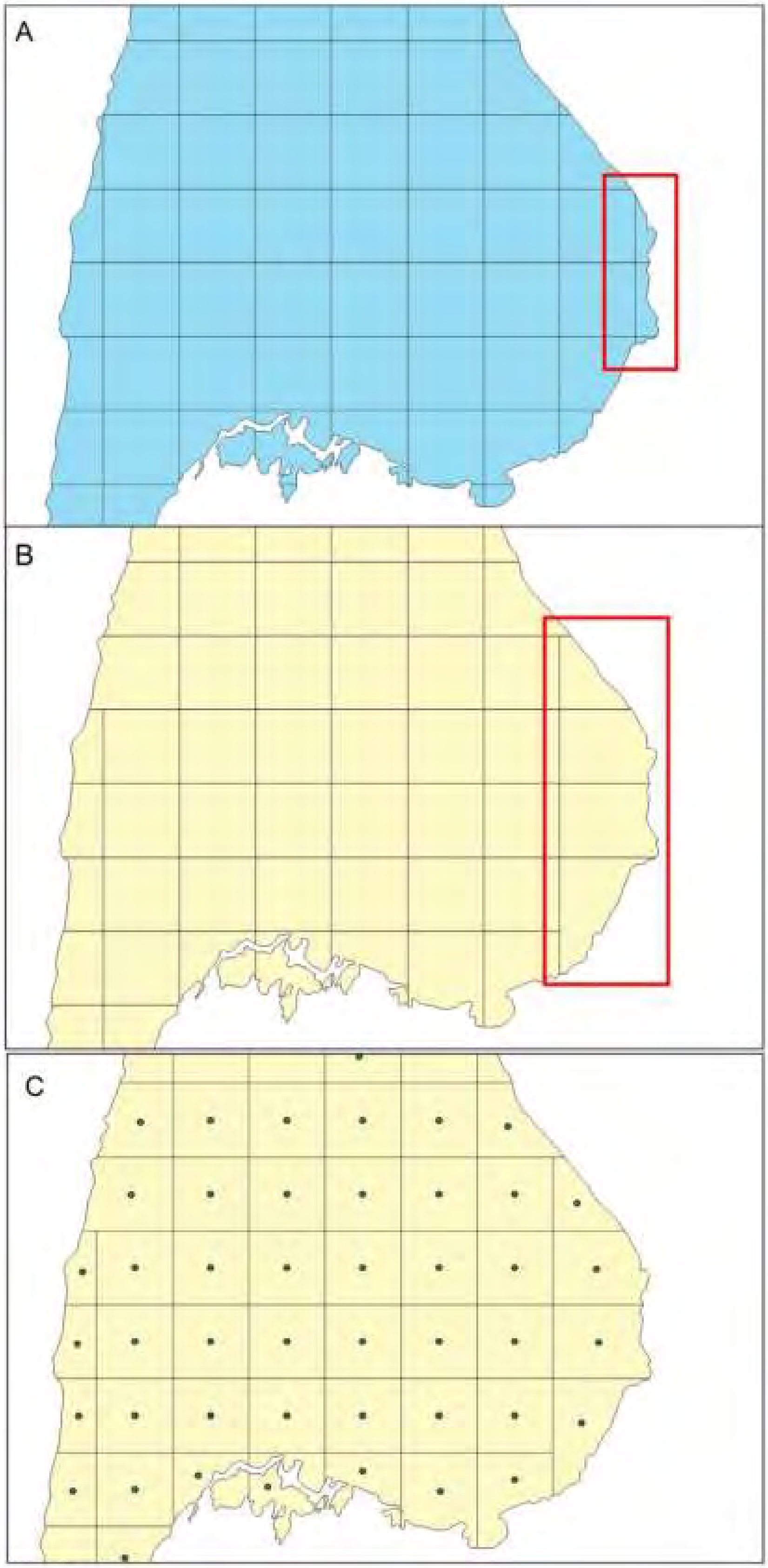


Figure 2.6: Maps of the study area showing the method I used to firstly overlay a grid system (A), then a clipped 1x1km fishnet grid, (B) and finally the merging of cells smaller than 25000m^2 and the insertion of GPS points as centroids for each cell (C).

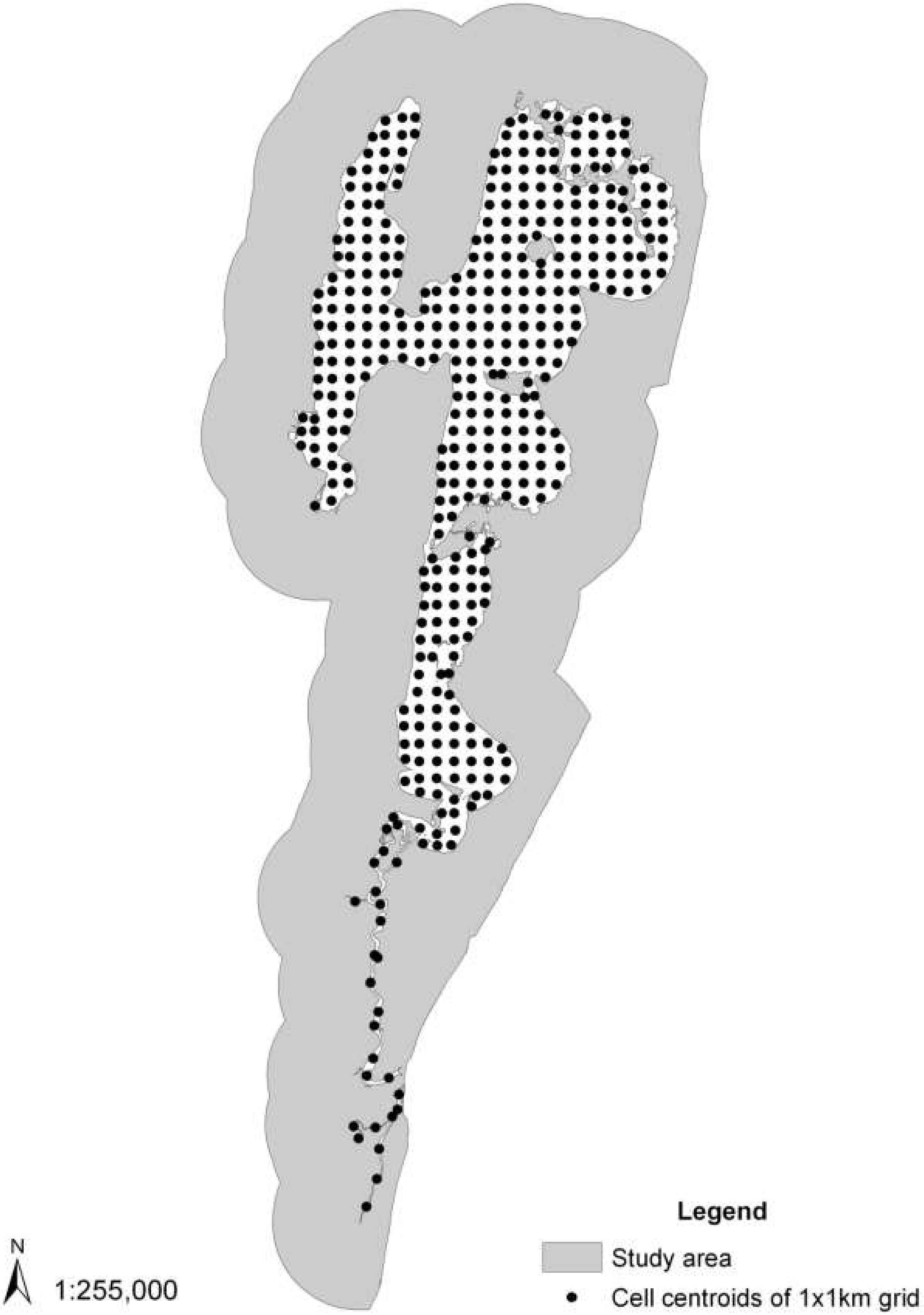


Figure 2.7: A map of the St Lucia Estuary showing the 1x1km grid of centroids (N=419) used for analysing the distance to river inlet, distance to human settlement, nearest vegetation type and dominant vegetation types.

Given the preference of hippos for slow-flowing, shallow systems (≤1.5m deep; Taylor 1980; Blowers *et al.*, 2010; Klingel, 2013), I distinguished between major aquatic biotopes. The Lakes were characterised by extremely shallow depth (>1.0m) with hyper-saline conditions reported during drought phases, with variable flow-rates (predominantly wind driven) (Whitfield & Taylor, 2009; Perissinotto *et al.*, 2010; Stretch & Maro, 2013). The Narrows was deeper (1.42m on average – based on direct measurements) and slow flowing, connecting the Lakes to the Mouth of the estuary. The Narrows experiences intermittent connection to the ocean and may experience fluctuations in salinity based on the distance from the estuary mouth. Rivers are of variable depth and flow rates, dependent on season and position within the watershed and provide freshwater to the estuarine environment (Været, *et al.*, 2009). I decided to use aquatic biotope as a categorical proxy for water depth in my broad scale data set, as direct measurement of water depth across the entire system was beyond the scope of this study. I hypothesised that a preference for the Narrows would indicate a preference for the associated deeper water depths (similar to those preferred by hippos elsewhere; Taylor, 1980; Blowers *et al.*, 2010; Klingel, 2013).

Using the 'selection tools', I selected all cell centroids along the periphery of the St Lucia Estuary (adjacent to the shore), defining these as sites which allow hippos direct access to the shore (1), and all other cells as those without direct access (0). I did this in order to evaluate the position of hippo territories in relation to the shore (with direct shore access or not). Hippos are known to defend territories along shorelines of lakes and rivers (Klingel, 2013); thus I hypothesised that hippo presence will exhibit a preference for sites along the periphery of the estuary.

I evaluated diurnal hippo presence in relation to two key environmental factors. Firstly, hippos are predicted to settle in water bodies that are in close proximity to their preferred vegetation type (i.e. short grasses found in open grassland, Eltringham, 1993; floodplain grasslands, Harrison *et al.*, 2007; or wetlands, Lewison, 2007; Mackie *et al.,* 2012). Thus, I tested the effect of nearest vegetation type on hippo presence by using the 'near tool' to calculate the distance from each centroid to the nearest vegetation type, thereby ascribing each cell with a nearest vegetation type. Secondly, according to Harrison *et al.,* (2007) habitat type has a greater effect on hippo distribution than distance from the water. I therefore predicted that hippos would preferentially occupy areas that have access to the largest area of their preferred habitat type. I generated a circular buffer of 5000m radius around each centroid (Fig. 2.8A) to represent the total area available to a given hippo when leaving the water to forage. The radius size selected represents the average distance a hippo travels from water per night (Klingel, 2013). As no such data exists for St Lucia Estuary itself, I used published data to determine the radius of the buffer used to delineate the effective foraging area from each centroid.

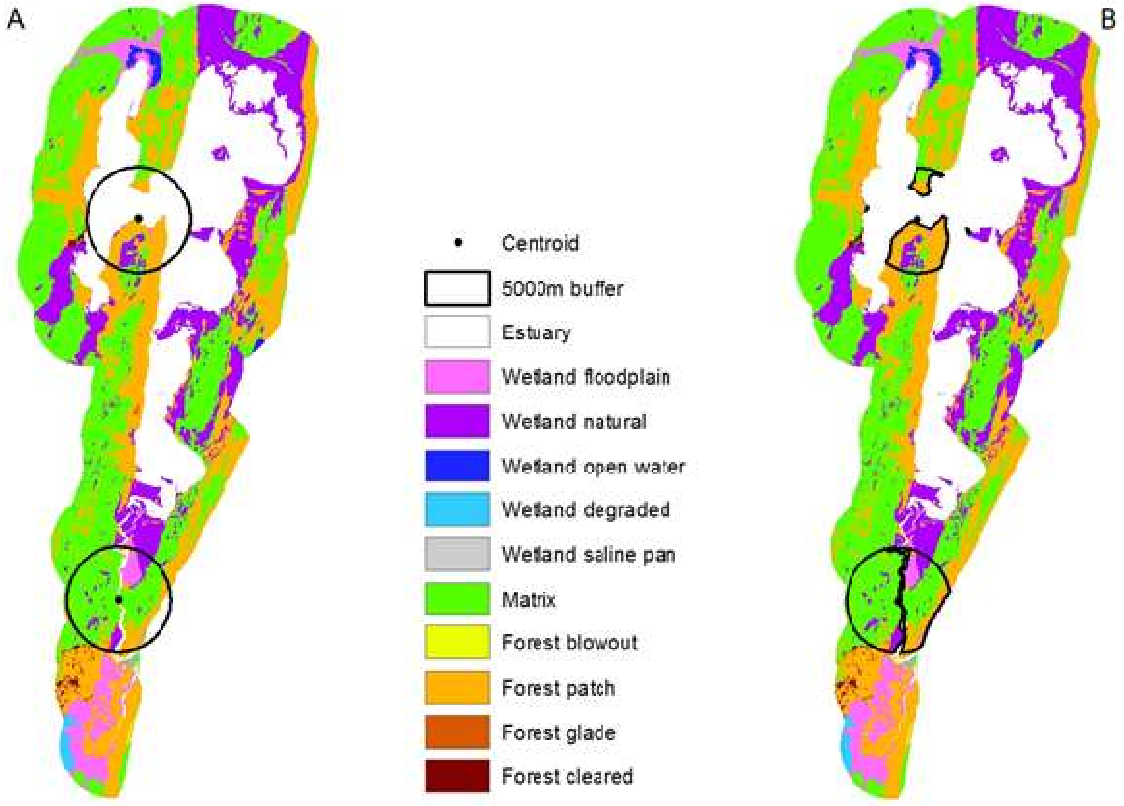


Figure 2.8: Maps showing the placement of the buffer circles around two selected centroids within the St Lucia Estuary study area (A), and the clipped buffer circles used to calculate the area of vegetation cover within each buffer circle (B).

For each circle I calculated the total area covered by each of the different vegetation types (i.e., Forest patch, Matrix, Natural wetland, Wetland floodplain and Forest cleared; as defined in Scott-Shaw & Escott, 2011) using the ‘tabulate area 2’ tool in ArcMAP 10.1 supplementary spatial analyst toolbox 1.3. I then identified the vegetation type covering the greatest area of each circular buffer and assigned this as the dominant vegetation type for each centroid. Given hippos preference for short grasses, I predicted that hippos would prefer areas where short grass vegetation dominates (i.e. Matrix, Natural wetland or Wetland floodplain) (Eltringham, 1993; Harrison *et al.*, 2007; Lewison, 2007; Mackie *et al.*, 2012; Attwell, 1963 in Chomba *et al.*, 2013).

I used overlays of the human settlement points (i.e., physical structures such as houses, schools, police stations; Fig. 2.9) to provide data on human presence. I excluded cultivated land or plantations as the associated land use layer was outdated and no longer represented the current state of the system. I also considered human settlements to represent, for the most part, high intensity land use and thus a better proxy for human presence within the study area. I predicted that hippo presence would increase with increasing distance from human settlements within the St Lucia estuarine system.

I used overlays of river line features (Fig. 2.10) to provide data on river features that may influence hippo presence. I did not distinguish between perennial (flows all year) and non-perennial (only flows during wet season, or following rainfall events) rivers, as the associated data were not available for all rivers within the layer. I edited the river line feature to erase all river lines except inlets (the point at which the river and the estuary converge) to generate the 'Inlet' variable. I predicted that hippo presence would decrease with increased distance from inlets.

Figure 2.9: A map showing the position of human settlements within the St Lucia Estuary study area, each dot signifies the location of a house, school, police station or shop, i.e. structures associated with human habitation.

Figure 2.10: A map showing the position of all rivers within the St Lucia Estuary study area. The point at which a river enters into the estuary was defined as an inlet.

Lastly I imported all GPS points where hippos were recorded (reported in the Ezemvelo KZN Wildlife June 2013 monitoring report, Taylor *et al.,* 2013b). Grid cells containing one or more hippo detection points were classified as cells with 'presence' (1) and those with no hippos detected were classified as 'absence' (0), giving rise to the binary data set (N=419, Presence=36, Absence=383).

After dividing the estuary into biotopes (lakes, Narrows, rivers), I used the 'measurement tool' to calculate the perimeter of the lakes and the distance along the central line of the Narrows and rivers respectively. I then summed the number of hippos counted per biotope and divided this by the measured distances, thereby calculating the hippo density within each biotope (hippos/km of river or per km of lake-shore respectively). This is in keeping with the current literature, which reports hippo densities as number of hippos per kilometre of river. I also calculated the area of each biotope using the 'calculate geometry' tool in order to allow for easy calculation of hippo density (individuals/km^2), for comparison with other mammalian species density distributions.

Fine-scale data

I used a motorboat to collect data on hippo presence/absence from the Mouth to the Forks (Fig. 2.1A). I excluded data from the lowest section (i.e., the bridge to the mouth, see Fig. 2.1C) as this area was subject to intermittent connections to the ocean via the Beach channel, resulting in marked short term fluctuations in water depth. Given the predicted importance of water depth to hippo presence, I excluded this area from the analyses as I was not able to sample water depth frequently enough to accurately reflect this variation. Above the bridge (approximately 4km upstream), water levels were much more stable and I thus included all presence and depth data from the Bridge up to the Forks (approximately 12.85km).

I used the same procedure as described for the Broad-scale data set to generate the Fine-scale data set. I generated a raster from the vegetation data at a resolution of 10m with cells sized 100X100m, in order to evaluate the fine scale habitat variables that may explain hippo distribution within the Narrows. I clipped the grid by erasing the lakes and the area downstream from the Bridge, resulting in some cells being smaller than 10000m^2 (Fig. 2.11A). As for the broad-scale data set, I incorporated cells >25% of the original cell size into adjacent cells, generating GPS positions corresponding to each of the grid cell centroids (Fig. 2.11B). These centroids were used in all subsequent distance and area calculations.

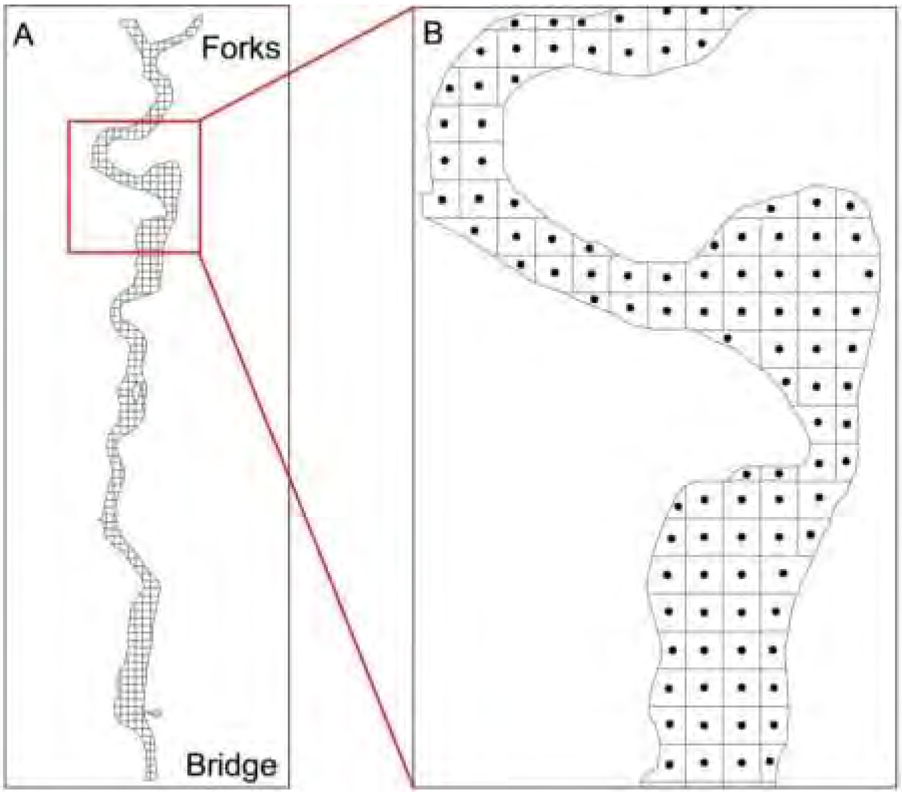


Figure 2.11: An illustration of the Narrows 100X100m fishnet grid system, extending from the Bridge to the Forks (A) and the GPS points inserted as centroids within the grid (B).

The position relative to the shoreline (adjacent to the shore/not), the distance to nearest human settlement (m) (Fig. 2.12A), distance to nearest inlet (m) (Fig. 2.12B), dominant vegetation type and nearest vegetation type (Fig. 2.12C) data were generated for the fine scale data set as described above for the broad scale data. However, given the fact that the Matrix vegetation is the dominant vegetation type for all cells within the Narrows data set, I removed the dominant vegetation variable from all subsequent analyses.

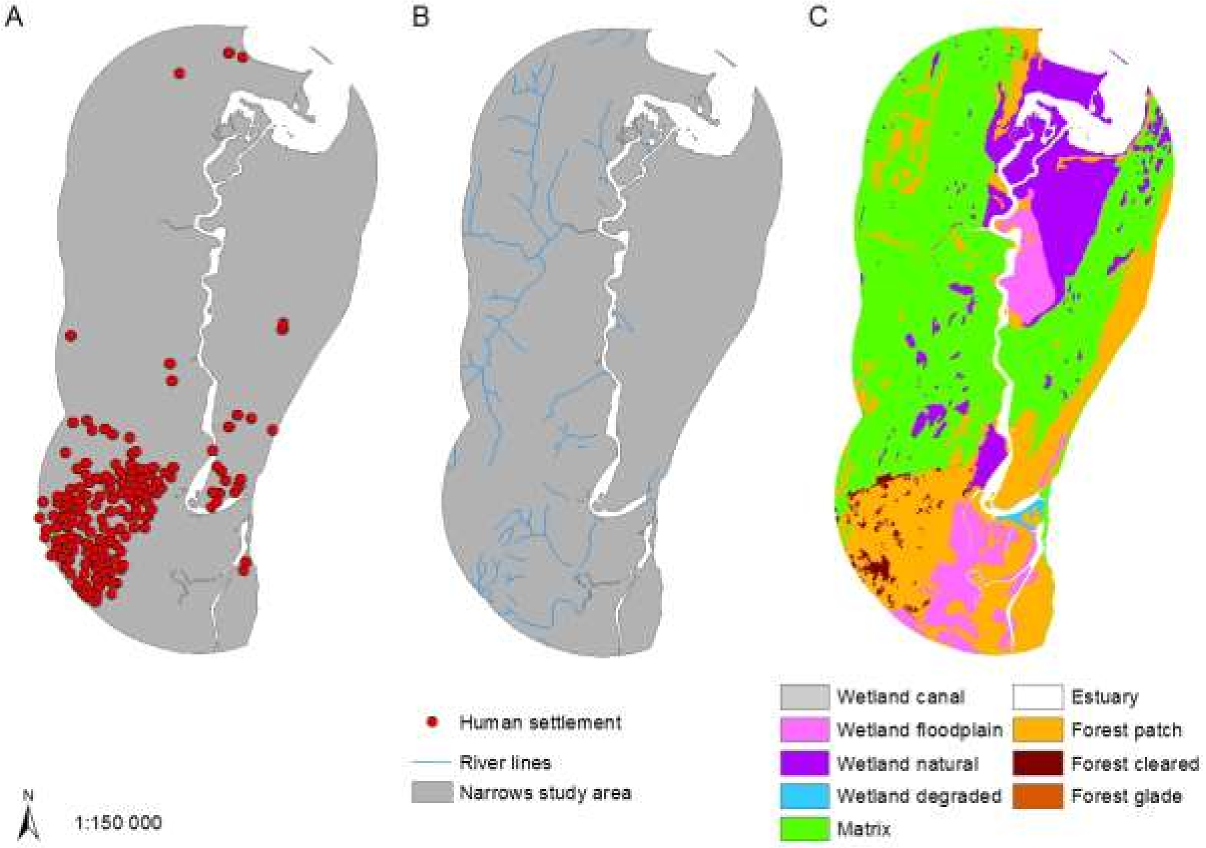


Figure 2.12: The 5000m buffer area surrounding the Narrows depicting human settlements (A), the river lines with associated inlet points along the banks of the estuary (B) and the vegetation types (C).

I imported the GPS positions with associated hippo counts and water depth data for each of the 10 census days performed during my boat based surveys. I calculated the average number of hippos observed per survey day. Using the ‘measurement tool’, I calculated the distance along the central line of the Narrows (12.85km). Subsequently, I calculated the density of hippos within the Narrows (number of hippos/km of river). I classified a group as being more than one hippo. I also imported the GPS positions and adjusted water depth data associated with hippo absence points. I subsequently projected these positions in Transverse Mercator, spheroid WGS84, central meridian 31. As with the broad scale data set, each grid cell within the Narrows data set containing one or more hippo points were classified as 'presence' cells (1) and those not containing any as 'absence' cells (0), giving rise to the binary data set (1/0; N=252, Presence=100, Absence = 152) for the Narrows. For each grid cell, I calculated the number of visits (i.e. the total number of times a group of hippos was detected within a cell on different days). Those cells containing only absence data points were classified as 0 visit cells.

I did not sample all cells within the Narrows for water depth as this was not logistically possible due the shallowness (<0.5m) of some sections of the estuary. Instead I included only cells with the associated water depth data into my analysis (n=252, hippos present=100 and hippos absent=152). I converted water depth into categories as follows; category 1 = 0.5 – 0.99m, 2 = 1.0 - 1.49m, 3 = 1.5 – 1.99m, 4 = > 2.0m. I included water depth categories into the analysis of hippo distribution in order to elucidate the preferred water depth for hippos in the St Lucia Estuary. Based on the average shoulder height of hippos (1.5m) I predicted that hippos within the system would select for water depth between 1.0 and 1.49m (i.e. Category 2) as this water depth will most easily facilitate submergence for thermoregulation and sun protection without having to use energy to surface for breath (Horikoshi-Beckette & Schulte, 2006; Blowers *et al.*, 2012).

To explore the potential influence of conspecifics on hippo intergroup distances (i.e. territoriality) and site fidelity, I calculated the distance (in meters) from the centroid of each grid cell to the nearest neighbour (those cells containing hippos) using the ‘near tool’. I predicted that distance to the nearest neighbour would increase with decreased hippo presence, i.e. occupied cells will be clustered throughout the system. I also predicted that the further apart occupied cells are, the fewer visitations those cells will have, (i.e., hippo frequency of occupancy decreases with increasing distance to nearest neighbour) indicative of a high degree of site fidelity and a preference for specific areas, irrespective of potentially increased hippo densities in favoured areas.

Spatial statistics

Data exploration and descriptive statistics

All data exploration and statistical analyses were undertaken using Excel (Microsoft, 2010), SPSS Version 22.0 (IBM Corp, 2013) and ArcMap 10.1 (ESRI, 2012). I explored my data by evaluating the zero-inflation within my data sets (the percentage of zero’s within my broad- and fine-scale data sets) and data dispersion (the ratio of variance to mean, whereby variance > mean represents over-dispersion and variance< mean represents under-dispersion). Both the broad-scale and fine-scale occurrence data sets were zero-inflated and under-dispersed whilst the fine-scale frequency of use data were zero inflated and over-dispersed (Potts & Elith, 2006; Appendix 1). The zero’s within my data sets are predominantly structural zero’s (i.e. absence of hippos due to cells being either unsuitable or suitable, but unused), however, a minimal number of zero’s within the broad-scale data set may be due to observer error during the fly-over.

I log-transformed the ‘Distance to human settlement’, ‘Distance to nearest inlet’, ‘Distance to nearest neighbour’ data, in an attempt to normalise these variables. Even though normality was not attained, the log-transformed data did improve subsequent model convergence. Therefore, log-transformed data were used for all continuous variables. I used non-parametric tests as all my data were non-normally distributed. I used Spearman ranked order correlation to simultaneously test for significant ($\alpha<0.05$) correlations between the dependant variable (hippo presence/absence or frequency of use) and selected predictor variables (broad-scale data, Appendix 2; fine-scale data sets, Appendix 3) and for multicollinearity among predictor variables (broad-scale data, Appendix 2; Fine-scale data sets, Appendix 4).

I evaluated the broad- and fine-scale data sets by comparing the available percentage of each predictor variable to the percentage of cells occupied by hippos within each selected category, thereby discerning the relationship between hippo occurrence and the predictor variables. The continuous data were evaluated using mean ± standard error (SE) and the range (min-max).

In order to evaluate the relationship between conspecifics I used the original field data, which is not grid-based (observed hippo groups, n=250). I calculated the distance from the centroid of each GPS point to the nearest neighbouring GPS point as recorded for hippo presence on that specific census day. I categorised the resulting data into 100m intervals, generating a frequency histogram of the distances at which hippos settled from their nearest neighbours (Appendix 5).

Furthermore, using an independent samples t-test I evaluated the difference between mean water depths of sites with and sites without hippos present, within the Narrows. Using an independent samples Kruskal-Wallis test I compared the total number of hippo groups, the size of each group and the total number of hippos recorded during the 10 non-consecutive survey days. Together these descriptive analyses provided me with a better understanding of my data set, which I then proceeded to test for spatial auto-correlation, and subsequently model as described in the next section.

Eliminating spatial autocorrelation

The 'fishnet tool' which I used to generate a grid system of cells for the broad- and fine-scale data sets has the unfortunate drawback of exacerbating spatial autocorrelation which was significant in all three data sets (Appendix 6). Consequently I used SPSS's random sampling tool (without replacement) to subsample my data and eliminate the spatial autocorrelation. In order to obtain fine-scale data sets that were comparable, I conservatively selected the sub-sampled data set that would eliminate the spatial autocorrelation within my fine-scale occurrence data (generating one sub-sampled data set to be used in both occurrence and frequency of use analyses).

Using the broad-scale data set as an example, I describe the procedure used to eliminate spatial autocorrelation from my data, thereby generating the final data sets that were used to model hippo spatial distribution (Appendix 7). The initial broad-scale data set contained 419 cases of which 36 were defined by hippo presence and 383 by hippo absence giving a 1:10.1 present/absent ratio (Fine-scale presence : absence ratio was 1:1.5). I subsampled my data proportionally, removing one presence point and as many absence points as was necessary to retain the 1:10.1 ratio. After each removal, I tested for spatial autocorrelation using the 'spatial autocorrelation (Moran's I) tool' in ArcMAP 10.1. Given the grid design of my data set, I conceptualized that hippo groups in bordering grid squares would have the greatest effect on one another. This led me to select a predefined conceptualization within ArcMAP, known as the 'Zone of indifference', to conceptualize the weights of the spatial relationships between grid cells when testing for spatial autocorrelation. The ‘zone of indifference’ weights cells as follows; nearest neighbours (those grid centroids within a predefined distance of one another; known as the ‘distance threshold’) are weighted as 1 and any centroids beyond the distance threshold would decrease in influence with distance. I set the distance threshold to 1000m, in order to conform to the broad-scale grid design (100m for the fine-scale data set), and standardised by row in order to account for the potential bias in the sampling design, as is best practise. I selected the largest subsampled data set that tested negative for spatial autocorrelation (Appendix 7). I generated graphic representations of the sub-sampled data sets in order to illustrate the hippo distribution data that were used to develop the statistical models (Fig. 2.13, Fig. 2.14 and Fig. 2.15).

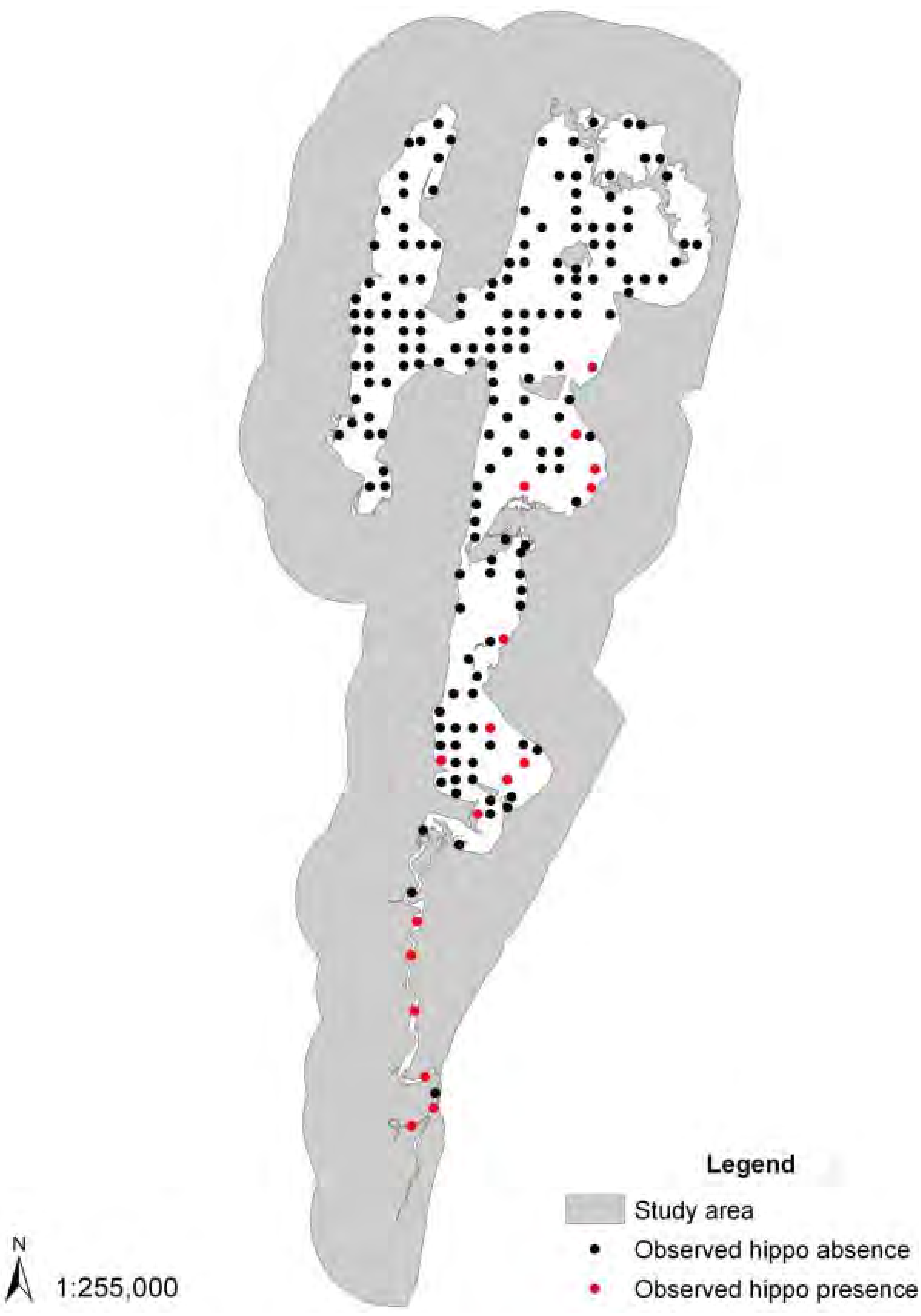


Figure 2.13: A map depicting the sub-sampled broad-scale hippo occurrence data (n=186; presence=17, absence=169), as used in the Binary Logistic model.

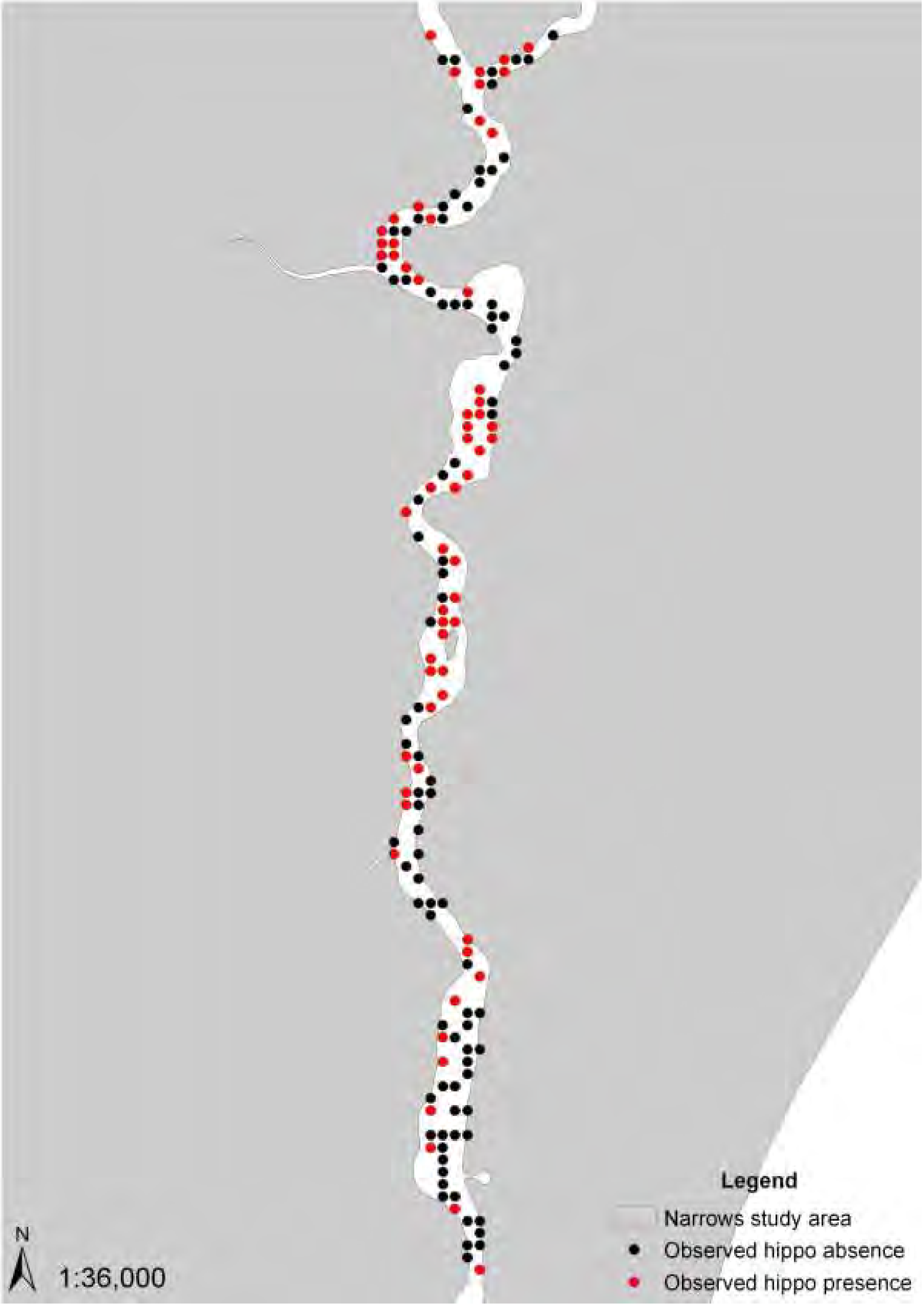


Figure 2.14: Map depicting the observed sub-sampled data (n=151; presence=60, absence=91) of hippo occurrence within the Narrows of the St Lucia Estuary, used in the Binary logistic regression model.

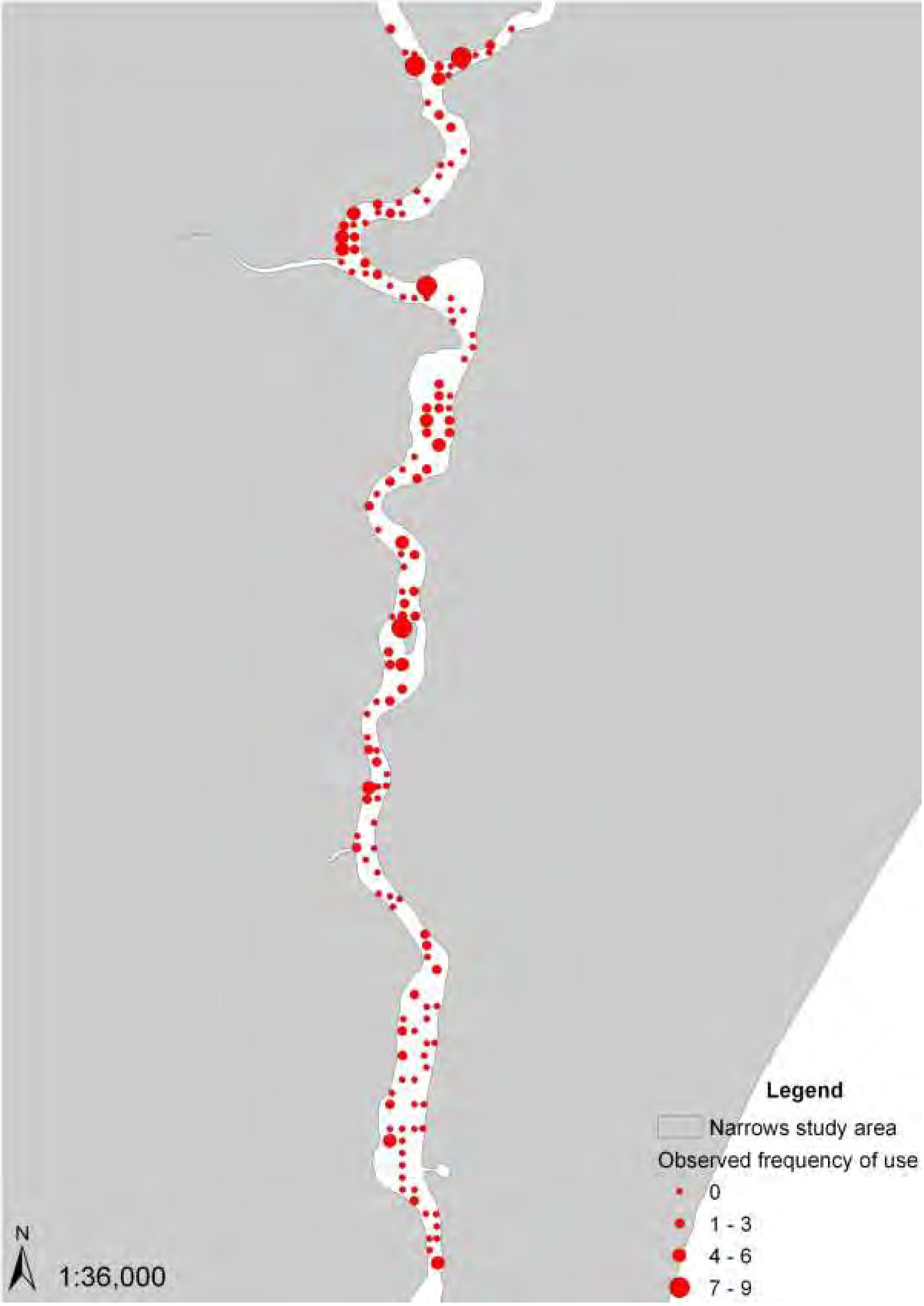


Figure 2.15: Map of the sub-sampled frequency of use data (N=151) used in the Negative Binomial log-link model to predict which habitat parameters best explains hippo use of certain areas within the Narrows of the St Lucia Estuary.

Model selection and evaluation

Given the need to eliminate spatial-autocorrelation from the original datasets, in order for model convergence to occur, I used the sub-sampled datasets, devoid of spatial-autocorrelation (Appendix 7, Fig 2.13, Fig. 2.14, Fig. 2.15), to develop and run the models. I used both backward – and forward stepwise modelling techniques with a p-value of 0.05 as the cut off, for all three models (one broad-scale occurrence model, one fine-scale occurrence model and a fine-scale frequency of use model).

Broad-scale hippo occurrence model

I used a Binary Logistic Regression to model occurrence (presence (1)/absence (0)) data, with presence as the response and absence as the reference category. The following predictor variables were included in the model, based on hypotheses outlined in the spatial data analysis section above:

1. Biotope (Lakes, Narrows, River) with Lakes set as the reference category,
2. In(Distance to Inlet),
3. Dominant vegetation type (Forest patch, Matrix, Natural wetland) with Forest Patch selected as the reference category,
4. Nearest vegetation type (Forest patch, Matrix, Natural wetland, Wetland floodplain, Forest cleared) with Forest patch selected as the reference category and
5. Shoreline (0=centre, 1=along the shoreline)
6. In(Distance to humans).

Fine-scale hippo occurrence and frequency of use models

I used a Binary Logistic Regression to model occurrence (presence (1)/absence (0)) data, with presence as the response and absence as the reference category and a Negative Binomial with log-link function to model the frequency of use. The following predictor variables were included in the model based on the hypotheses as stipulated in the spatial data analysis section:

1. Water depth categories: Category 1 = 0.5-0.9m,
   Category 2 = 1.0-1.49,
   Category 3 = 1.5 -1.99m,
   Category 4 ≥2.0m (reference category)
2. In(Distance to Inlet)
3. In(Distance to Nearest neighbour)
4. Nearest vegetation type (Forest patch, Matrix, Wetland Natural, Wetland floodplain), with Matrix vegetation set as the reference category.
5. Shoreline (0=centre, 1=along the shore)
6. In(Distance to humans)

I selected a model by comparing the finite sample corrected Akaike's Information Criterion (AIC_C), values and the overall model p-values, selecting for the model with the lowest AICc values and a correspondingly significant p-value. I chose to use AICc as the $n/K < 40$ for the model with the most parameters (K) (Burnham and Anderson, 2004). I ran the selected models using the sub-sampled datasets in order to generate predicted values (probability of occurrence/predicted frequency of use). I used the predicted values to evaluate the selected models using two different procedures, one for the occurrence models (for both broad- and fine-scale data sets) as per Pearce and Ferrier (2000), and one for the frequency of use model as per Potts and Elith (2006). This was necessary as binary data (0/1) could not be evaluated using the same method as applied to the count data used in the frequency of use dataset.

Occurrence model evaluation

I generated a Relative Operating Characteristic (ROC) curve, under non-parametric assumptions, to evaluate the model's ability to distinguish between occupied and unoccupied cells. SPSS generates a statistic (Discrimination capacity) with 95% confidence intervals, standard error and the coordinate points used to generate the ROC curve. The Discrimination capacity is calculated as the area under the ROC curve (broad-scale data, Appendix 10; fine-scale data, Appendix 11), generated by plotting the proportion of observed positives (Sensitivity, Appendix 8) against the probability of a false positive (False positive fraction, Appendix 9) at each interval (predicted probability of occurrence values generated by the model).

I evaluated the occurrence model's goodness-of-fit (calibration) by fitting a linear regression to the logit (natural logarithm, ln) of the proportion of observed occurrences (within each of the predicted probability of occurrence intervals) versus the logit of the median of predicted probability intervals (Pearce and Ferrier, 2000). I generated this graph in Excel and obtained the linear regression equation and the associated R^2-value. By evaluating the slope and intercept values I was able to describe the reliability with which the model predicted the probability of occurrence. Subsequently I qualitatively described the potential sources of error given the outcome of the above evaluation. A slope between zero and one suggests that the model predicted values <0.5 are underestimating occurrence, while predicted values >0.5 are potentially overestimating occurrence. The intercept, $b > 0$, illustrate that the broad-scale model consistently overestimates the probability of occurrence; while the intercept, $b < 0$, illustrates that, the fine-scale model is consistently underestimating the probability of occurrence (Pearce & Ferrier, 2000; Potts & Elith, 2006).Furthermore, I used the ROC outputs to select an appropriate threshold value, thereby generating a map of the predicted distribution of hippos.

Frequency of use model evaluation

I used Pearson correlation coefficient (r) and Spearman's ranked correlation coefficient (R) to evaluate the correlation between the observed and predicted values of hippo frequency of use. I assessed the model goodness-of-fit by fitting a linear regression to the observed versus predicted data in Excel, generating the linear equation and the associated R^2-value. I evaluated the differences between observed data and the model predictions by calculating the Root mean squared error (RMSE) and Average Error (AVE error) of model residuals (Potts & Elith, 2006; Hoffman & O'Riain, 2012).

For both the occurrence and frequency of use models, I also visually evaluated the model results for any obvious structure by graphing the relationships between the Standardised Pearson residuals and Cook's Distance and the predicted value of the linear predictor (continuous predictor variable).

B: Activity budget and behaviour of hippos

Spatial features of the focal group’s territory

The Mouth group’s territory is located at the most southern extent of the St Lucia Estuary (Fig. 2.1 A & C; Fig 2.16), bordered on the northern bank by the town of St Lucia. The St Lucia Ski-boat club, which is a local restaurant and pub, a parking lot, camp site and pedestrian walkway extends along the northern bank of this group’s territory, with the beach forming the eastern boundary between the Mouth group’s territory and the Indian Ocean (this was once the site of the St Lucia Estuary mouth; Fig. 2.16). Tourists and anglers enter the Mouth group’s territory both from the bank as well as on private watercraft and tourist barges. Thus, the Mouth group experiences a high degree of human presence and have subsequently become habituated to humans. Part of the southern bank of the Mouth group’s territory has recently been excavated to create the beach channel that forms the intermittent connection to the Mfolozi River (Fig. 2.16). Fluctuating water levels in the Mfolozi therefore influence the water levels experienced at the Mouth group’s lie-up site.

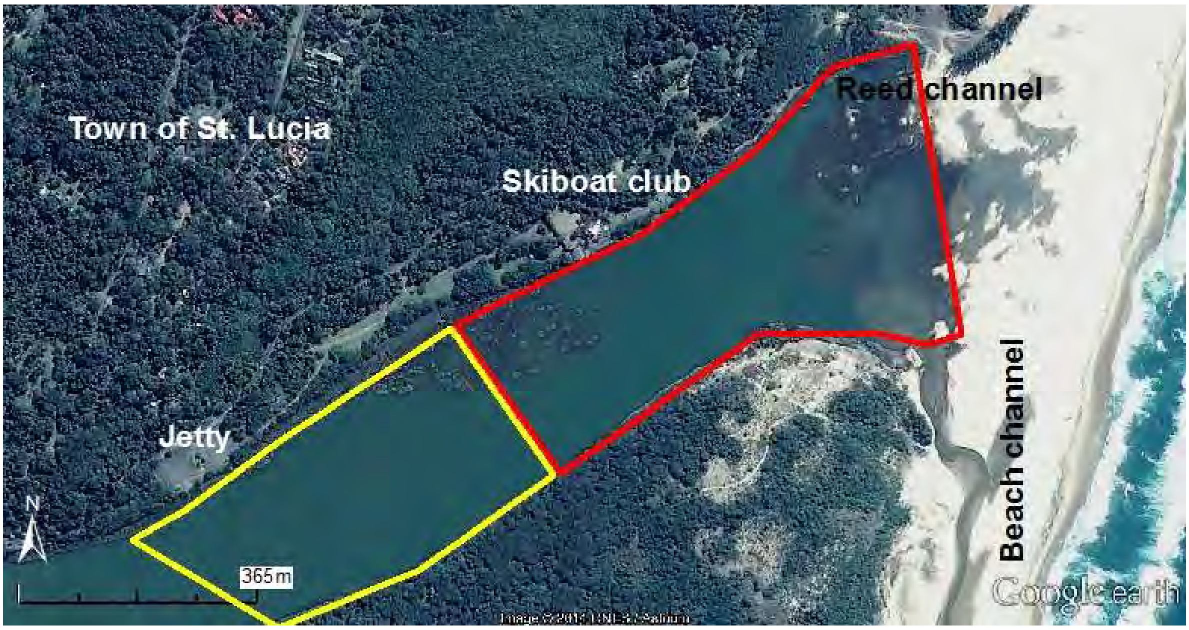


Figure 2.16: A modified Google Earth image depicting the extent of the Mouth Group's territory with notable features in the surrounding landscape. The red polygon depicts the original territory; the yellow polygon depicts the section added to the territory following a territorial take-over.

I used ArcMAP 10.1 and the methods described above (in Section A) to evaluate the Mouth groups' effective foraging range (5km radius around their territory, Fig. 2.17). Forest patch vegetation dominates this area and is the nearest vegetation on the northern banks of the territory. However, hippos from this group have access to both degraded wetland and matrix vegetation on the southern and eastern banks of their territory respectively. It is important to note that there are ample wetland floodplains within the Mouth group's foraging range (extending from the reed channel onto the northern banks and on the southern bank approximately 1.5km from the Mouth group's diurnal lie-up site), as well as the town of St Lucia's residential lawns, which are often grazed upon by hippos from this group. Unfortunately, my study did not evaluate the evening grazing activities of the mouth group's hippos. As such my interpretation of their activity budget and behaviours are based on the resources and potential disturbances known to occur within the 5km radius from the Mouth group's territory.

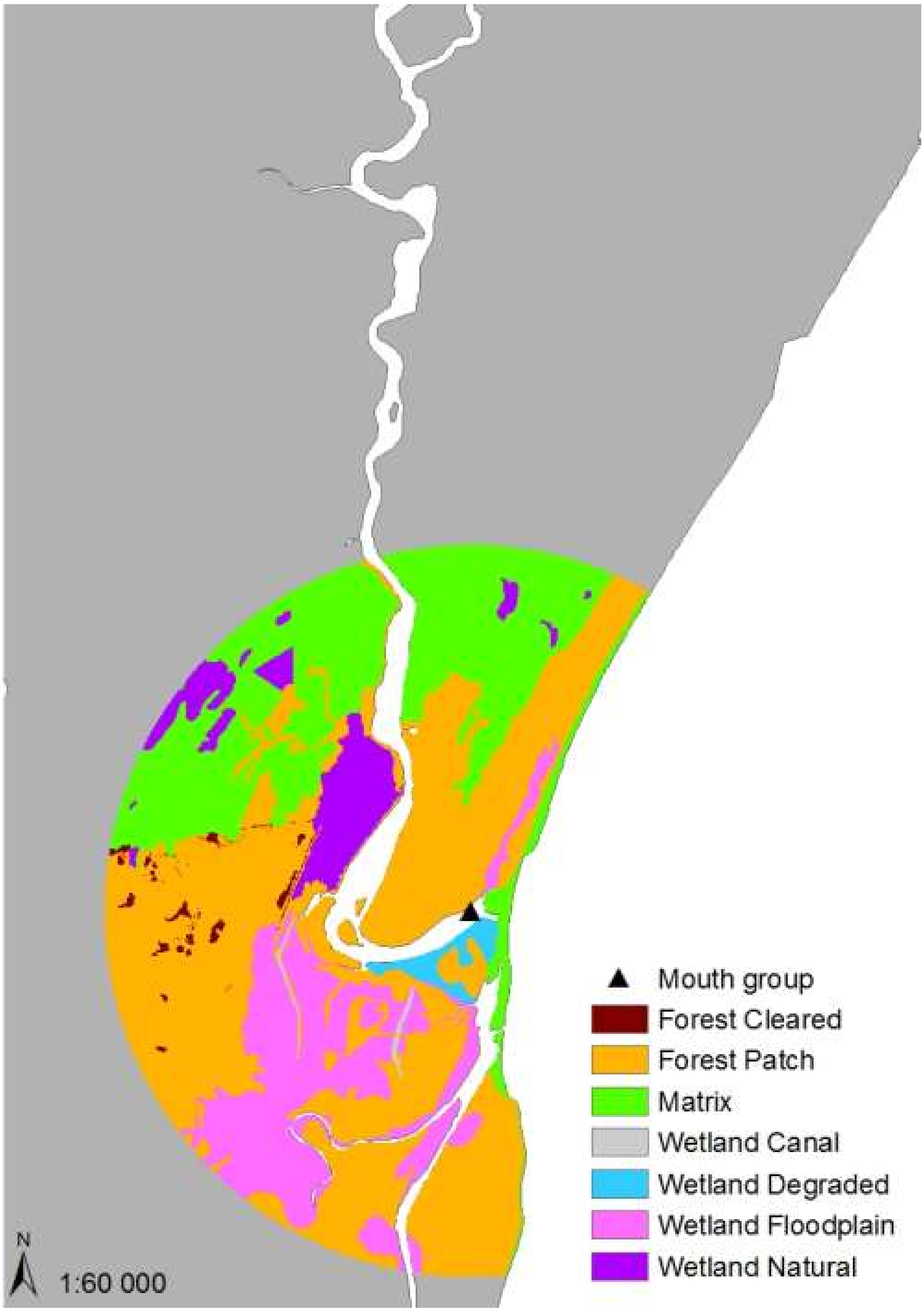


Figure 2.17: Map depicting the 5km effective foraging range and associated vegetation of the Mouth group hippos, relative to the extent of the Narrows.

The Mouth group was selected as the focal group as they were habituated to boat based observations, easily accessible and were comprised of 12 individuals which is close to the average group size (11 hippos/group) for hippos in the Narrows.

Behavioural data collection

Boat-based behavioural observations were conducted over a three-month period from April to June 2013. A total of 139.75 hours of observations were performed on 13 non-consecutive (independent) days. Observations were conducted from sunrise (06h00) to sunset (17h00) on ten out of the thirteen days (110 hours). On three days (29.75 hours), observations were either curtailed or started later due to unforeseen circumstances (e.g. a change in weather or engine trouble). On arrival at the group, the boat was anchored at a safe distance from the hippo group. The safe distance varied throughout the day (estimated mean = 40m, range = 30 – 150m) in accordance with hippo general behaviour but was never less than 30m. The boat remained stationary when group members moved, allowing the hippos to settle in a new area before I considered relocating the boat. Group fission was a common occurrence throughout the day, but observations on the entire group were almost always possible. On the rare occasions (n=4) that the whole group moved off during observations (e.g. during a submerged movement event), we performed no-wake speed transects throughout their home range until the group was relocated. In the rare event (n=37 out of 293 observation periods of 30min each) that an individual or small group moved from sight in such a way that we could not relocate them, we remained with the majority of the group.

Activity budgets

Instantaneous scans (Altmann, 1974) were performed every 30 minutes between 06:00 and 17:00. I recorded the behaviour of all visible individuals through direct observations using binoculars (mag = 7 X 40). Data were recorded on a prepared spreadsheet within 1 minute of the start of each scan. Whenever possible (e.g. calm conditions with limited group spread), direct observations were supplemented with a photograph of the group using a digital camera.

The behaviour of hippos was recorded within one of five mutually exclusive behavioural categories: resting, feeding, moving, socialising or out of sight (Table 2.2; Fig. 2.18). The number of individuals out of sight at each interval was determined using the maximum number of individuals seen during the day minus the cumulative number partaking in the remaining four behavioural states per interval. Unsighted individuals may have been submerged during sampling, obscured by vegetation or may have left the group.

Table 2.2: Ethogram of hippo activities used to develop hippo activity budgets.

Behaviour	**Description**	**References**	**Figure**
Feeding	Chewing motion with jaw while consuming plant material.	Blowers, *et al.*, 2010	2.18A
Moving	Walking around, in or out of water, and porpoising (moving rapidly through water in an up, out and back into the water motion).	Blowers, *et al.*, 2010	2.18B
Resting	Animals remain inactive, either congregating in a bundle (rafting) or alone.	Blowers, *et al.*, 2010	2.18C
Socialising	Interacting with other individuals including mating, fighting, and vocal communication.	Own classification	2.18D
Out of sight	Hippo obscured from view, the animal is either fully submerged, hidden behind vegetation or has left the observation area.	Own classification	-

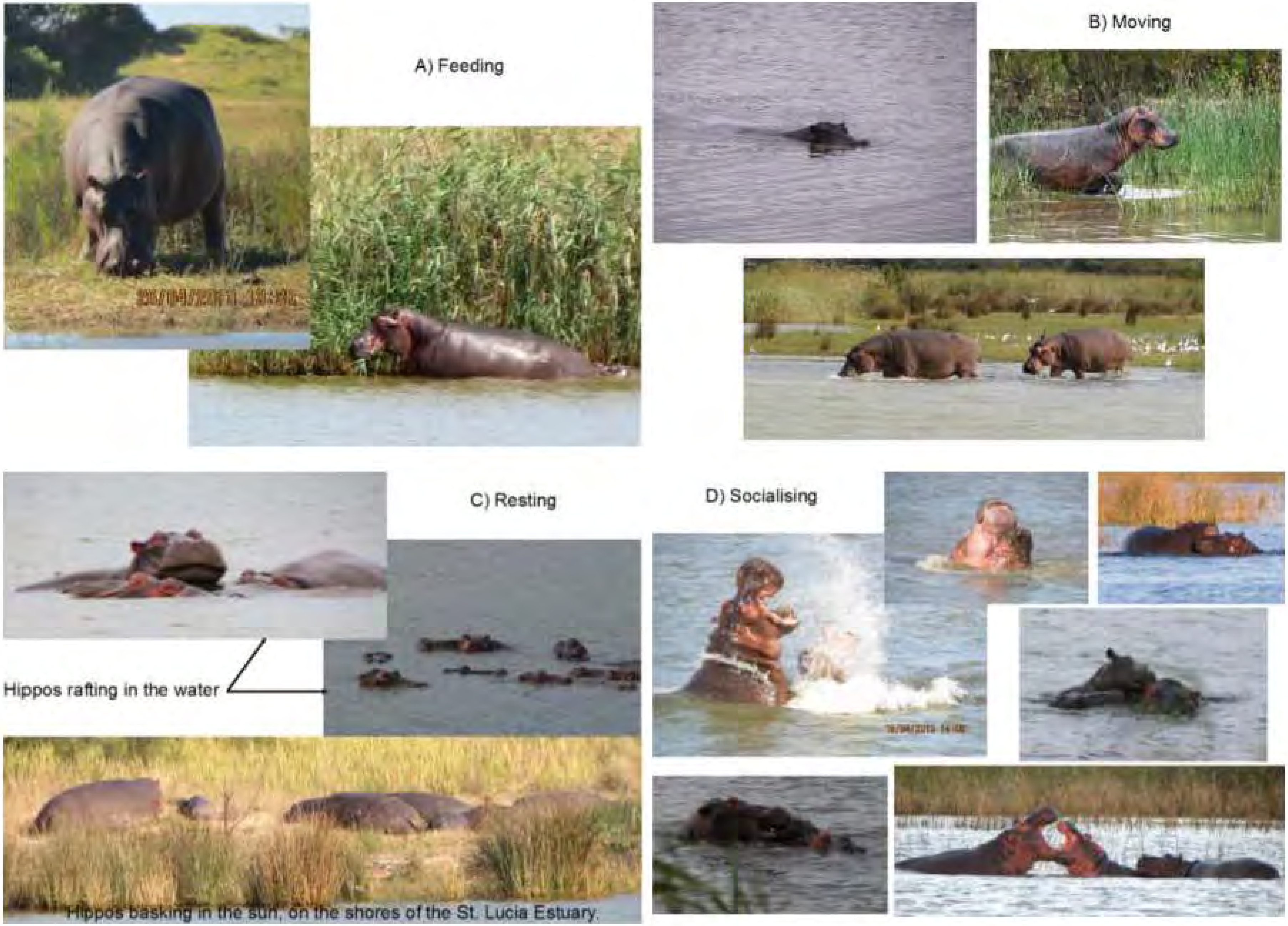


Figure 2.18: Photographs depicting some of the behaviours which were recorded during 13 independent days of observation, (classified according to behavioural states: A) Feeding, B) Moving, C) Resting and D) Socialising), used to determine the diurnal activity budgets of a group of wild hippos in the St Lucia Estuary.

Ad libitum data

I used continuous sampling (Altmann, 1974) to record social behaviours (vocalisation, yawning, dung showering and tail paddling; Table 2.3; Fig. 2.19) that were rare or of short duration and thus unlikely to be adequately sampled using the instantaneous scan. I recorded the start and end time of each behaviour to obtain a duration estimate. I selected the wheeze-honk vocalisation, as it is an amphibius call functioning as both a disturbance and a contact call (Karstad & Hudson, 1986; Barklow, 2004; Klingel, 2013).

Table 2.3: Ethogram of hippo social behaviours used for continuous behavioural observations.

Behaviour	**Description**	**Proposed function**	**References**	**Figure**
Yawn	Open mouth exposing tusks.	Expression of excitement.	Blowers, *et al.,* 2010 Klingel, 2013	2.19A
Vocalisation	General contact calls comprising of a wheeze followed by several guttural honks.	This behaviour is contagious, being started by one individual and is quickly repeated by others in the group.	Karstad & Hudson, 1986 Blowers, *et al.*, 2010 Klingel, 2013	-
Tail paddling	Tail moves from side to side at the surface of the water.	A submissive behaviour.	Blowers, *et al.,* 2010 Klingel, 2013	2.19B
Dung showering	Animal tail paddles whilst defecating.	Used to advertise and reinforce dominance.	Karstad & Hudson, 1986 Blowers, *et al.,* 2010	2.19C

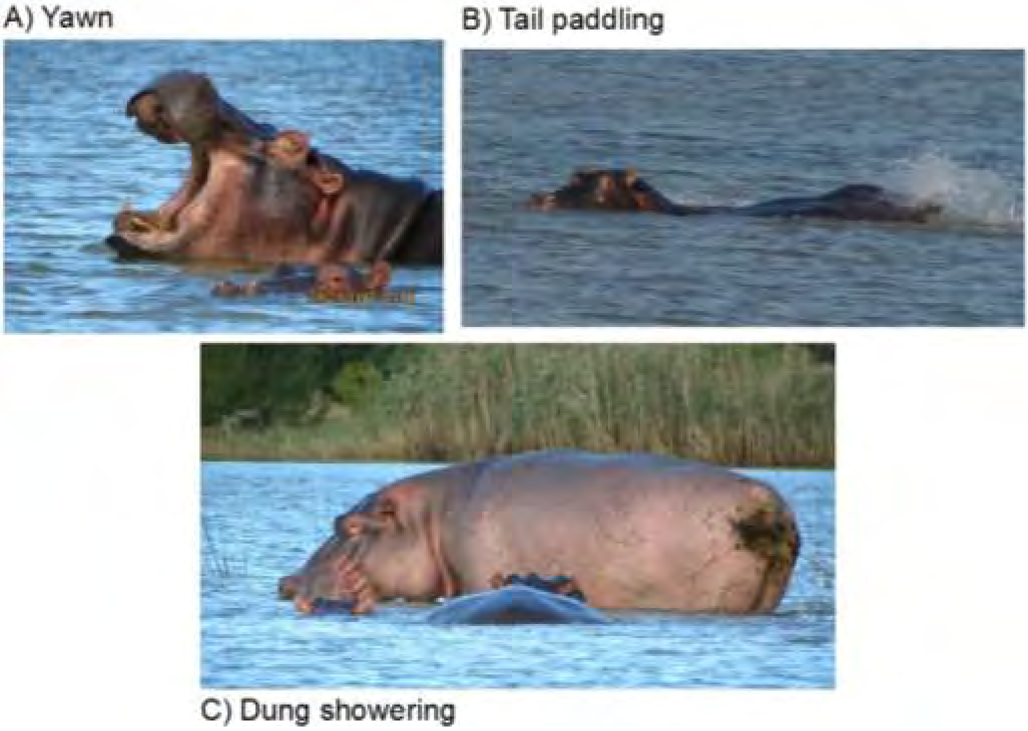


Figure 2.19: Photographs illustrating the social behaviours recorded during the continuous observations on a group of wild hippos in the St Lucia Estuary.

Behavioural data analyses

A lack of individually recognisable external features on the heads of the study group prevented me from being able to identify each hippo in the study group. Consequently, the data I collected represent a group average, with the assumption that in any given sampling event the behaviour of one individual does not affect the behaviour of another and furthermore that I did not resample the same individual twice. Meeting both of these assumptions is facilitated by the generally sedentary nature of this species in water and the speed with which I was able to complete the scans.

Visibility

Given the amphibius nature of hippos, not all animals were visible during each of the scans. The proportion of the group that was visible at each scan was thus calculated using the number of hippos recorded during the scan divided by the total number of hippos observed on that particular day, multiplied by 100 to give a percentage. Given the non-normal distribution of the group visibility data (Kolmogorov-Smirnov: statistic=0.091, df=299, ρ<0.001), I applied non-parametric statistical analyses to all subsequent evaluations. I used a Wilcoxon signed ranks test to determine if group members were more often visible than not visible in order to quantify the proportion of hippo behaviour that could be observed. Kruskal-Wallis analysis of variance was used to evaluate the visibility of hippos between observation days as well as between times of day (defined as follows; 06:00 – 08:00, early morning (EM), 09:00 – 11:00, late morning (LM), 12:00 – 14:00, early afternoon (EA) and 15:00 – 17:00, late afternoon (LA)).

Activity budgets and social behaviour

I calculated the daily average proportion of time the group spent on each of the four behavioural states (resting, feeding, moving, socialising) by summing the total number of individuals taking part in each activity, divided by the total number of visible hippos, averaged over the number of sample periods in a day. The average activity budget of the hippo group was calculated over the 13-day sampling period with days treated as independent sample units. Given that the data were non-normally distributed (Kolmogorov-Smirnov: feeding 0.478, degrees of freedom=150, ρ<0.001; moving 0.290, df=150, ρ<0.001; resting 0.210, df=150, ρ<0.001; socialising 0.390, df=150, ρ<0.001) I used non-parametric tests for all subsequent statistical analyses. Kruskal-Wallis analysis of variance was used to analyse the difference between the average time spent engaged in each activity. Friedman's one-way ANOVA was used to analyse the difference in time spent engaged in each activity between study days. A Wilcoxon Signed Rank test with a Bonferroni correction (used to adjust for the increasing type I error rates associated with multiple comparisons) was used for the Post hoc analysis in order to determine which days differed significantly. The adjusted significance level was set at α=0.00064; which is 0.05/number of pairwise tests, all subsequent adjustments were calculated in a similar manner.

The temporal activity pattern was analysed by dividing the daily observation period into four consecutive two hour intervals; 06:00 to 08:00, categorised as the early morning (EM); 09:00 to 11:00, late morning (LM); 12:00 to 14:00, early afternoon (EA) and 15:00 to 17:00, late afternoon (LA). Data were averaged within these intervals and then averaged across the 13 days for each of the activities. Friedman's one-way ANOVA was used to analyse the difference in each activity (i.e. each activity; feeding, moving, resting and socialising, were analysed separately) between different times of day.

Ad libitum data were collected as counts of each behaviour (vocalising, yawning, dung showering and tail paddling) per hour. The hourly data were converted to an average count per day for each behaviour. The average temporal pattern of behaviour was also calculated for each of the time intervals each day (EM, LM, EA and LA) and expressed as an average count across the 13 days. Using Kolmogorov-Smirnov test for normality I determined that the data were non-normally distributed (dung showering 0.454, df=142, ρ<0.001; tail paddling 0.298, df=142, ρ<0.001; vocalising 0.105, df=142, ρ=0.001, yawning 0.243, df=142, ρ<0.001) thus I used non-parametric tests. Friedman's one-way ANOVA was used to analyse the difference in the daily average count per behaviour between study days. Post hoc analysis used Wilcoxon Signed Rank test with a Bonferroni adjustment (α=0.00064) to determine which days differed significantly from the rest. Friedman's one-way ANOVA with post hoc Wilcoxon signed rank testing with a Bonferroni adjustment (α=0.0083) was used to analyse the difference in each behaviour (i.e. dung showering; tail paddling, vocalising and yawning, were analysed separately) between different times of day.

Chapter 3: Results

A: Spatial ecology of hippos

Broad-scale descriptive data

The June 2013 aerial census provided an estimate of 986 hippos within the St Lucia Estuary. Of these, 0.51% was located within rivers, 46.65% in the lakes and 52.84% within the Narrows (Table 3.1). Fig 3.1 shows that of the 419 cells within the data set, 36 were occupied by hippos; of which 22 were located within the lakes, 12 within the Narrows and 2 within the Mfolozi River.

Table 3.1: The number and density of hippos in each of the three main biotopes that together comprise the St Lucia Estuary. Count data are from the 2013 aerial survey. Density was calculated as the number of hippos divided by the distance (km) of lake shore or channel.

Biotope	**Number of hippos**	**Surface area (km^2)**	**Distance along shore or channel (km)**	**Density (hippos/km)**
Lakes	460	337.82	336.41	1.37
Narrows	521	6.76	25.26	20.62
Rivers	5	1.14	13.21	0.38
Total	986	345.72	374.88	2.63

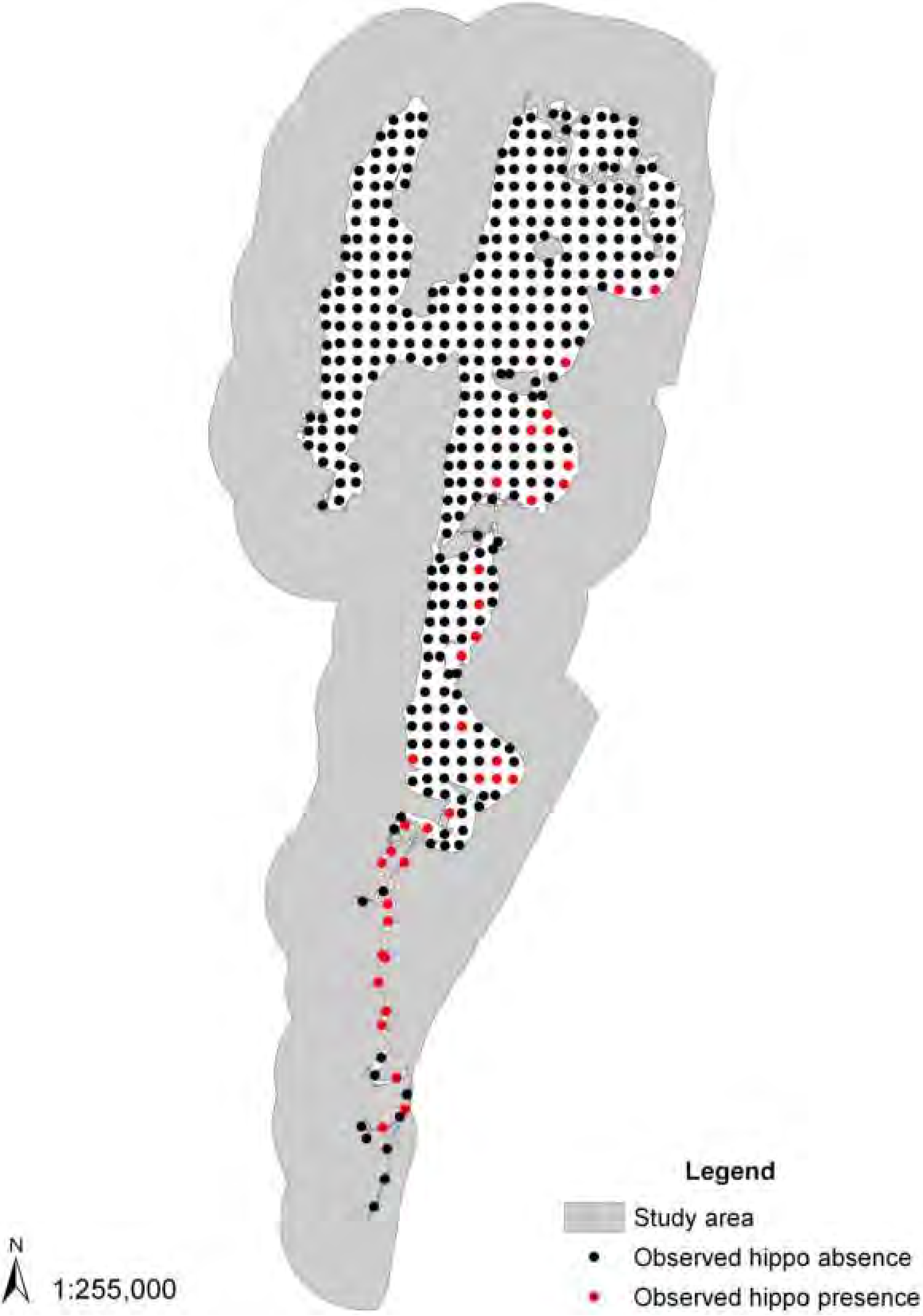


Figure 3.1 Map showing observed hippo distribution within the St Lucia Estuary (N=419, Presence = 36, Absence = 383).

Table 3.2: Predictor variable descriptive statistics for the Broad-scale data set. Available % refers to the percentage of cells within the data set (n=419) to which the specified variable category have been assigned. The Used % refers to the percentage of cells within the specified category occupied by hippos. Mean ± 1 standard error (SE) and the range (min – max) for continuous variables.

Predictor variables	Categories	Available %	Used %
Site	Rivers	2.1	22.2
	Narrows	4.3	66.7
	Lakes	93.6	5.6
Shoreline	Yes	58.0	11.1
	No	42.0	5.1
Nearest vegetation type	Forest cleared	0.7	0
	Forest patch	32.7	8.8
	Matrix	5.5	17.4
	Wetland floodplain	3.1	15.4
	Wetland natural	58.0	7.4
Dominant vegetation type	Forest patch	40.3	9.5
	Matrix	28.4	9.2
	Wetland natural	31.3	6.9
	Mean	±SE	Range
Distance to human settlement (m)	3416	117	204 – 11057
Distance to inlets (m)	2275	78	146 - 7200

Proportionately more cells within the Narrows were occupied by hippos than in the Lakes or Rivers (Table 3.2). More cells within the data set had direct access to the shore than not. Natural wetland was the most common ‘nearest vegetation’ type (58% of all cells within the broad-scale data set). Fifty percent of occupied cells were nearest to Natural wetland vegetation. Thereafter hippo presence was associated with Forest patch (33.3%), Matrix vegetation (11.1%) and Wetland floodplain (5.6%). Furthermore, I evaluated the type of vegetation that dominated (covering the largest area) the ‘effective foraging range’ (circle with 5km radius) of resident hippos. Forest patch vegetation (40.3%) was most often the dominant vegetation type (covering the largest area) within a 5km radius of each of the cells, with Natural wetland (31.3%) and Matrix vegetation (28.4%) accounting for the rest of the cells with roughly proportionate occupancy by hippos of 44.4%, 30.6% and 25.0% respectively. There was no clear relationship between vegetation types (both nearest and most dominant) and hippo occupancy.

Fine-scale descriptive data

Hippos occupied 40% of the cells within the Narrows (Fig. 3.2). The number of individual hippos (Kruskal-Wallis test statistic= 9, df =9, ρ =0.437) as well as the number and size of groups (Kruskal-Wallis test statistic = 6.771, df= 9, ρ =0.661) within the Narrows did not vary significantly between survey days. During the 10 survey days, I counted an average of 270.7 hippos (±11.78 SE) equating to a density of 21.07 hippos/km in the Narrows. An average of 25 groups (± 0.92 SE) was counted, with an average of 10.83 (±0.55 SE) hippos per group.

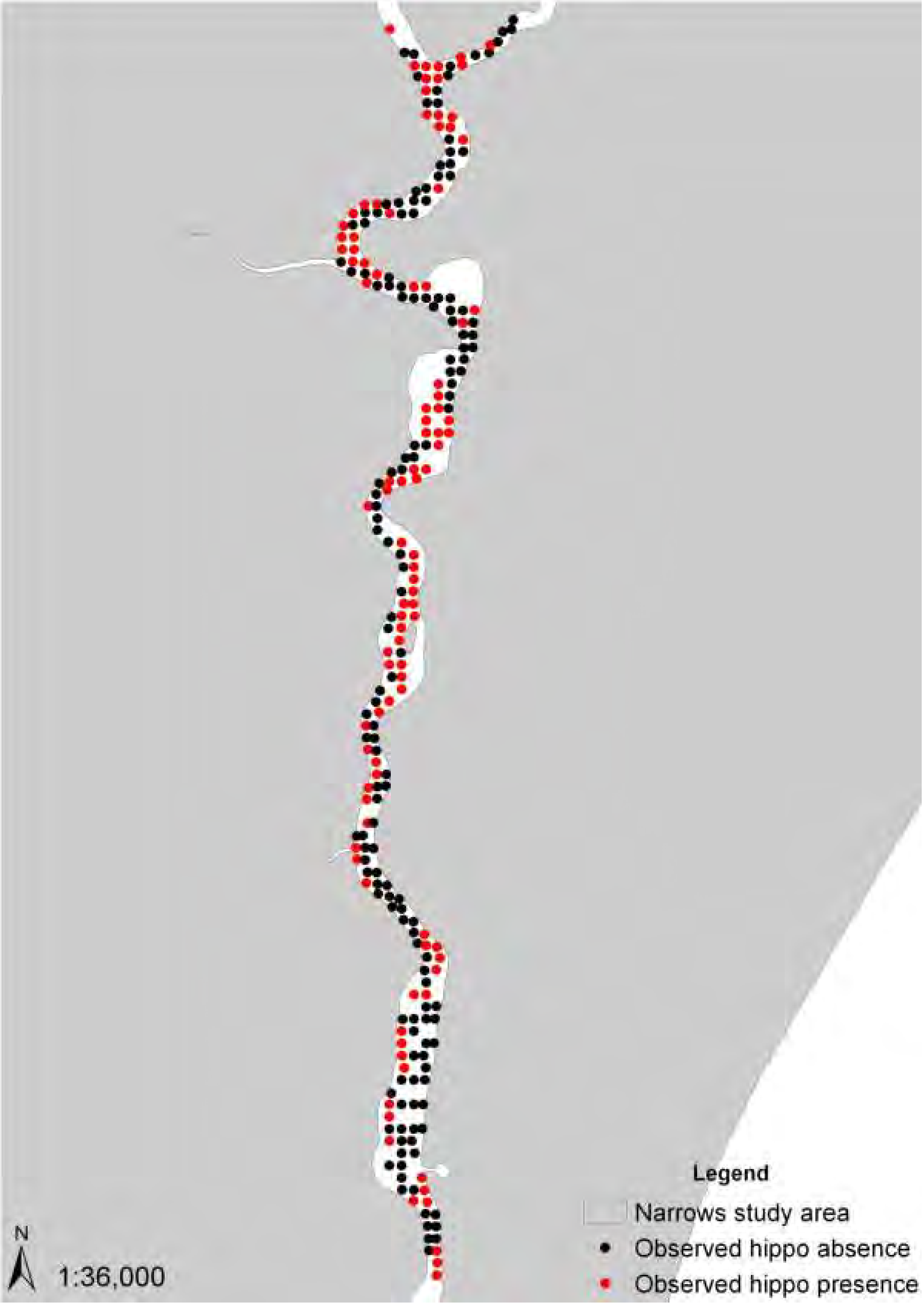


Figure 3.2: Map showing the observed hippo distribution within the Narrows of the St Lucia Estuary (N=252, presence= 100, absence=152).

Table 3.3: Predictor variable descriptive statistics for the Fine-scale data set. Available % refers to the percentage of cells within the data set (n=252) to which the specified variable category have been assigned. The Used % refers to the percentage of cells within the specified category that were occupied by hippos. Mean ± 1 standard error (SE) and the range (min – max) are provided for continuous variables.

Predictor variables	Categories	Available %	Used %
Water depth categories	1 (0.5 – 0.99m)	9.5	58.3
	2 (1.0 – 1.49m)	50.4	54.3
	3 (1.5 – 1.99m)	33.3	16.7
	4 (≥ 2m)	6.7	17.6
Shoreline	Yes	84.9	41.1
	No	15.1	31.6
Nearest vegetation type	Forest patch	38.1	43.8
	Matrix	32.1	24.7
	Wetland floodplain	14.7	56.8
	Wetland natural	15.1	44.7
	Mean	±SE	Range
Water depth (m)	1.42	0.023	0.70 – 2.37
Distance to human settlement (m)	2759.6	98.78	114 - 5115
Distance to inlets (m)	810.36	32.61	28 - 2061
Distance to nearest neighbour (m)	122.38	3.53	49.9 – 445.86

Hippos occupied 41.72% of sites nearest Forest patch vegetation, which was the most dominant near shore vegetation (38.1% of sites) along the Narrows. Matrix vegetation dominated the effective foraging range of all sites within the Narrows and was the second most dominant near shore vegetation (Table 3.3) yet merely 19.82% of occupied sites were nearest Matrix vegetation. Sites that were nearest Wetland vegetation (29.8% of all sites) were disproportionately more often occupied by hippos, accounting for 37.76% of occupied sites.

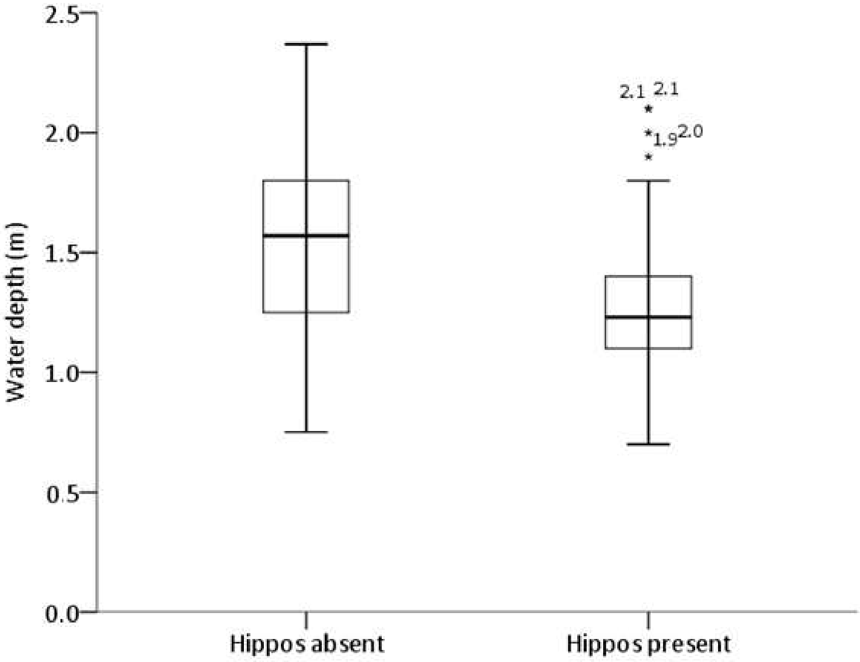


Figure 3.3: Boxplot showing average water depth at cells with and without hippos present (N=252) Note: Water depth measurements were not made at sites <0.5m deep, due to inaccessibility by boat.

Overall the Narrows had an average water depth of 1.42m (Table 3.3). However, there were significant differences in water depths (Fig. 3.3; t =-6.846, df =239.636, ρ<0.001) between cells with (mean= 1.25m ± 0.029 SE, n=100) and without (mean=1.53m±0.029, n=152) hippos.

Broad-scale occurrence model

The broad-scale occurrence model (AICc =97.796, Likelihood ratio X^2 = 26.281, df= 4, ρ< 0.001; Table 3.4 and Fig. 3.4) indicated that hippo presence is primarily influenced by biotope type (Wald X^2 = 13.440, df=2, ρ=0.001). Hippos were 24.71 and 34.42 times more likely to occur in the Narrows and rivers, respectively than in the Lakes. Hippos also exhibited a preference for sites closer to river inlets (Fig. 3.5), being 0.59 times less likely to occupy a site for every 1 unit increase in distance from a river inlet. Hippo presence was 2.86 times higher as distance from human settlements increased by 1 unit (Fig. 3.6).

Table 3.4: Results of the broad-scale habitat occurrence model including the coefficient estimates (β), standard errors (SEM), Wald Chi-squared-statistics and *p*-values for each predictor. Biotope types are italicised and significant values (ρ < 0.05) are marked in bold.

Parameter	**β**	**SEM**	**Wald X^2**	**ρ-value**
Intercept	-4.457	3.697	1.453	0.228
River	3.538	1.408	6.319	**0.012**
Narrows	3.207	1.038	9.540	**0.002**
ln(Distance to Humans)	1.050	0.501	4.394	**0.036**
In(Distance to Inlet)	-0.901	0.423	4.494	**0.034**

The following figures depict predicted (Fig. 3.4) hippo distribution, and the predicted hippo distribution in relation to the significant predictor variables (distance to river inlets, Fig. 3.5; distance to human settlement, Fig. 3.6) as highlighted by the model results (Table 3.4).

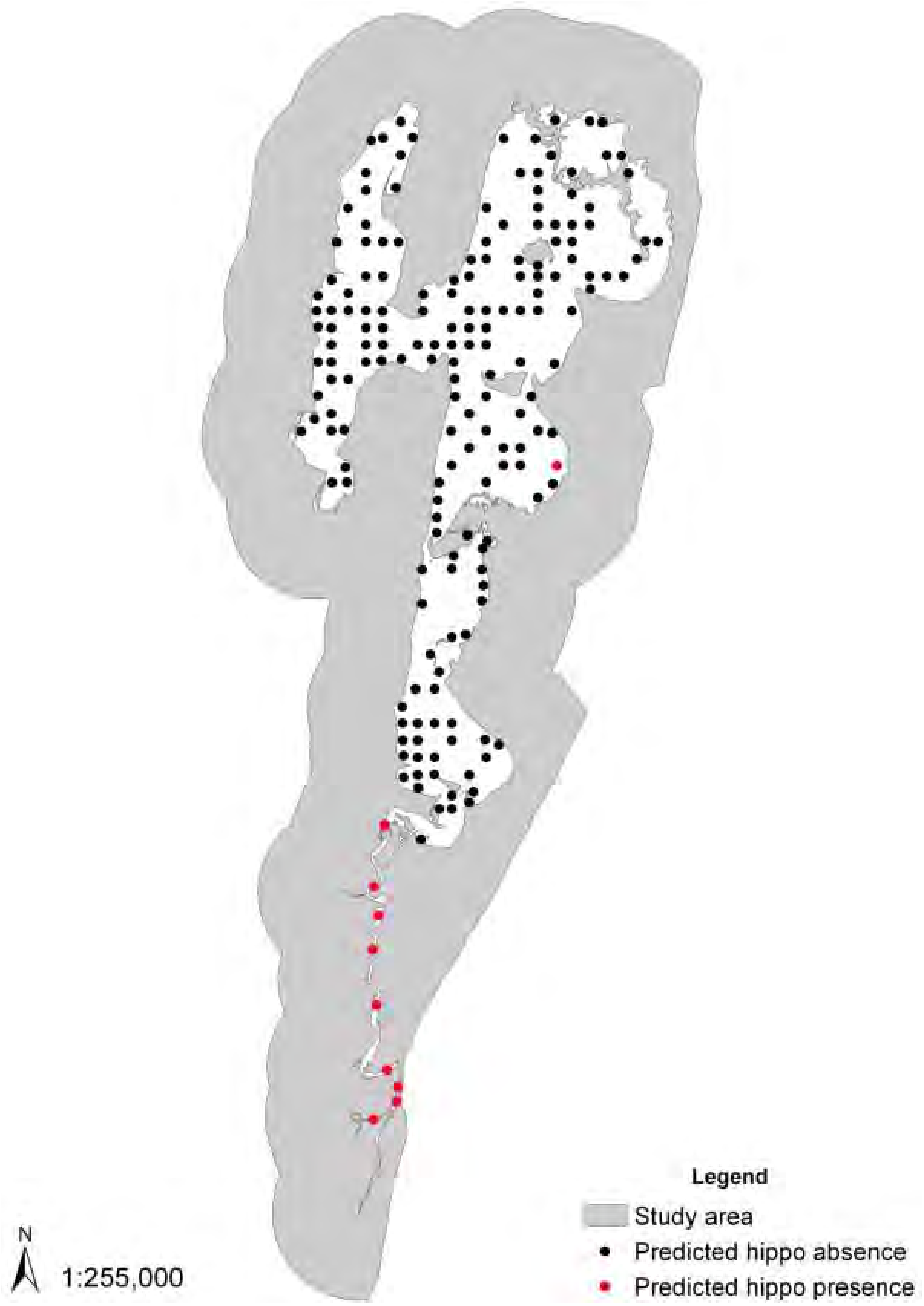


Figure 3.4: Map of the predicted occurrence of hippos within the St Lucia Estuary.

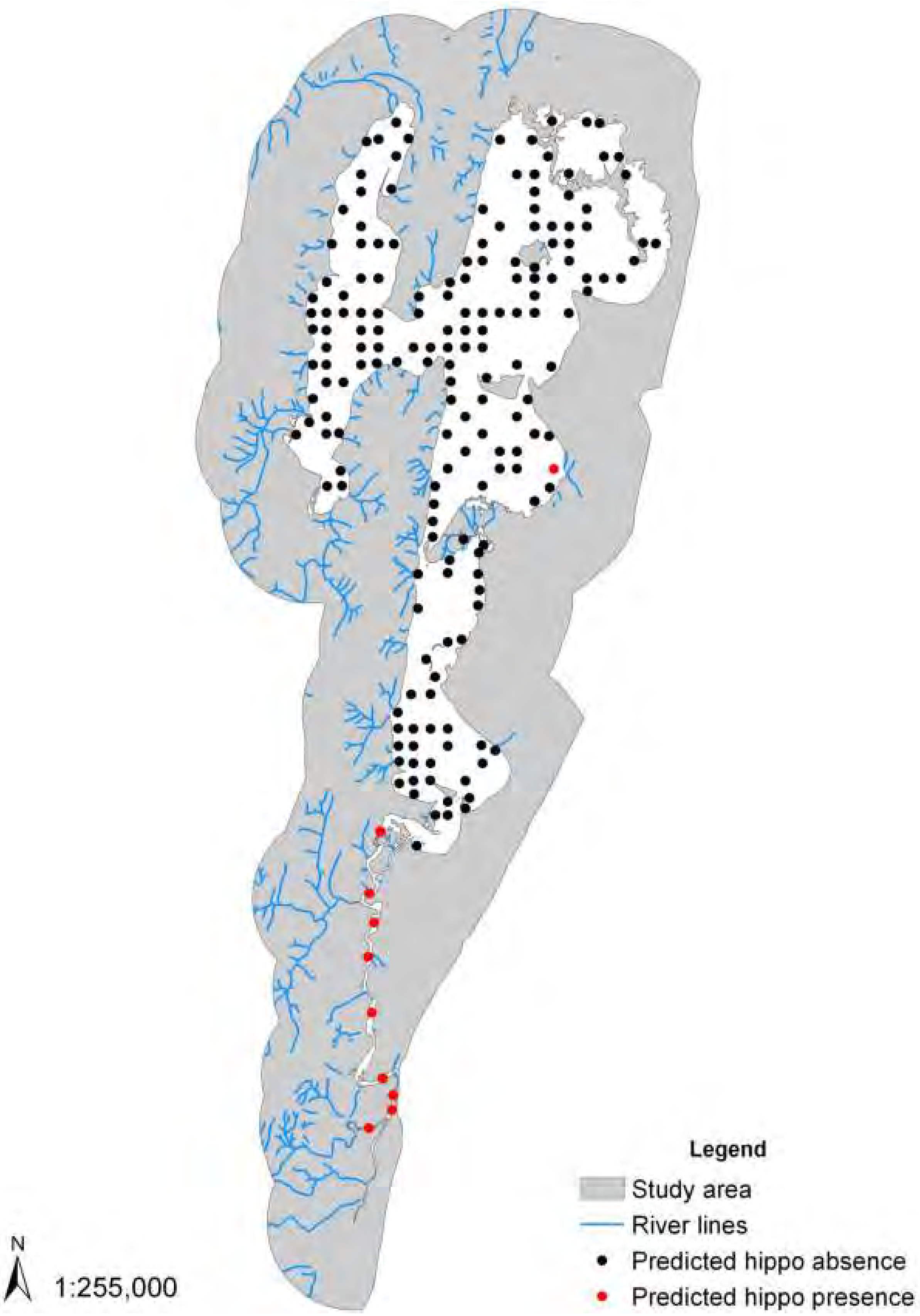


Figure 3.5: Map of the predicted hippo distribution within the St Lucia Estuary in relation to river inlets (the points at which river lines enter the St Lucia Estuary).

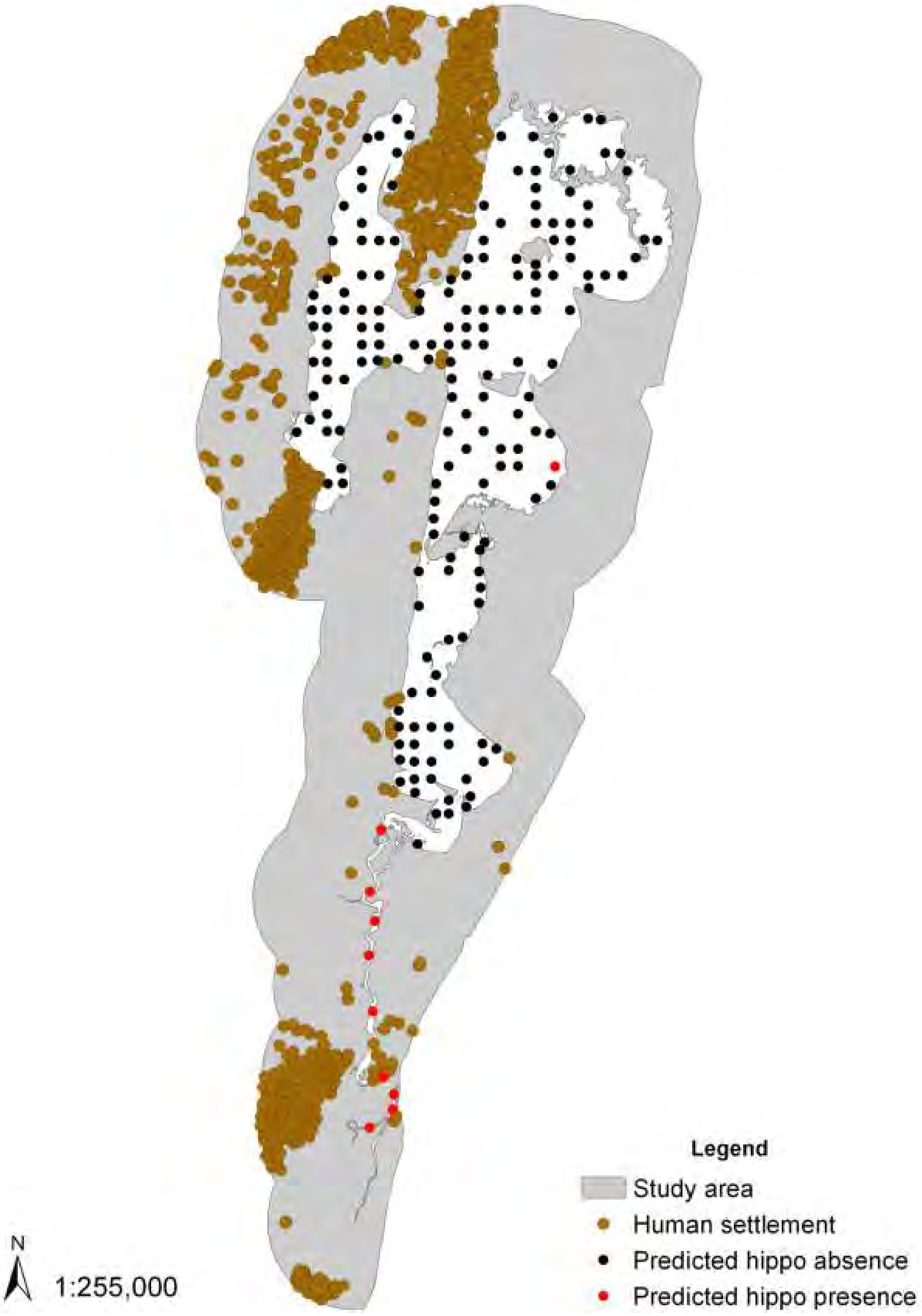


Figure 3.6: Map of the predicted hippo distribution within the St Lucia Estuary in relation to human settlements.

Fine-scale occurrence model

The fine-scale occurrence model (AICc= 176.619, Likelihood ratio X^2 = 38.89, df= 5, ρ< 0.001; Table 3.5) predicted that distance to humans had a significant effect on the hippo presence (Figure 3.8), which was 2.49 times more likely to occur in an area when it is 1 unit distance further from human settlements (Table 3.5). The distance to nearest neighbour was the second most important parameter predicting hippo presence in the Narrows. Hippos were 0.7 times less likely to occupy an area that is one unit distance further from conspecifics. Hippo presence was primarily influenced by water depth category (Wald X^2=21.842, df=3, ρ,0.001; Category 1: 0.5-0.99m; Category 2:1.0-1.49m; Category 3: 1.5-1.99m and Category 4:> 2m). Using the deepest water depth (Category 4) as a reference, hippos were 2.42, 15.95 and 23.87 times more likely to occur in Category 3, 2 and 1 water depths respectively (Fig. 3.10).

Table 3.5: Results of the fine-scale occurrence model including the coefficient estimates (β), standard errors (SEM), Wald Chi-squared-statistics (X^2) and *p*-values for each predictor. Water depth categories are denoted in italics: WD1= 0.5- 0.99, WD2 = 1.0-1.49, WD3= 1.5-1.99, WD4≥ 2m and the Natural logarithm (In) for each of the continuous variables. Significant ρ-values are in bold.

Parameter	**β**	**SEM**	**Wald X^2**	**ρ-value**
Intercept	-3.969	3.854	1.061	0.303
WD 1 (Ref. WD 4)	3.172	1.233	6.622	**0.010**
WD 2	2.769	1.104	6.296	**0.012**
WD 3	0.886	1.131	0.614	0.433
In(Distance to Human)	0.911	0.290	9.870	**0.002**
In (Distance to Nearest Neighbour)	-1.191	0.587	4.112	**0.043**

The following figures compare the observed and predicted hippo occurrence within the Narrows, illustrating each in relation to distance to human settlement (Fig. 3.7 and Fig. 3.8), and the water depth (Figure 3.9 and Fig. 3.10).

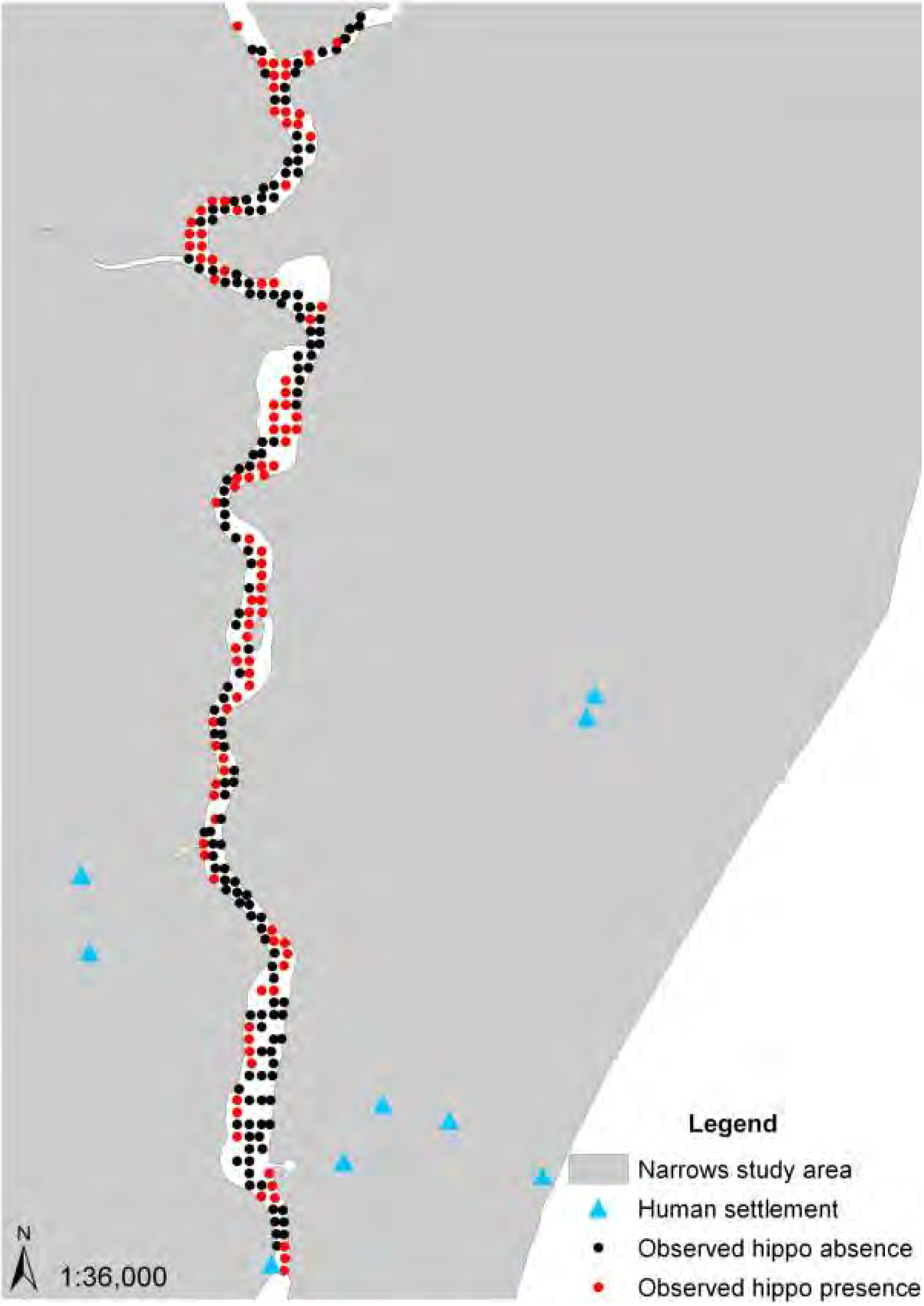


Figure 3.7: Map of the observed occurrence of hippos within the Narrows of the St Lucia Estuary in relation to human settlements (N=252, Presence = 100, Absence = 152).

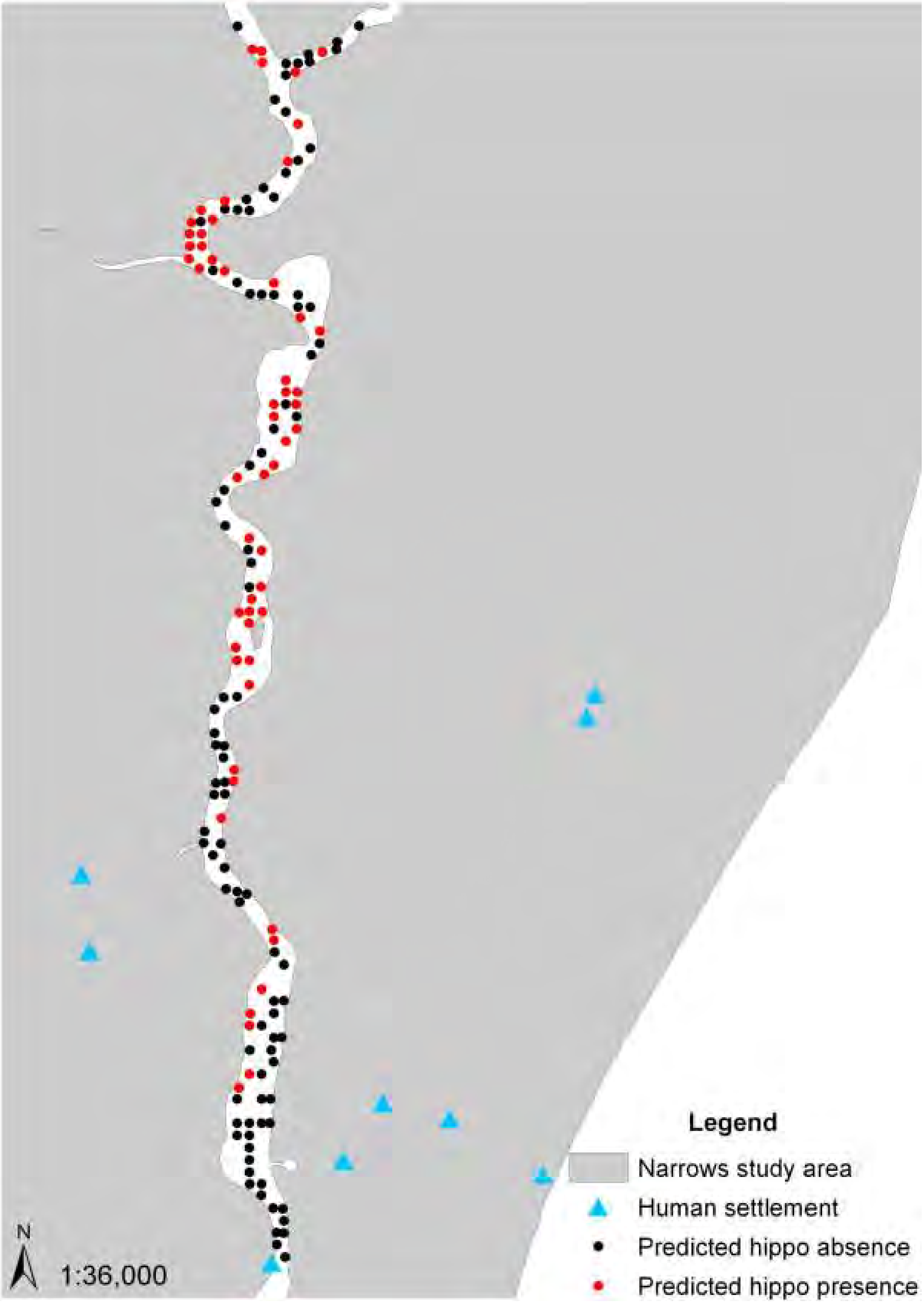


Figure 3.8: Map of the predicted hippo occurrence within the Narrows in relation to human settlements (N=151).

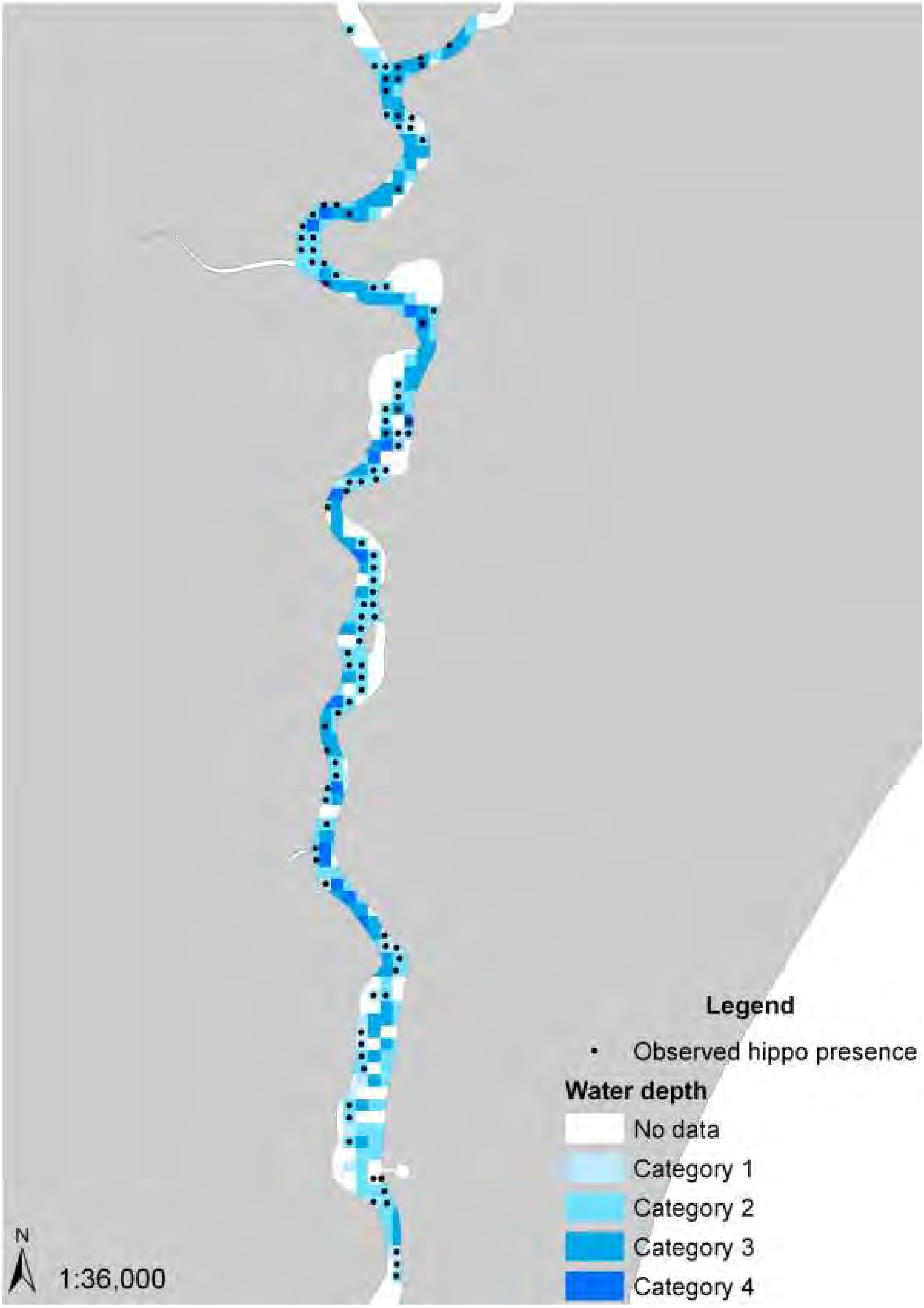


Figure 3.9: Observed hippo distribution within the Narrows, in relation to the water depth categories (Category 1 = 0.5 -0.99m; Category 2 = 1.0 – 1.49m; Category 3 = 1.5 – 1.99m and Category 4 ≥ 2m).

Figure 3.10: Predicted hippo distribution within the Narrows, in relation to the water depth categories (Category 1 = 0.5 -0.99m; Category 2 = 1.0 – 1.49m; Category 3 = 1.5 – 1.99m and Category 4 ≥ 2m).

Frequency of occurrence within the Narrows

The fine-scale frequency of use model (AICc= 375.827, Likelihood ratio X^2 = 54.250, df= 7, ρ< 0.001) indicated that water depth was the most important predictor (Wald X^2=26.574, df=3, ρ<0.001) of the frequency of cell use. Hippos were 14.72 times more likely to occupy cells, of Category 2 (1.0- 1.49m; Table 3.6) than category 4 (≥2m) water depths. Water depth category 1 (0.5- 0.99m) and 3 (1.5- 1.99m) did not significantly affect the frequency of cell use within the Narrows. Hippos were 7.87 and 2.89 times more likely to frequent category 1 and 3 water depths than category 4 water depths. The distance to nearest neighbours was the second strongest determinant of hippo cell use (Wald X^2=8.106, df=1, ρ=0.004). Hippos were more likely to visit cells in close proximity to other hippos (mean ± SE = 122.38m ± 3.53), with a decrease in frequency of use (0.72 times less likely to use a cell) as the distance to nearest neighbours increased. Vegetation type also influenced the frequency of hippo use of particular cells (Wald X^2=12.185, df=3, ρ=0.007; Fig. 3.12), with hippos significantly less likely to return to sites that are adjacent to Matrix vegetation. With Matrix vegetation as a reference, hippos are 1.94 times as likely to return to a site nearest to forest patch vegetation, 2.28 times as likely to return to sites nearest Wetland floodplain vegetation and 4.11 times as likely to return to a site in close proximity to Wetland-natural vegetation (Table 3.6). The following figures compare the observed (Fig. 3.11) and predicted (Fig. 3.12) frequency of hippo cell use in relation to nearest neighbour and nearest vegetation type.

Table 3.6: Results of the fine scale frequency of use models including the coefficient estimates (β), standard errors (SEM), Wald Chi-squared-statistics and *p*-values for each predictor. Water depth categories are denoted by WD1= 0.5- 0.99, WD2 = 1.0-1.49, WD3= 1.5-1.99, WD4≥ 2m. Nearest vegetation type are denoted in italics by FP = Forest patch, WF = Wetland floodplain, WN = Wetland-natural and M = Matrix vegetation. The Natural logarithm for the distance to nearest neighbour is denoted by In(NN). Significant values (ρ < 0.05) are in bold.

Parameter	**β**	**SEM**	**Wald X^2**	**ρ-value**
Intercept	4.466	2.2738	3.857	0.050
WD 1 (Ref. WD 4)	2.063	1.1293	3.339	0.068
WD 2	2.690	1.0752	6.260	**0.012**
WD 3	1.061	1.1132	0.909	0.340
FP (Ref. M)	0.664	0.333	3.977	**0.046**
WF	0.825	0.410	4.056	**0.044**
WN	1.413	0.414	11.657	**0.001**
In(NN)	-1.275	0.4495	8.045	**0.005**

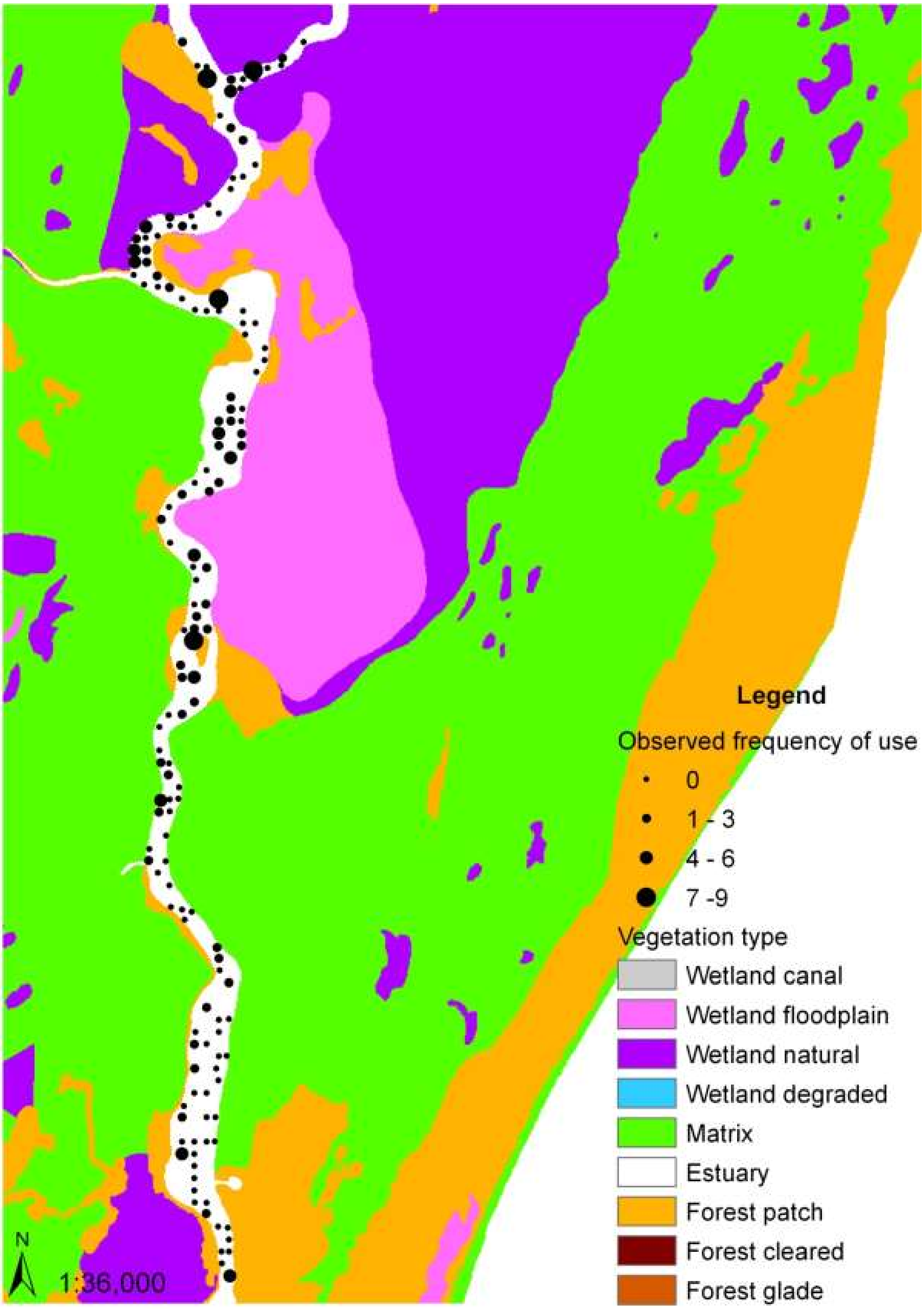


Figure 3.11: Map of the observed frequency of use of cells within the Narrows of the St Lucia Estuary in relation to the type of nearest vegetation.

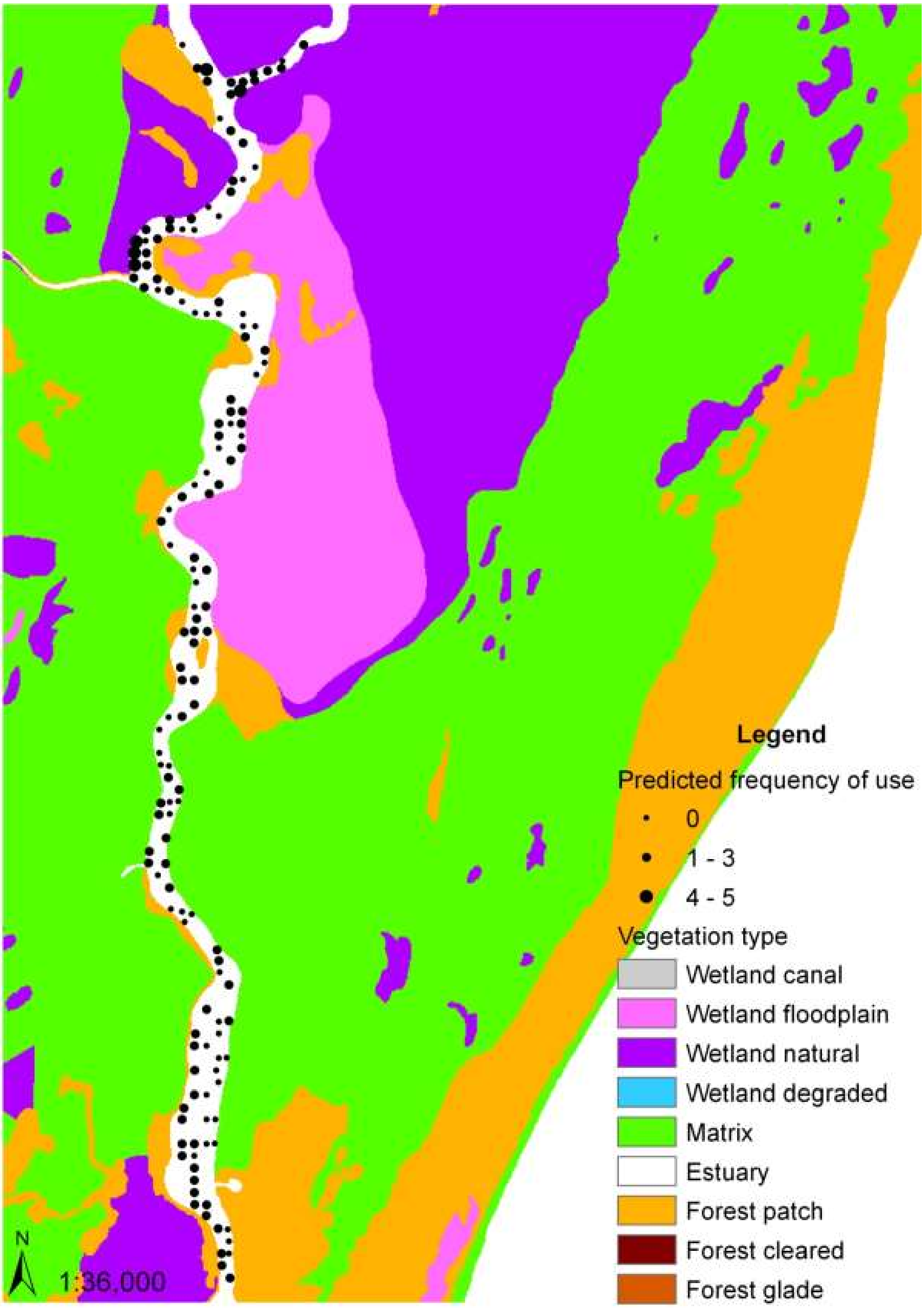


Figure 3.12: Map of the predicted frequency of use of cells within the Narrows of the St Lucia Estuary in relation to the type of nearest vegetation.

Model evaluation

A brief summary of the model evaluation parameters and associated R^2-values denoting each models predictive capabilities is included in Tables 3.7 (occurrence models) and 3.8 (frequency of use model) below. The binary model evaluation procedures generated exceptionally good model fit statistics (Table 3.7) although the high zero-inflation argues for some caution in the confidence of these values (Appendix 1).

Table 3.7: Broad - and fine-scale occurrence model evaluation statistics; corrected Akaike's Information Criterion (AIC_C), Discrimination capacity (i.e. area under the Relative Operating Characteristic curve) and associated 95% Confidence Interval (CI) and standard error (±SE); the calibration statistics; slope (m), intercept (b) and R^2 –value.

Model	**AIC_C**	**Discrimination capacity**				**Calibration**		
		Area	**95% CI** **Lower**	**Upper**	**SE**	**m**	**b**	**R^2**
Broad-scale occurrence	97.796	0.805	0.683	0.927	0.062	0.907	0.0036	0.76
Fine-scale occurrence	176.641	0.779	0.704	0.853	0.038	0.977	-0.0013	0.84

From the occurrence model evaluations (Table 3.7) it is evident that the broad-scale model performed best at discriminating between occupied and unoccupied sites, correctly identifying sites 80.5% of the time, whilst the fine-scale occurrence model performed best at reliably predicting the probability of occurrence ($R^2 = 0.84$). Both the broad- and fine-scale model calibration values for slope (broad-scale: 0.907; fine-scale: 0.977) and intercept (0.0036; -0.0013) indicate that the models are performing well.

Evaluating the broad-scale calibration statistics (slope and intercept values), and the large proportion of zero's within the lakes I concluded that the model consistently overestimates the probability of occurrence (Pearce & Ferrier, 2000; Potts & Elith, 2006) within the rivers and Narrows, whilst under-predicting occurrence within the Lakes (Table 3.7). Despite these caveats the broad-scale binary model correctly predicted the presence of hippos within the lakes (using only presence/absence data; Fig. 3.4), at the site with the highest observed hippo count (99 hippos counted in Tewate bay during aerial survey).

As with the broad-scale model, the fine-scale occurrence model's intercept value suggests that the model is underestimating occurrence when the predicted probability is less than 0.5, and overestimating occurrence when the predicted probability is >0.5. However, the negative slope value illustrates that the fine-scale occurrence model is consistently underestimating the probability of occurrence (Table 3.7). This may explain why the model tends to predict fewer occupied sites within the lower reaches of the Narrows (Fig. 3.8) than were observed (Fig. 3.7).

Table 3.8: Fine-scale frequency of use model evaluation statistics, with the finite sample corrected Akaike's Information Criterion (AIC_C) Pearson correlation coefficients (r) and Spearman ranked correlation (R), slope (m), intercept (b), average error (AVEerror) and root mean square error (RMSE).

Model	**AIC_C**	**Correlation**		**Calibration**			**Error**	
		r	**R**	**m**	**b**	**R^2**	**AVE error**	**RMSE**
Fine-scale frequency of use	375.827	0.37	0.47	0.68	0.27	0.136	0.05	1.65

The fine-scale frequency of use model exhibits relatively low correlations between the observed and predicted values (Table 3.8). This suggests that the model was better at predicting the sites that were most frequented (Spearman's ranked correlation (R)=0.47), than it was at predicting the frequency with which sites were used (Pearson correlation (r)=0.37). The model fit is also relatively poor, explaining only 13.6% of the variation between the observed and predicted values. Similarly to both of the hippo occurrence models above, the calibration statistics indicate that the frequency of use model predictions were less accurate at the extremes of observations. Thus, the model predicted (Fig. 3.12) more sites with lower frequency of use than observed (Fig. 3.11), and fewer sites with high frequency of use. Yet overall the average model predictions are correct (evidenced by the small error values; AVE error = 0.05 and RMSE = 1.65). All three models exhibited some structure potentially explained by the zero inflation inherent in the data (Fig. 3.13).

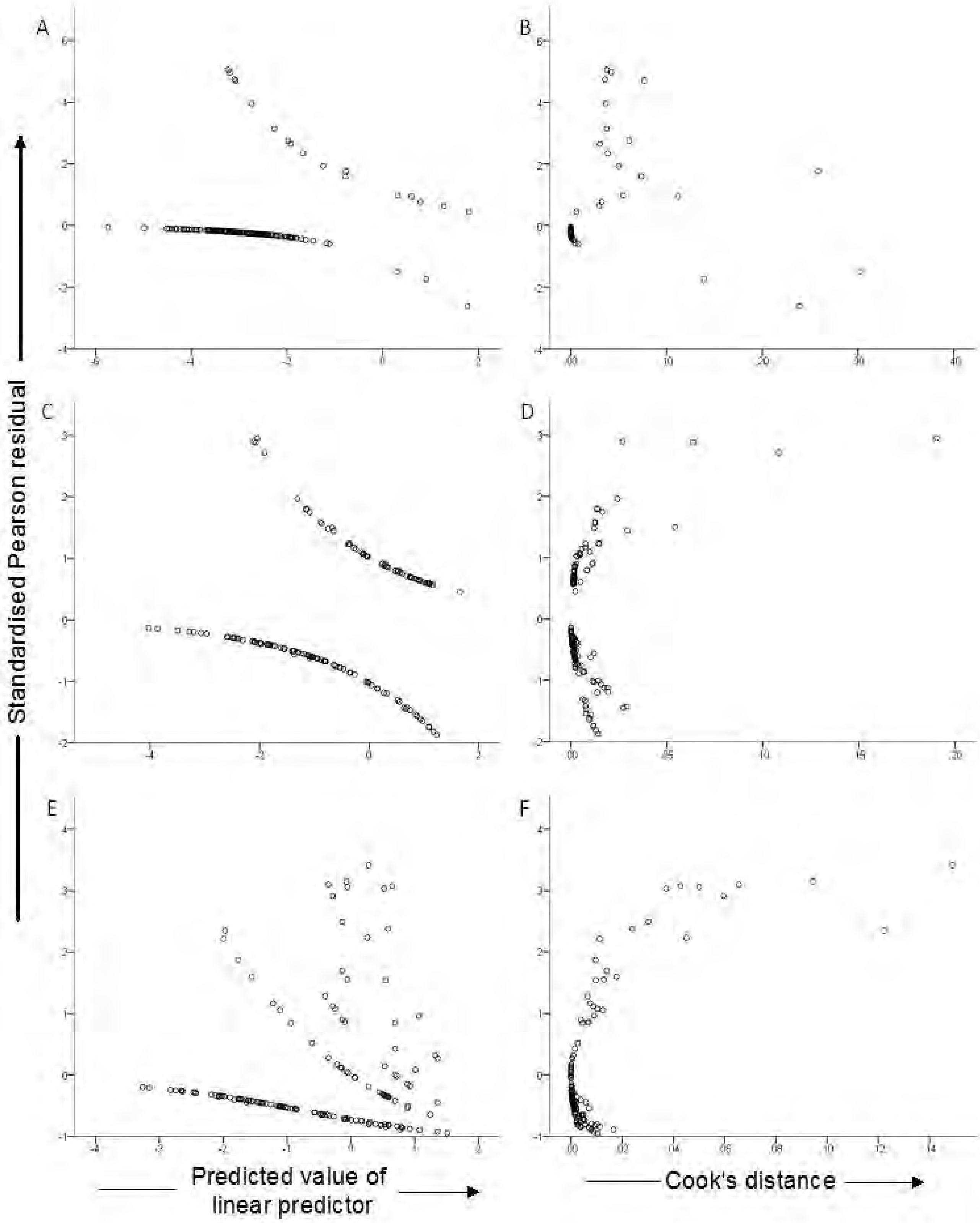


Figure 3.13: Graphed model evaluations of the Predicted values and Cook's distance against Standardised Pearson residuals for the broad-scale occurrence model (A&B), the fine-scale occurrence model (C & D) and the fine-scale frequency of use model (E & F).

B: Activity budget and behaviour of the focal hippo group

Group size and visibility

The average size of the focal group was 12 hippos (range 7 to 14) during the observation period with 56.45% (± 0.0147 SE) of hippos being visible during the 139.75 hours of scan observations (Wilcoxon Signed Ranks Test: Z= -4.304, ρ<0.001; Fig. 3.14). Sexing and classifying hippos according to age group is particularly difficult in the field given the fact that sub-adult males are similar in size to adult females (Beckwitt *et al.*, 2002). As such, I was unable to discern group composition by the end of the study. However, I did determine that the focal group was indeed a nursery group, as there were at least two females with calves.

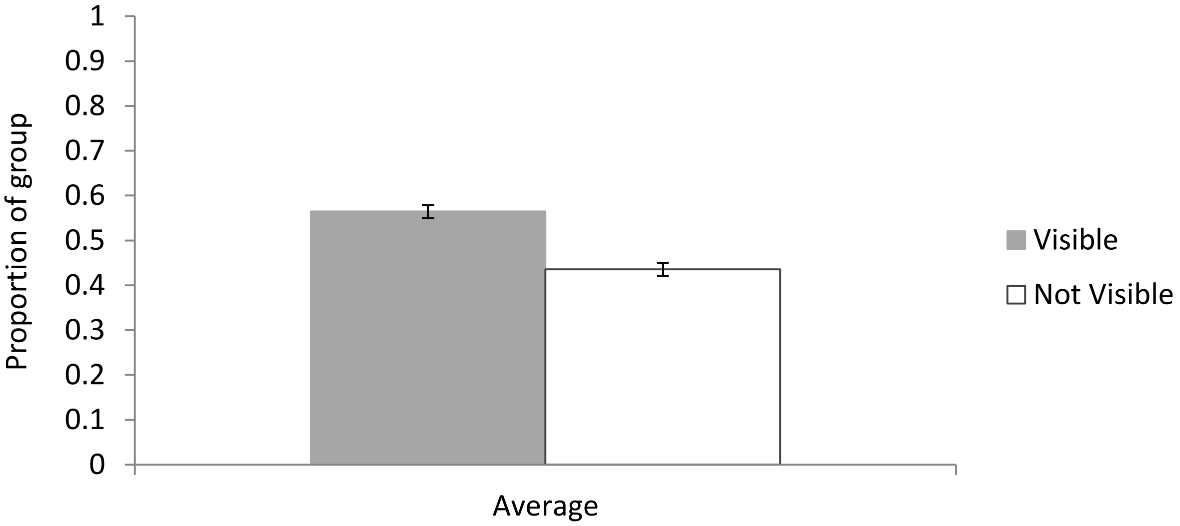


Figure 3.14: Difference in the proportion of hippos (average ± SE) in the focal group that were visible and not visible during the observation period (significant difference; ρ < 0.001).

The proportion of the group that was visible on each day of the study varied significantly (Kruskal-Wallis test: $H_{(df=12,n=299)}$=57.451, ρ<0.001) with three of the thirteen days having <50% of the group visible on average across all scan samples (days 4, 7 and 13; Fig. 3.15).

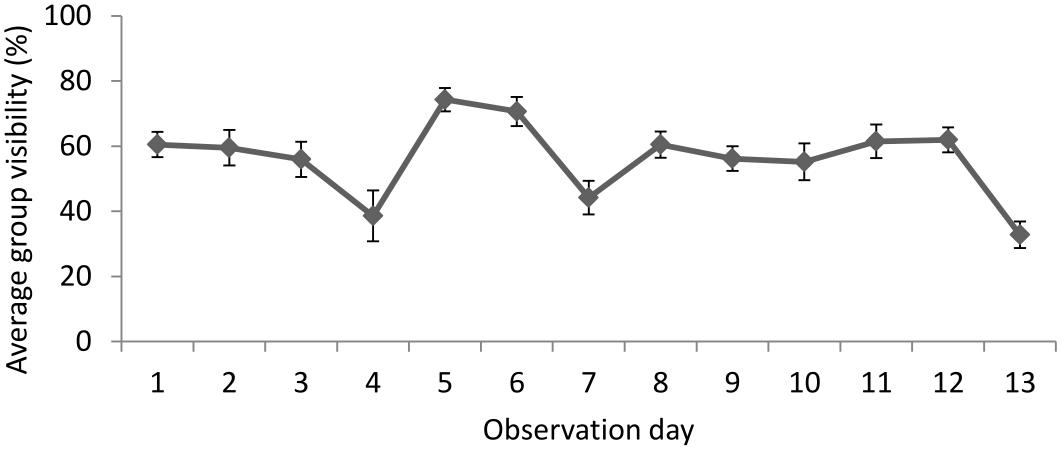


Figure 3.15: Variation in daily visibility of the focal group of hippopotamus. Closed circles: mean, vertical error bars: standard error.

Visibility differed significantly between times of day (Kruskal-Wallis test: $H_{(df=3,n=299)}$=16.524, ρ=0.001; Fig. 3.16); hippos were significantly less visible in the late afternoon (15:00 to17:00) than they were in the early morning (06:00 to 08:00; X^2=50.155, adjusted ρ=0.003) or late morning (09:00 to11:00; X^2=52.649, adjusted ρ=0.002). All subsequent results are based on the behaviour of individuals that were visible during the scans.

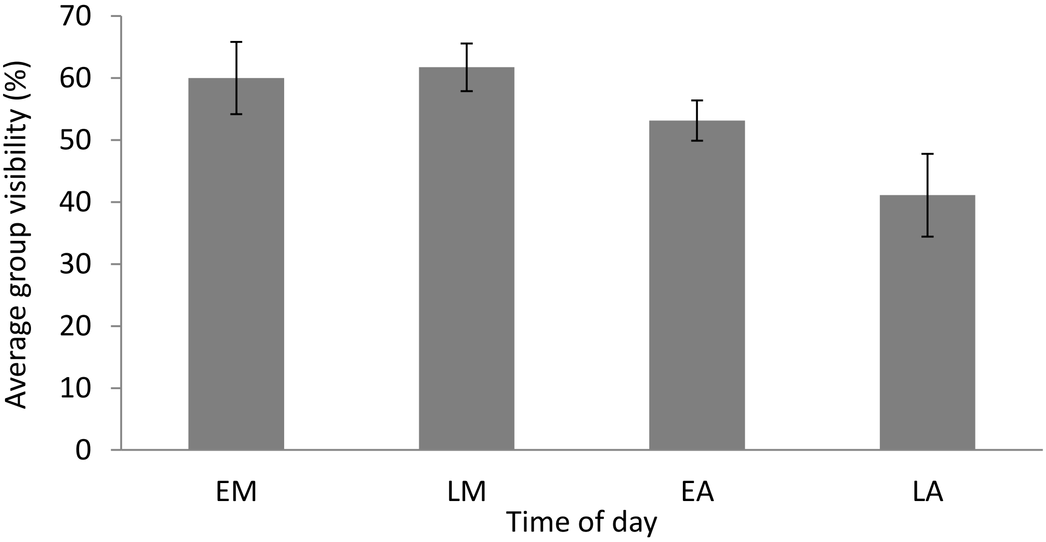


Figure 3.16: Differences in visibility (average ± SE) of the focal group of hippopotamus between different times of day (EM=Early morning, 06:00-08:00; LM=Late morning, 09:00-11:00; EA=Early afternoon, 12:00-14:00; LA=Late afternoon, 15:00-17:00).

Activity budget

Hippos allocated significantly more time (Kruskal-Wallis test: $H_{(df=3,n=600)}=376.907$; $\rho<0.001$) to resting 79.39% (± 3.95) than all other activities including moving (10.44% ± 2.04), socialising (7.92% ± 2.19) and feeding (2.24% ± 0.91, Fig. 3.17). The proportion of time engaged in feeding, resting and socialising differed significantly with day of study (Friedman's One-way ANOVA: Feeding $X^2_{(12,9)}=24.440$, $\rho=0.018$; Resting $X^2_{(12,9)}=22.057$, $\rho=0.037$; Socialising $X^2_{(12,9)}= 24.782$, $\rho=0.016$; Fig. 3.18). However, a post-hoc analysis using a Wilcoxon Signed Rank Tests, with a Bonferroni correction, (significance level set at $\rho < 0.00064$), reported no statistically significant differences. There were no significant differences in the distribution of behaviours across different times of day (Friedman's One-way ANOVA: Feeding $X^2_{(df=3,n=12)}=2.905$, $\rho=0.407$; Moving $X^2_{(df=3,n=12)}=0.923$, $\rho=0.820$; Resting $X^2_{(df=3,n=12)}=4.109$, $\rho=0.250$; Socialising $X^2_{(df=3,n=12)}=1.364$, $\rho=0.714$, Fig. 3.19).

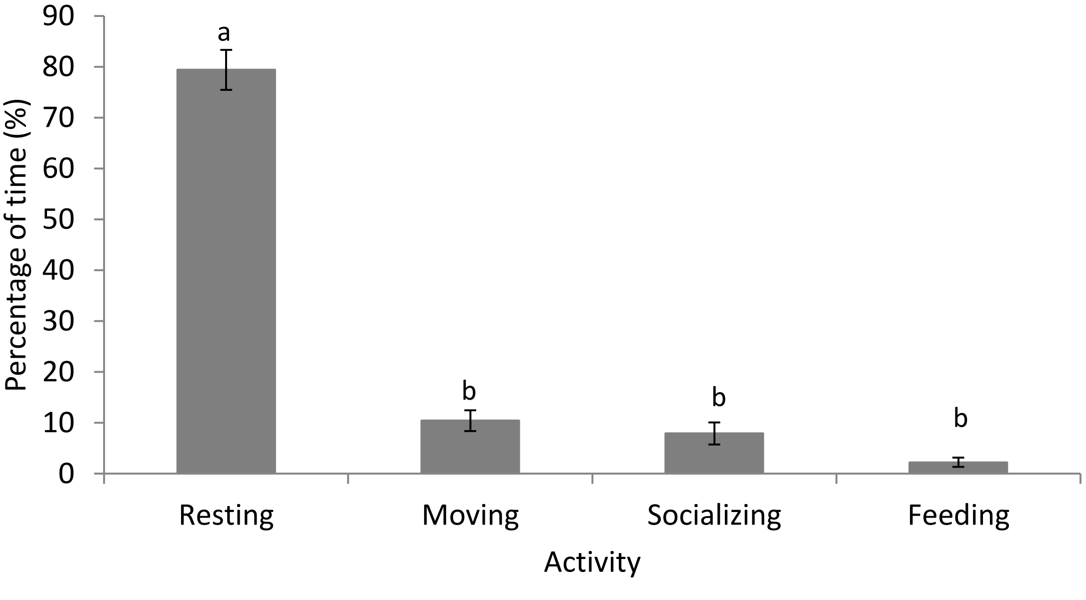


Figure 3.17: Percentage of diurnal time (average ± SE) spent engaged in each of the four activities (resting, moving, socializing, feeding) by the visible component of a focal hippopotamus group (a is significantly different from b; $\rho < 0.001$).

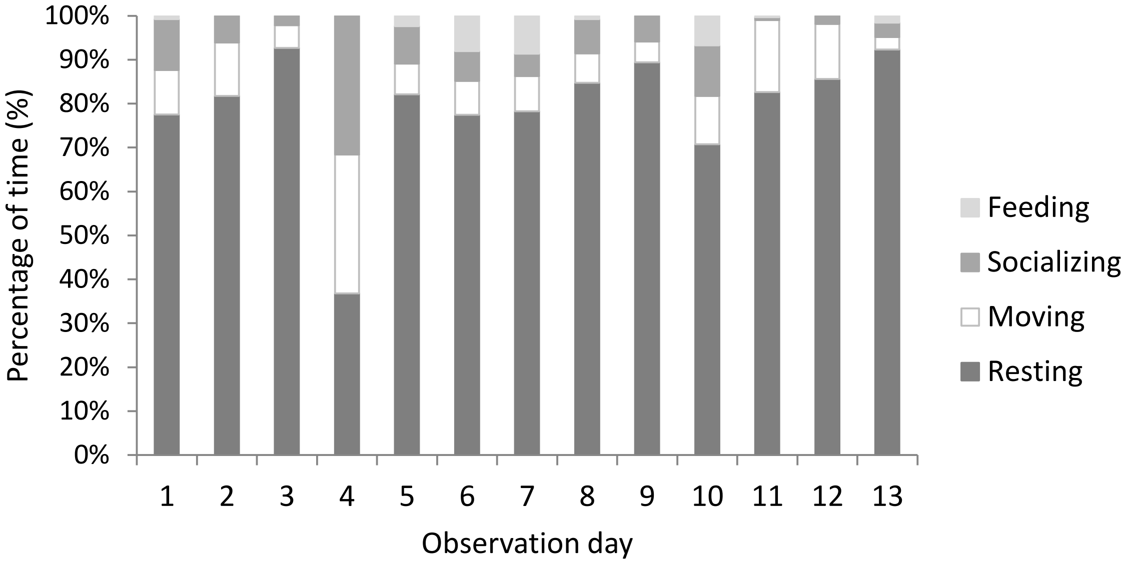


Figure 3.18: Variability of daily activity budget of the visible component of a hippopotamus group.

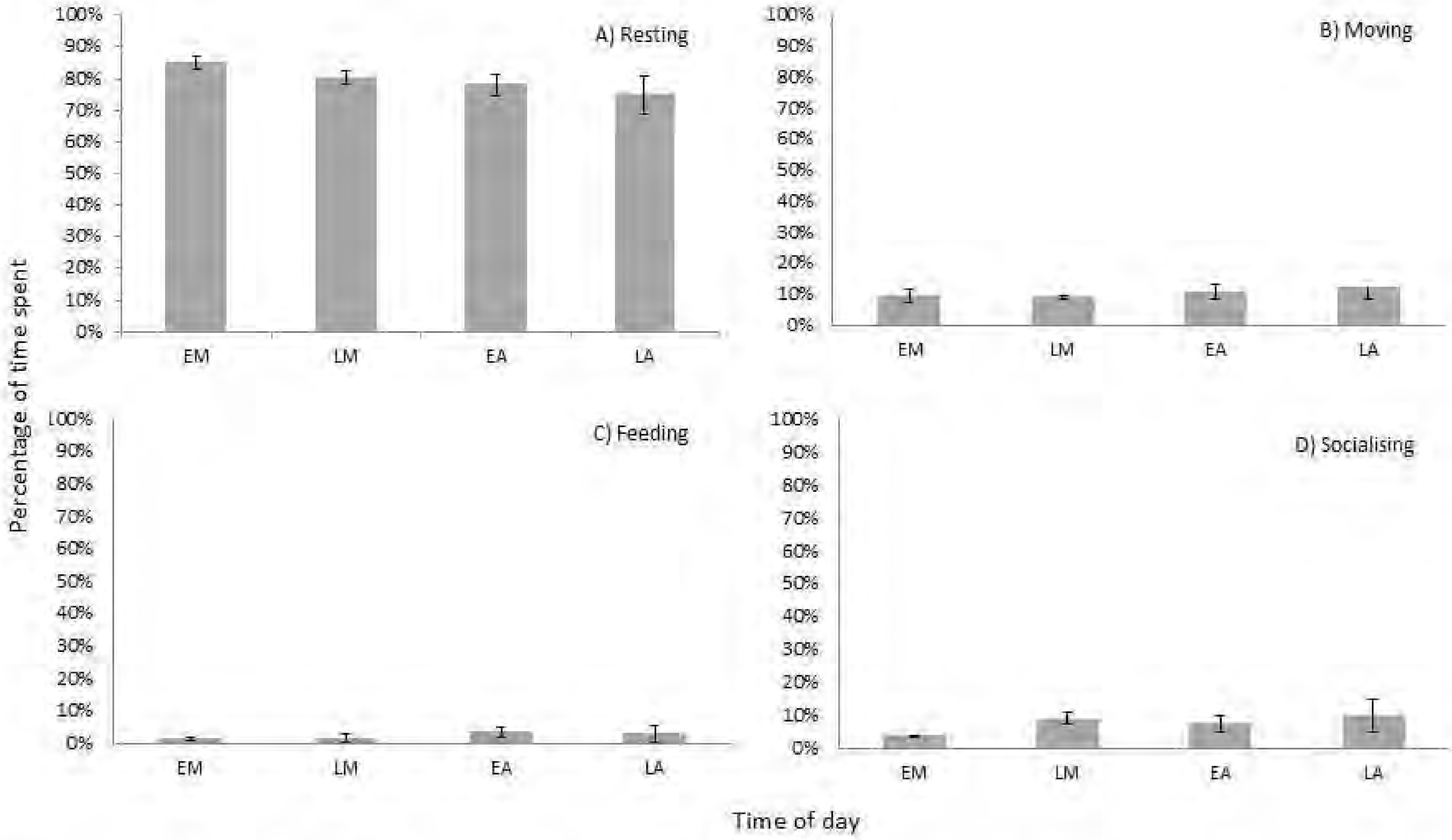


Figure 3.19: Differences in the average percentage of time allocated by the visible component of the hippo group to each of the four activities [A) Resting, B) Moving, C) Feeding and D) Socialising] between different times of day (EM=Early morning, 06:00-08:00; LM=Late morning, 09:00-11:00; EA=Early afternoon, 12:00-14:00; LA=Late afternoon, 15:00-17:00).

Social behaviours

Significant differences in the number of events per day of observation were recorded for dung showering, tail paddling and vocalising (Friedman's One-way ANOVA: Dung showering $X^2_{(12,10)}$=37.335, ρ<0.001; Tail paddling $X^2_{(12,10)}$=24.638, ρ=0.017; Vocalising $X^2_{(12,10)}$=35.469, ρ< 0.001; Fig.3.20). A Post Hoc test using the Wilcoxon Signed Rank Test, with a Bonferroni adjustment (significance level set at ρ<0.00064; significance level of 0.05/76 pair-wise tests, give 13 days of observation) did not reveal any differences between observation days for the different behaviours.

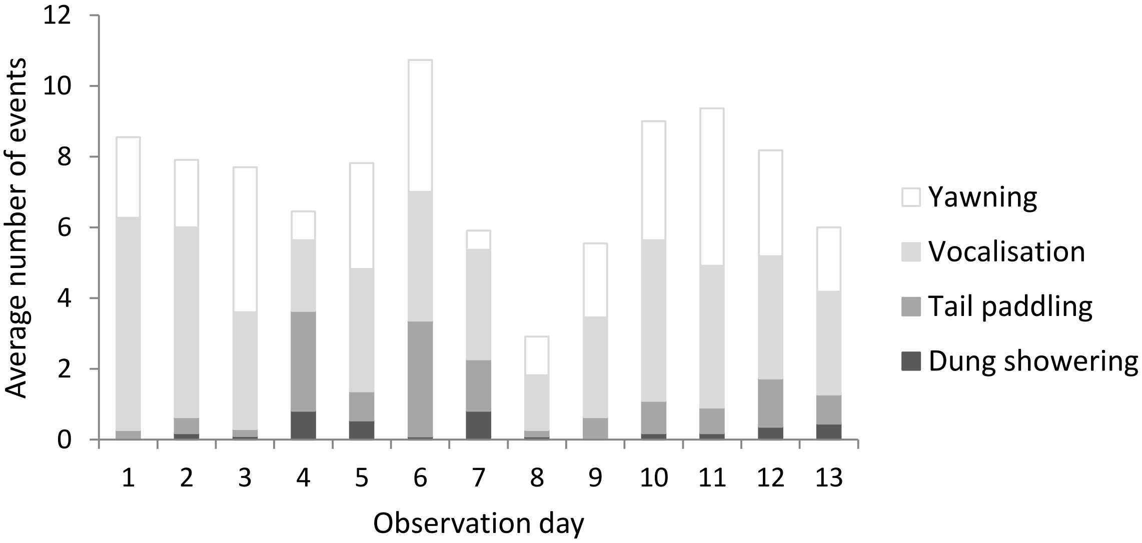


Figure 3.20: Variability of daily social behaviours of the visible component of a hippopotamus group.

Hippo yawning behaviour exhibited significant differences across different times of day (Friedman's 1-way ANOVA: $X^2_{(3,13)}$=14.328, ρ=0.002). Post Hoc analysis with Wilcoxon Signed Rank Tests and a Bonferroni adjustment (significance level set at ρ< 0.0083) revealed that hippos yawned significantly less in the early morning (EM) than during the late morning (LM; Z=-2.675, ρ=0.007) or late afternoon (LA; Z=-3.076, ρ=0.002, Fig. 3.21).

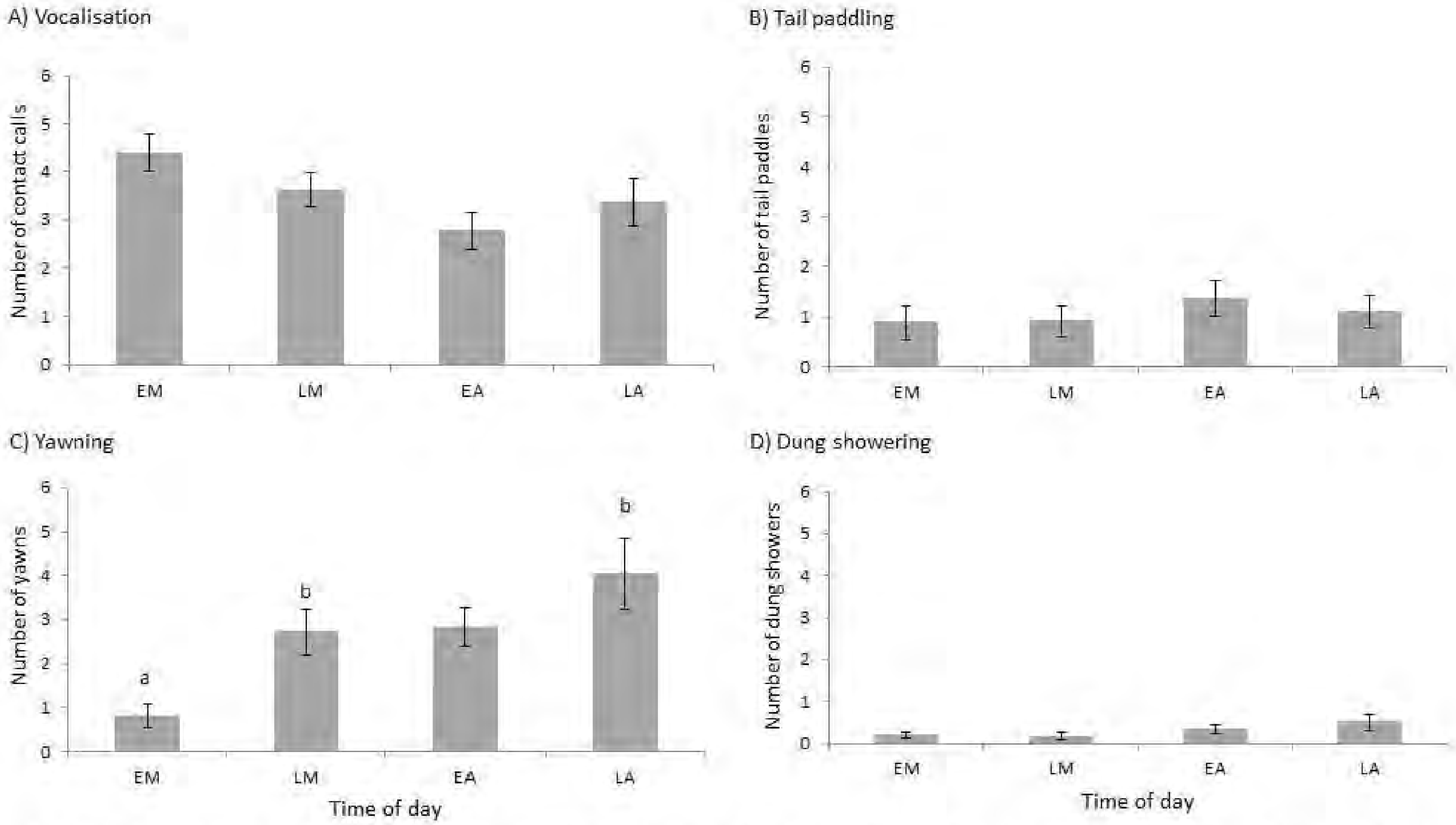


Figure 3.21: Differences in the average number of events (±SE) of; A) Vocalisation, B) Tail paddling, C) Yawning and D) Dung showering, between different times of day (EM=Early morning, 06:00-08:00; LM=Late morning, 09:00-11:00; EA=Early afternoon, 12:00-14:00; LA=Late afternoon, 15:00-17:00; a differed significantly from b, $p < 0.008$).

Chapter 4: Discussion

In this chapter, I place my findings, both spatial and behavioural, into the broader context of current threats facing *Hippopotamus amphibius*, a vulnerable species. Focussing on the key habitat variables as identified by my broad- and fine-scale spatial models, I evaluate the potential implications of changes to this already heavily impacted system on the future of the St Lucia hippo population. Furthermore, I discuss the limitations of my study and make suggestion for future research.

A: Spatial Ecology

Population density and distribution

The high degree of variability in hippo densities across their sub-Saharan range has been attributed to a number of local factors, including season, water levels, and the suitability of surrounding habitat (Viljoen, 1995; Bennett *et al.*, 2000; Kanga *et al.*, 2011; Chomba *et al.*, 2012). The overall population density within St Lucia Estuary (2.63 hippos/km of river) is comparable to that obtained within the Black Volta River in Ghana (2.11 hippos/km of river; Bennett *et al.*, 2000). However, it is considerably less than the estimated density of hippos within the Luangwa River in Zambia (35 hippos/km of river; Chomba *et al.*, 2012). Hippo densities are notoriously variable, not only between but also within systems, as illustrated by Viljoen (1995), who reported hippo densities varying between 2.9 and 11.6 hippos/km between five river sections in the Kruger National Park, South Africa. Similarly, the St Lucia Estuary also had highly variable hippo densities between each of its three major biotopes (Table 3.1).

Broad-scale results from the aerial survey data revealed that hippo density is highest (20.62 hippos/km) in the Narrows biotope. Importantly the boat-based census, which was restricted to the Narrows, provided a similar density estimate (21.07 hippos/km of river). The standard error for the 10 boat-based population estimates was low, suggesting that this is a reliable method for estimating population size within this biotope. The agreement in hippo population estimates in the Narrows using both aerial and boat based surveys increases confidence in aerial survey estimates of hippos in the lakes of the St Lucia system were boats have limited access. Boat-based surveys of the Narrows provide cost-effective, high-resolution hippo distribution data, providing accurate data on group sizes and intergroup distances (not available from aerial surveys). Both the number of groups (24.9 ± 0.94 SE groups) and group sizes (10.86 ± 0.55 SE hippos/group) were remarkably stable within the Narrows suggesting both site and group fidelity. I elected to analyse the hippo distribution data in terms of occurrence (both broad- and fine-scale data) and frequency of daily use (fine-scale data only). This provides insight into the landscape level requirements of the resident hippo population.

The importance of water depth

Chief among those factors affecting hippo distribution and behaviour, in this as well as other systems throughout their range, is water availability. This study identified water depth and distance to river inlets as important factors affecting hippo distribution within the St Lucia Estuary as a whole. The higher presence of hippos in the Narrows suggests a preference for water depths greater than in the lakes (Fig. 3.1). The Narrows is on average 1.42m deep while the Lakes are shallower (<1m deep) and more susceptible to dry outs during droughts (Taylor *et al.*, 2006a, 2006b ; Whitfield & Taylor, 2009; Chrystal & Scharler, 2014). Within the Narrows, hippos favoured water depths between 1.0 and 1.49m (Table 3.3; Table 3.5; Table 3.6; Fig. 3.9; Fig. 3.10); results which are similar to those from a previous study (1.37m ±

0.028 SE) in the St Lucia Estuary (Taylor, 1980). Hippos rest in water in order to maintain body temperatures, reduce sun exposure and minimise energy expenditure. Sites that are shallow enough to stand in, yet deep enough to remain submerged in would thus be ideal diurnal refuges (Horikoshi-Beckett & Schulte, 2006; Coughlin & Fish, 2009; Blowers, *et al.*, 2010; Klingel, 2013). Given the average shoulder height of hippos is 1.5m, it is not surprising that much of the lakes are too shallow for hippos, and predictions by the broad-scale model indicate that hippos selectively settle within the deeper Narrows and the associated river segments (Fig. 3.4).

Hippo distribution within the Lakes is linked to the presence of river inlets, specifically those along the eastern shores (Fig. 3.1, Fig. 3.5), where groundwater seepage ensures some water inflow/upwelling year-round (Taylor *et al.*, 2006b; Været *et al.*, 2009; Kelbe *et al.*, 2013; Taylor, 2013). Given the hypersaline (exceeding 35 ‰) conditions experienced within the lakes during drought phases, river inlets provide an important source of fresh drinking water for hippos (Taylor 1980) in the St Lucia estuary, often in the form of groundwater seepage (Taylor *et al.*, 2006b; Været, *et al.*, 2009; Whitfield & Taylor, 2009; Kelbe *et al.*, 2013; Whitfield, 2013; Taylor *et al.*, 2015;). The fact that hippos occupied only 36 out of the 419 cells available, predominantly along the eastern shores of the lakes and within the Narrows (Fig. 3.1), suggests a clustered distribution pattern. This may be explained by the fact that inter- and intra-group distances are likely to decrease as resources, specifically water depth, become limited (Klingel, 2013), with numerous groups coalescing into one. As the system dries during severe droughts, inlets with groundwater seepage (e.g. Nkazana and Tewate streams; Taylor *et al.*, 2006b; Været *et al.*, 2009) become the last refuges, forming pools for the lake hippos to lie-up in (Kelbe *et al.*, 2013; Taylor, 2013). Tewate Bay is one such refuge, as evidenced by the more than 300 hippos that aggregated there during the

2002 extended-drought phase (Kelbe *et al.*, 2013; Taylor, 2013). The broad-scale model results correctly predicted hippos to settle in Tewate Bay (Fig. 3.5), thereby highlighting the importance of river inlets to hippo persistence within the lakes. According to Bennett *et al.*, (2000) and Chansa, *et al.*, (2011b), river inlets are often associated with greater hippo densities as they are sites of increased sediment deposition, thereby generating sandbars that are ideal for providing a gradient of depths that hippo can use for behavioural thermoregulation.

At the scale of the whole St Lucia estuarine system, proximity to river inlets is an important factor predicting hippo distribution, as discussed above. However, this variable is not an important predictor of hippo presence within the Narrows. This may be because the Narrows has a much higher density of inlets (2.07 river inlets/km^2) compared to the Lakes (0.169 river inlets/km^2) and hence it is less of a limiting and hence defining variable in this biotope. However, it must also be borne in mind that the fine-scale data set evaluated the Narrows at a much smaller scale (100x100m instead of the 1x1km broad-scale data), which is potentially too fine to detect the relationship between distance to river inlets and hippo distribution.

Direct and indirect effects of human encroachment

This study revealed a negative correlation between hippo distribution and distance to human settlements at both broad - and fine-spatial scales (Table 3.4, Fig. 3.6 and Table 3.5, Fig. 3.8 respectively). It is possible that human presence has both direct (e.g. harassment) and indirect effects (e.g., land-use change and competition with livestock for grazing, decreasing water level due to water abstraction) on hippo, which may explain the negative relationship.

The inverse relationship between hippo distribution and human settlements is similar to the findings of Mackie *et al.*, (2012), who reported a decrease in hippo range with increased anthropogenic activity. Similarly, Kujirakwinja (2010), in the Virunga National Park, Democratic Republic of Congo, reported greater hippo densities in areas where human settlement was sparse or absent. An exception to the latter is provided by Kujirakwinja (2010), who reported an increase in hippo presence and density around ranger stations, which was attributed to hippos seeking refuge from poaching pressure.

The mechanisms by which humans disturb hippo habitat selection within the St Lucia Estuary are unknown. iSimangaliso Wetland Park is a protected area; however there are numerous human settlements within and around the park. Higher levels of human presence and activities such as fishing, tourism and poaching associated with human settlements have the potential to generate significant disturbance to resting hippos (Onyeanusi, 2004). Work by Richardson & Würsig (1997) and Gordon *et al.* (2004) on marine mammals suggest that individuals at rest are more susceptible to disturbances (predominantly human). A variety of effects (including displacement from biologically important habitats, competition for resources, alteration of activity budgets and behaviour) associated with increased human disturbance have been documented for numerous species (marine mammals, Richardson & Würsig, 1997; Weilgart, 2007; Luís, *et al.*, 2014; hyenas, Kolowski, *et al.*, 2007; ungulates, Averbeck *et al.*, 2012; Sönnichsen, *et al.*, 2013). Thus the lack of hippo occupancy observed along the Western Shores of the Lakes (Fig. 3.1) and the lower occupancy (Fig. 3.7) and frequency of use (Fig. 3.11) observed within the lower reaches of the Narrows (closer to human settlements) may be indicative of the direct effects of human disturbance. There were both fewer (Fig. 3.2) and smaller (personal observation) hippo groups settling within the lower reaches of the Narrows where human presence is particularly high. It is worth noting that hippo groups may become habituated to humans, even foraging in residential areas, as is the case in the town of St Lucia where numerous hippos come to graze on residential lawns (Taylor, 2013). This is currently still the exception and not the norm. However, as natural forage availability becomes limited during severe drought conditions hippos may become increasingly reliant on these man-made lawns, thereby increasing the potential for human-hippo conflict.

The decreased presence of hippos near human settlements may also be explained by competition with domestic livestock for access to grazing areas (Wengström, 2009). Roaming herders graze their cattle on communal lands in and around the iSimangaliso Wetland Park, hippos are therefore potentially at risk of being excluded from these grazing areas, either through negative interactions (e.g. competition, avoidance) with cattle or the conversion of hippo grazing areas into unsuitable fields by cattle grazing and trampling (Wengström, 2009). In this way, humans may indirectly affect the vegetation type, quality and quantity available to hippos for grazing. In contrast, Kanga *et al.*, (2011) reported an increase in the density of hippos in areas along the Mara River, Kenya associated with pastoral ranches. However they attributed this to a drastic range contraction for hippo (due to habitat loss and a shortage of resources) and a concomitant increase in density in the least impacted areas i.e., pastoral ranches.

Encroachment by a growing human population into the buffer zone surrounding the iSimangaliso Wetland Park is placing more pressure on the water and potentially encroaching on areas once utilised for grazing (Whitfield & Taylor, 2009; Taylor *et al.*, 2015). By abstracting water and diverting rivers, neighbouring communities are drying out wetlands and creating space for illegal cultivation in both the northern lakes region and the lower reaches of the Mfolozi River (Whitfield &Taylor, 2009; Stretch & Maro, 2013; Taylor, 2013b; Whitfield *et al.*, 2013; Taylor *et al.*, 2015). Together these practices are resulting in rapid land-use change and degradation of the available wetland vegetation (Whitfield &Taylor, 2009; Ellery *et al.*, 2013; Whitfield *et al.*, 2013; Taylor *et al.*, 2015). These changes in turn may influence both the distribution of lie-up sites and the suitability of foraging sites for hippos. The combined effect could force hippos into smaller areas with increased human presence.

The role of wetland vegetation and nearest neighbours

Hippo occurrence (Table 3.5) and frequency of cell use (Table 3.6) within the Narrows was positively influenced by distance to nearest neighbours, with hippos settling in close proximity to sites that were previously, or were at that time, occupied by hippos. This resulted in a clustered pattern of site selection, as is evident in both the observed and predicted hippo distribution maps. Cells in the upper reaches of the Narrows are characterised by higher presence (Fig. 3.7, Fig. 3.8) and frequency of use (Fig. 3.11, Fig. 3.12).

Within the Narrows, the average distance to the nearest neighbouring group was 122.38m (Table 3.3), resulting in a clumped distribution with only 39.7% of the total area of the Narrows being occupied by hippos. Nineteen percent of sites used within the Narrows were used repeatedly (50 and 90% of the survey days). These estimates are however, likely to be conservative as they are influenced by the scale at which sites were delineated. Sites were defined as cells with a dimension of 100X100m, based on the known territory sizes of riverine hippos elsewhere in Africa (50 - 100m along the shore, Klingel, 2013). However, my observations on a group of hippos (Chapter 3) within this system revealed that its territory may include several areas that are used alternately by either the entire group or subgroups as their individual needs or the micro-environmental conditions alter. Thus for example, females and calves may move from the core area (most frequented) to shallower areas (less frequented) to nurse; or the entire group may move to what was once a shallower area following an increase in water levels or a change in wind direction or strength. These findings are supported by other studies (e.g., Wittemyer *et al.*, 2005; Klingel, 2013) which have shown that environmental conditions drive changes in group composition and distribution. Together these lines of evidence suggest that the cell sizes for sites, although based on previous estimates of territory size in hippo, may have been too small. A larger cell would have included more GPS points and hence higher estimates of site fidelity.

The fact that hippo groups space themselves out into smaller units within certain areas of the Narrows, may indicate that groups converge on areas that offer the most favourable combination of resources. Numerous studies have suggested that abiotic features of a site, such as water depth and distance to grazing are more important than for example group composition in determining the suitability of a site (Barklow, 1997; Karstad & Hudson, 1986; Viljoen, 1995, Klingel, 2013). Female hippos are known to select sites based on habitat suitability, with sites that fulfil key requirements occupied more frequently and by larger groups (Karstad & Hudson, 1986; Viljoen, 1995; Barklow, 1997; Klingel, 2013). Thus selecting sites that are in close proximity to conspecifics may be indicative of high levels of competition for shared resource (e.g. lie-up sites of adequate water depth, forage availability).

In the present study, model results indicated that hippo distribution within the Narrows is strongly influenced by water depth (Table 3.5; Table 3.6). Despite this there were still many sites within the optimal water depth range (1.0 – 1.49m) that were not occupied by hippos (Table 3.3), suggesting it is not a limiting resource and that other variables may explain presence. The frequency of cell use increased with decreasing proximity to natural wetland and wetland floodplain vegetation, whilst hippos avoided using sites in close proximity to the Matrix vegetation type (Table 3.6; Fig.3.12). Utilisation of wetland vegetation for grazing may explain the seemingly compressed distribution of hippos into the upper reaches of the Narrows, where there is more natural - and floodplain wetland vegetation. These wetland areas may be of particular importance during the dry season and especially so during extended droughts, providing grazing grounds when other areas, further afield, are potentially overgrazed or unproductive due to a lack of water (Taylor, 2013).

It is worth noting that natural wetland vegetation dominated the near shore area, and was the second most dominant vegetation type within 5km (Table 3.2). Furthermore, the majority of wetland vegetation is on the eastern shores of the St Lucia Estuary (Fig. 2.4), often associated with ground-water seepage (Ellery *et al.*, 2013). Elsewhere in Africa, studies have highlighted both proximity (a preference for settling closer to wetlands: Lewison, 2007; Mackie *et al.,* 2012; and short grass grasslands: Eltringham, 1999) and dominant vegetation type (floodplain grasslands: Harrison *et al.*, 2007) as important factors affecting hippo distribution. However, with so few occupied cells within the estuary the model results indicate no clear relationship between vegetation types (both nearest and most dominant) and hippo occupancy. Instead, I suggest that at the broadest scale hippo occupancy is primarily driven by the need for water availability, and that the avoidance of areas densely populated by human settlements may be a confounding effect of the anthropogenic influences on water availability and vegetation type and quality along the Western shores of the lakes.

B: Activity budget and social behaviour

By evaluating hippo distribution, we gain an understanding of the factors that may influence hippo habitat selection. However, by evaluating hippo activity budgets and behaviour, we may gain insight into their behavioural responses to a changing environment. Given their dependence on water as a refuge, and their central place foraging strategy, any changes to aquatic habitats or the surrounding vegetation and land-use is likely to be expressed as changes in hippo activity budgets or social behaviours (Timbuka, 2012). For example, behavioural observations on the Mouth group revealed that an increase in water levels resulted in (1) the group moving upstream into a lone bull’s territory, (2) a territorial dispute and (3) the eviction of the Mouth group’s dominant bull (day 4 of observations). Similar results have been reported in other studies in Africa, noting that fluctuating water levels were associated with more territorial disputes, whilst hippo groups exhibited greater social equilibrium under static water level conditions (Karstad & Hudson, 1986).

Visibility

Given the amphibious lifestyle of hippos, numerous activities and behaviours occur underwater, or out of sight of observers (e.g. in reeds, under riparian vegetation). For the most part, there is no reason to believe that any activity (resting, moving, socialising or feeding) would disproportionately occur out of sight of the observer. By quantifying the proportion of behaviours observed, my results revealed the cryptic nature of hippo behaviour and subsequently highlighted some of the limitations of a behavioural study on wild hippos. On average, the majority (56.45%) of the Mouth group were visible during scans (Fig. 3.14). However, visibility was variable throughout the observation period, with significant differences noted between days (Fig 3.15) and between times of day (Fig 3.16).

The fact that hippo visibility differed between and within days suggests that hippo space use and surfacing behaviour are temporally variable. Such variability could be due to variation in abiotic (wind speed, wind direction, cloud cover, air temperature, water depth, water temperature) and social factors (responses to territorial disputes, calf introductions, underwater communication) (Barklow, 2004; Noirard, 2008; Klingel, 2013). A study by Noirard (2008) found that hippos in the Niger River, Niger Republic, adjusted their sun exposure (basking and surfacing) depending on water and air temperatures. Hippos exposed their bodies to the sun for longer during colder periods. I also noticed that hippos submerged more of their bodies and remained submerged for longer periods when the wind speed increased (usually later in the day), resulting in hippos relocating to sheltered areas such as reed channels or a lie-up site under riparian vegetation. Behavioural thermoregulation may therefore explain daily and temporal variability in hippo visibility. Changes in wind speeds or decreases in air temperatures in the late afternoon may explain the significant decrease in visibility of hippos at this time of day (Fig. 3.16). I collected wind strength data as perceived at my location; on board a stationary boat, approximately 40m from the nearest hippo. Given the safety limitations I was often positioned in a more exposed area than where hippos were located. Thus the subjectivity of designating wind strength (perceived wind speed at a specific point in space and time; categorized as wind strength 1 = 0–4 knots, wind strength 2 = 5–9 knots, etc.) combined with the resultant small sample size obtained during my observations lead me to discard the wind related data.

Hippos are generally most socially active and vocal in the period between 15:00–18:30 (Karstad & Hudson, 1986; Barklow, 1997). Barklow (2004) observed that hippos were submerged for 77% of the time between 16:00 to 19:00, and attributed the increased submergences of hippos late in the day to their increased use of underwater sounds and social communication. I also observed a decrease in visibility of the focal group in the late afternoon (15:00 to 17:00) relative to the early (06:00 to 08:00) and late morning (09:00 to 11:00; Fig. 3.16). In addition, there was decreased visibility on the fourth observation day, which coincided with a territorial dispute (Fig. 3.15). It is possible that both events are associated with increased underwater communication and hence more time below water. Based on these observations I suggest that the decrease in visibility of hippos are most likely as a result of increased subsurface communication, instead of wind speeds as previously suggested. However, visibility was not only hampered by submergence behaviour, but relocation within the group's territory as well. Thus wind speed and direction may affect hippo fine-scale space use.

Barklow (2004) observed that hippos decreased time spent under water as they approached their haul-out time, at the end of his observation period (19:00). Typically, group members haul-out en masse at dusk (Klingel, 2013). However, the Mouth group were much more cryptic in this behaviour, and the decrease in hippo visibility in the late afternoon often resulted in the majority of the group being unaccounted for in the final scan of the day, possibly indicating that hippos haul out en masse in areas where they were unobserved or as individuals. It is possible that the more discrete behaviours of the Mouth group, and the possible alteration in emergence times, is an attempt to avoid the many tourists that congregate at the group in the late afternoon when hippos would normally be leaving their day time lie-up sites. Such a notion is supported by the work of Onyeanusi (2004) who observed a group of hippos in Kainji Lake National Park, Nigeria and reported that emergence time shifted as a function of human presence.

Activity Budgets

Hippos are nocturnal and thus expected to allocate the majority of their diurnal activity budget to resting in an attempt to conserve energy, maintain their body temperature, and ferment and digest the previous night's forage (Klingel, 2013). My findings are in agreement with this general prediction. Hippos spent the majority of their daytime hours resting (79.39%) in the water or on the banks of the estuary, with only a small portion of their diurnal activity budgets being allocated to moving (10.44%), socialising (7.92%) or feeding (2.24%, Fig. 3.17). The lack of behavioural studies on hippos within South Africa lead me to compare my results to those obtained during a similar study conducted by Timbuka (2012) on wild hippos in the Katavi region in Tanzania. The Mouth group allocated substantially more of their diurnal activity budget to resting, and less to feeding or moving than hippo groups in the Katavi region (average time spent resting and standing = 53.3%, feeding= 19.3%, moving = 18.05%; Timbuka, 2012). The differences between these findings may be explained by the environmental differences between these localities. Tanzania is located near the tropics and thus experiences longer days and shorter nights, compared to St Lucia Estuary. Thus hippos residing in the Katavi region may have less time available to feed during the night resulting in more diurnal foraging behaviour being recorded. For hippos, resting is much more than an energy conservation strategy but fulfils both thermoregulatory and digestive functions too. Potentially, resting serves a social function as well, with rafting behaviour having been proposed as reinforcing social bonds (Blowers *et al.*, 2010).

Timbuka (2012) also noted that hippo were most active (feeding, moving) during the early morning (07:00 to 07:30) and the early evening (19:00 to 19:30), with most resting occurring in the middle of the day (09:00 to 17:30), potentially when temperatures (and UV exposure) are highest (Timbuka, 2012). In my study, the Mouth group exhibited no statistically significant differences in the temporal allocation of activities (Fig. 3.19), suggesting that hippos are equally likely to be resting, moving, socialising or feeding in the early morning as any other time of day. It is possible that observations in the seasonal extremes of winter and summer (I collected my data in autumn) might produce more marked diurnal patterns in activity budgets. Hippos in the Katavi region of Tanzania allocated more time to feeding during the cooler, wet season than during the dry season when increased air temperatures and decreases in the availability of forage resulted in increases in the resting behaviour and decreases in the time spent foraging and walking (Timbuka, 2012).

It is possible that the Mouth group hippos allocated more time to resting than either feeding or moving in response to a lack of forage in close proximity to the diurnal lie-up site. This is similar to findings by Timbuka (2012) who showed that hippos adjusted their diurnal activity budgets in response to forage availability near their lie-up sites in addition to water availability and air temperatures. Forest patch vegetation dominates the focal group's effective foraging range (5km radius); however, small areas of matrix vegetation (predominantly sand dunes and beach, with sparsely settled dune vegetation; Taylor *et al.*, 2013a), degraded wetland (severely impacted by human activities) and wetland floodplain vegetation are accessible from their diurnal water refuge (nearest vegetation types; Fig. 2.17). The feeding bouts that I observed included grazing in both wetland degraded and matrix vegetation types, as well as numerous instances of browsing on riparian vegetation such as reeds, or hibiscus plants, or feeding on unidentified aquatic plants. Harrison *et al.*, (2007) suggested that feeding on aquatic plants by hippos may be indicative of limited grazing availability in nocturnal foraging areas. The latter may well be one of the factors contributing to the increased resting behaviour, as continued human encroachment and land-use change (e.g., illegal agricultural activities, human settlement) affects the availability and accessibility of wetland vegetation within the lower reaches of the Mfolozi river (Taylor *et al.*, 2015), part of the area potentially utilised by the Mouth group hippos.

Social behaviours

The social behaviours displayed by hippos in the focal group differed significantly between observation days (Fig. 3.20), suggesting that hippos were responding to external factors (e.g. water levels, weather conditions, intra-group dynamics) or endogenous factors (e.g. hormonal status, reproductive status). Vocalising, tail paddling and dung showering differed significantly between observation days, yet exhibited no obvious diurnal patterns (Fig. 3.21 A, B, D).

I expected vocalisation to occur most often during fission-fusion events, when individuals join the group in the early morning after an evening of solitary grazing and late afternoon, around dusk when hippos congregate before they leave to graze. However, my data illustrated no such patterns (Fig 3.21 A); instead, hippos vocalised randomly throughout the day. Karstad and Hudson (1986) noted that hippos were most social and most vocal in the late afternoon and early evening (15:00 to 18:30) - an observation confirmed by Barklow (2004). Barklow (2004) suggested that the dominant bull usually initiated these amphibious calls resulting in nearly all hippos within the group surfacing and responding in chorus. I was seldom able to identify the hippo that initiated the call, due to the close proximity of group members. However, my data suggest that once initiated, the majority of the group responded in chorus. Furthermore, calls were randomly distributed throughout the day, lacking the dawn and dusk peaks present in other studies. It is possible that high levels of human activity (i.e., fishing, horseback riding, tourist barges, boating) in and around their territory, interfere with intragroup communication and elicit vocalisations throughout the day.

I also expected submissive (Tail paddling, Fig. 3.21B) and dominant (Dung showering, Fig. 3.21D) behaviours to be more frequent in the early morning and late afternoon as these times of day are potentially associated with the affirmation of hierarchies immediately after and prior to group fissioning for terrestrial foraging. Again, no such temporal patterns were observed and similar to vocalisations, both behaviours were performed with similar frequency throughout the day. There was however variation in both these behaviours between observation days (Fig 3.20) suggesting that these behaviours are potentially influenced by environmental or social factors that I was not able to quantify. I did note that dung showering and submissive tail paddling were more frequent following a territorial dispute with a neighbouring bull (day four, Fig. 3.20). Thus, it is possible that the increase in dominant and submissive displays following the territorial take-over is indicative of a hippo group in social flux, during which a new hierarchy is being established. Blowers *et al.*, (2010) suggested that a lack of aggressive interactions and dominance displays (tail paddling, dung showering, etc.) observed during their study was due to an already established dominance pattern existing between familiar or related group members.

Yawning behaviour is associated with an expression of excitement and has been observed to increase as hippos prepare to leave for foraging (Karstad & Hudson, 1986). Consequently, I had expected yawning behaviour to be greatest in the late afternoon just prior to the hippos exiting the water to commence feeding. My results supported this prediction as hippos yawned significantly less in the early morning than they did in the late morning or late afternoon (Fig. 3.21C). This pattern was consistent between days (Fig. 3.20) and suggests that yawning fulfils an important social function.

Management applications of this study

The greatest threat to hippo persistence within St Lucia will almost certainly result from reduced inflow or increased abstraction with a concomitant reduction in water levels. This would be especially pertinent for hippo populations within the lakes, with current water levels less than 1m deep (Whitfield & Taylor, 2009), where further shallowing of the lakes would further limit the number of potential diurnal lie up sites available. This restriction may influence both the social dynamics (e.g. crowding) of the resident hippo population as well as the surrounding habitat structure (e.g. overgrazing). Hippos are known to be ecosystem engineers in both their aquatic and terrestrial environments, thus changes in their distribution and density may have important effects for other species and system functioning (McCarthy *et al.*, 1998; Kanga, *et al.*, 2011; Klingel, 2013; Taylor, 2013).

Under the conditions evaluated during this study, hippos within the Narrows were not restricted by the availability of sites with preferred water depths. However, if water levels drop below some critical threshold (yet unknown) and more hippos become restricted to the Narrows (moving south from the Lakes), the availability of lie-up sites may become a limiting factor. Higher hippo densities and increased aggression under resource-limited conditions may result in a decrease in conception rates or survival, which may impact hippo populations within the St Lucia Estuary (Smuts & Whyte, 1981; Eltringham, 1993). During this study I never observed hippos in sites less than 0.5m deep, however my inability to access such shallow sites (the boat’s hull was too deep) precluded me from obtaining direct water depth measurements and the associated data required to verify such an observation statistically.

Recent reports on the state of the St Lucia estuary indicate that declining water depth is a potential threat to the system as a whole (Taylor *et al.*, 2015), which may impact on the future of the St Lucia hippo population. Increasing pressure on the freshwater resources by growing human settlements on the fringes of the iSimangaliso Wetland Park, and the lower than average rainfall conditions have resulted in the system as a whole 'drying-down' (Whitfield & Taylor, 2009; Whitfield *et al.*, 2013; Taylor *et al.*, 2015). Water levels have dropped by 60cm in 9 months, (Lake; July 2014–April 2015) and salinities are increasing (with fresher water in the Narrows and salinities exceeding that of seawater (35parts ‰) in the northern sections of the system; Taylor *et al.*, 2015). Although the annual report suggests that hippos are currently moving northwards within the system, following the southward contraction associated with drought conditions, the northward migration could also be driven by the recent re-linkage of the Mfolozi River and associated positive effects on water levels in the lower (southern) reaches of the Narrows.

The reconnection of the Mfolozi River to the St Lucia Estuary was identified as one of the most important factors in securing the future sustainability of the estuary (Lawrie & Stretch, 2011; Whitfield *et al.*, 2013). However, Whitfield & Taylor (2009) have cautioned against the premature reconnection of these two systems, citing the higher rates of siltation as a potential problem. Whitfield & Taylor (2009) recommended that the Mfolozi river water pass through a re-established Mfolozi swamp first allowing the sediment to be filtered. The advice of Whitfield & Taylor (2009) was not heeded and the Mfolozi River - St Lucia Estuary link was re-established in July 2012, without a swamp filter (Perissinotto, *et al.*, 2014).

The reconnection of both the freshwater source (Mfolozi River water) and marine water has had many positive effects on the estuarine system, with increased productivity and recruitment of marine species into the estuary (Taylor *et al.*, 2015). However, it has also brought both fine-grained Mfolozi sediment and coarse-grained sea-sediment into the St Lucia system, specifically in the lower reaches of the Narrows, potentially causing a shallowing of the system (Taylor *et al.*, 2015). Not only could the water level change due to sedimentation but water levels may also fluctuate more often due to the intermittent connection with the Mfolozi, and as the amount of water that flows into the system via the link varies with rainfall events, mouth state (open/closed) and over-topping of seawater (Taylor *et al.*, 2015). Given the sensitivity of hippos to fluctuating water levels and their dependence on the Narrows as a refuge, fluctuations in water levels associated with this link may alter hippo behaviour and distribution within the system. Karstad & Hudson (1986) reported increased aggression and territorial disputes when water levels were actively fluctuating.

The gradual infilling of the mouth region of the Narrows with Mfolozi and ocean sediments may benefit hippo settlement by converting areas that were normally too deep for hippos into sites with suitable water depths. The problem though is that the mouth region of the Narrows lacks natural wetland and wetland floodplain vegetation along its banks, making these sites less favourable for hippos. Furthermore, the mouth region of the Narrows is heavily impacted by human settlement, both with regard to proximity to humans, and with regard to the variety of anthropogenic activities that occur in this area (i.e., expanding human settlements, land-use change to cultivated land, fishing and tourism). Hippos are thus unlikely to settle in this part of the system in great numbers. If they should, the potential for human-hippo conflict is great.

A study by McCarthy *et al.* (1998) attributed the fluvial system characteristics of the Okavango delta’s fan to hippo engineering. Similarly, hippo distribution and habitat use may influence the system connectivity and water flow within the wetland vegetation surrounding the St Lucia Estuary. Hippo engineering capabilities may be beneficial to the regeneration of the Mkhuze and Mfolozi swamps filters (Fig. 1.3), thereby enhancing their ability trap sediment and ensure the maintenance of sufficient water levels within the St Lucia estuary (Taylor, 1980; Whitfield & Taylor, 2009; Whitfield *et al.*, 2013). Thus by limiting human encroachment and its associated impact on wetlands, hippos might be encouraged to return to these swamplands, thereby re-engineering them, and ensuring the future sustainability of this system.

The protection and management of the wetland vegetation types surrounding the St Lucia Estuary and associated groundwater sources are imperative for the growing hippo population. This is especially pertinent in the context of the increased duration and severity of recent droughts in the system, during which hippos are thought to rely more heavily on this habitat for grazing (Taylor, 2013). Not only do wetlands provide forage for hippos during the dry-season, but they potentially provide hippos with lie-up sites during the wet season (Taylor, 2013), thus decreasing the distance that hippos need to travel to foraging areas. Taylor (2013) reports a gradient of hippo grazing intensity, with the most heavily grazed areas closer to the estuary shore and other wet season lie-up sites (swamps and pans on eastern and western shores of the estuary).

Recent reports of habitat loss due to illegal land-use change within the park boundaries is also of great concern (Taylor *et al.*, 2015), as this suggests increased competition with humans and their livestock for grazing. I suggest that management and conservation authorities can mitigate the effects of human encroachment and habitat loss by maintaining and managing the buffer zone around the iSimangaliso Wetland Park. Granted this is an enormous task given the size of the system and the interconnectivity of rivers and roads entering and leaving the area, however focussing efforts on wetland vegetation zones is of vital importance, not only to the hippo population but to the system as a whole. These are indeed trying times for a system in flux, yet these are potentially also the best times to study a species as sensitive yet adaptable to change as hippo. Continued monitoring of hippo numbers in space and time through boat based counts in the Narrows and an aerial survey of the lakes will allow for an assessment of impacts under changing environmental conditions.

Study limitations

The current study was limited to the diurnal spatial distribution and behaviour of hippos. The results from this study highlights the need for data on the nocturnal habits of hippo, in order to better inform future ecological models (both spatial and behavioural). Remote tracking methods for wildlife are fairly advanced but the difficulties of securing such devices to hippo are substantial and hence were not considered for this or other studies with similar goals. Mapping hippo grazing lawns, by either following hippo paths from the estuary into the surrounding habitat or using satellite imagery, may add to our understanding of hippo ecology however, even these data do not allow for mapping of individuals or groups of hippo onto a particular grazing area. I was not able to measure how far hippo travelled to their foraging sites and the amount of time they spent feeding. This was predominantly due to the logistical difficulties associated with following hippo to obtain such data. Consequently I assumed a maximum nightly distance moved of 5km from hippo diurnal lie-up sites and used this to draw potential foraging circles (the area that is theoretically available to hippos on any given foraging trip) in the habitat surrounding each grid centroid within the associated data set (broad- or fine-scale). Subsequently I used vegetation maps to quantify the areas of the main vegetation types surrounding hippo lie-up sites.

Given the surface area (337.82km^2) and shallow nature of the lakes (<1m deep, too shallow for the boat to safely travel in) it was logistically unfeasible to directly measure water depth and hippo distribution in this biotope. As such all fine-scale data are restricted to the Narrows. The difference in the size of the lakes versus the Narrows (Table 3.1) made selecting an appropriate scale at which to model the whole system rather difficult. The final grid scale of 1x1km, while appropriate for the variables I explored in my model did have the disadvantage of potentially masking some important predictors of hippo presence.

The primary limitation within the behavioural data set is its relatively small sample size (n=13 non-consecutive days, which amounted to a 139.75 hours of observation), which was smaller than I had hoped to collect (three days a week, over ten weeks; amounting to 330 hours). This was largely a result of an unreliable boat and the unavailability of skippers. Furthermore, the park authority requested that I limit my boat-based observations and surveys to week days, in order to avoid disturbing tourism and recreational activities over weekends and public holidays. The small sample size limited my ability to explain variation in the behavioural data both diurnally and across days. I did learn and hope to have successfully communicated that diurnal observations are limited by the reduced visibility of hippo and the difficulty of individual identification given only a small portion of their bodies is visible. Thus I would consider diurnal activity budgets to be a lower long term research priority than either routine presence scans and the quest to devise methods for monitoring nocturnal foraging behaviour.

Suggestions for future hippo research in the St Lucia system

Changes in hippo group size and inter-group distances may offer management authorities the initial indicators of environmental changes within the system. However, for this to be effectively implemented as a management tool, more data would be required on hippo group sizes and locations, preferably linked with environmental data such as water depth. High resolution data on the latter, obtained using side-scan sonar equipment, would refine understanding of contemporary drivers of hippo distribution within the system and concurrently enhance abilities of management to predict future hippo distributions under different environmental condition. The additional value of such information is that management may be alerted to the potential ramifications of shifts in hippo distribution for the surrounding landscape (e.g. over grazing, increased human-hippo conflict). I recommend that future research focus on a comparative study between wet- and dry-season hippo distributions, as no such data yet exist, and understanding hippo landscape level use under different water availability conditions is paramount to understanding the impacts that future climate change may exert on the St Lucia estuarine system and associated hippo population.

The lower reaches of the Narrows are associated with a closer proximity to human settlements and potentially a greater degree of human disturbance in the form of tourist barges and private watercraft. Displacement of hippos by direct effects of human encroachment in the form of disturbance, and potentially harassment, may explain the lower site occupancy (Fig. 3.7), frequency of use (Fig. 3.11) and density of hippos within the lower reaches of the Narrows. The increased ecological productivity associated with the reconnection of the marine and freshwater sources (Taylor *et al.*, 2015) may encourage greater numbers of recreational fishermen to utilise the estuary. With a greater number of private watercraft utilising the lower reaches of the Narrows, hippos may be displaced from these areas, much in the same way as numerous species have been displaced from important habitats or resources (Richardson & Würsig, 1997; Kolowski, *et al.*, 2007; Weilgart, 2007; Averbeck *et al.*, 2012; Sönnichsen, *et al.*, 2013; Luís, *et al.*, 2014;). Studies on manatees have illustrated that animals respond variably to anthropogenic disturbances (noise, presence, vessel approaches) depending on their group composition and activity (Miksis-Olds, *et al.*, 2007; Miksis-Olds & Wagner, 2011). Manatees altered behavioural responses, increasing swim speed and moving to deeper waters, depending on vessel type (greater avoidance of private watercraft) and vessel speed (faster vessel approaches elicited greater responses; Miksis-Olds, *et al.*, 2007). Thus I recommend that future studies evaluate hippo distribution and site use in response to type and frequency of human disturbances, as human activities may need to be managed in order to mitigate the potential effects of increased boat-noise and anthropogenic activities along the shore on hippo spatial distribution and behaviour.

Hippos are highly gregarious during their diurnal rest periods, yet they are predominantly solitary nocturnal grazers, returning to the same site to form relatively stable group compositions with high site fidelity (Klingel, 2013). The Mouth group exhibited similarly high levels of site fidelity and a relatively stable group composition, with 8 out of 12 individually identifiable hippos returning to the site on a daily basis. Stable group compositions may yield both social and reproductive advantages. Hippos that are more familiar with one another, or perhaps related to one another may engage in more affiliative behaviours and less agonistic behaviour as illustrated by a study on captive hippos (Blowers *et al.* 2010). There is also reason to believe that kin selection may drive allo-suckling behaviour, as observed in a captive hippo group (Pluháček & Bartošová, 2011). Cases of allo-suckling have been recorded for wild populations as well (Marshall & Sayer, 1976; Smuts and Whyte, 1981; personal observations). Both genetic data combined with long-term observational studies (with individual identification) on wild hippos are required to further support these observations. The social importance of site fidelity and group living is yet unexplored among wild hippo populations. Given the fact that hippos exhibit mating territoriality it is possible that changing environmental conditions will alter hippo spatial distribution and group sizes and potentially impact on the genetic viability of the hippo population.

Conclusion

This study has identified water depth, proximity to humans and proximity to wetland vegetation as the primary factors influencing hippo distribution within the St Lucia system. I have also provided the first study on the activity budget of a hippo group within the Narrows which may serve as a reference for future studies. This study provides a foundation from which future studies can build, in the hopes of incorporating hippo habitat selection and landscape level requirements into a systems level management approach.

I believe that in order to conserve hippos as a species, as well as in order to manage the often isolated populations currently persisting on the continent, we must generate a thorough understanding of the species, their spatial ecology, behaviour and genetics. Increasing pressure on water and wetland resources by human settlements and farming, combined with climate-change associated variations in the extent and severity of droughts, will result in decreased availability of water within the Lakes and decreasing freshwater availability in the surrounding landscape (Whitfield & Taylor, 2009; Whitfield *et al.*, 2013; Været, 2008). Thus, there is great scope for future research on hippos, particularly in the St Lucia Estuary where fluctuating environmental conditions may offer researchers the opportunity to evaluate how human driven abiotic changes influence hippo distribution and behaviour. This quasi-experimental setup may lead to insights into hippo ecology and behaviour not yet gleaned from previous studies.

Reference list

Altmann J. 1974. Observational study of behavior: Sampling methods. *Behaviour* 49: 227–267.

Aschoff J. 1966. Circadian activity pattern with two peaks. *Ecology* 47: 657-662.

Attwell RIG. 1963. Surveying Luangwa hippo. *Puku* 1: 29-50.

Austin M. 2007. Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling* 200: 1-19.

Averbeck C, Plath M, Wronski T, Apio A. 2012. Effect of human nuisance on the social organisation of large mammals: group sizes and compositions of seven ungulate species in Lake Mburo National Park and adjacent Ankole Ranching Scheme. *Wildlife Biology* 18: 180-193.

Barklow WE. 1997. Some underwater sounds of the hippopotamus (*Hippopotamus amphibius*). *Marine and Freshwater Behaviour and Physiology* 29: 237-249.

Barklow WE. 2004. Amphibious communication with sound in hippos, *Hippopotamus amphibius. Animal Behaviour* 68: 1125-1132.

Beckwitt R, Shea J, Osborne D, Krueger S, Barklow W. 2002. A PCR-based method for sex identification in *Hippopotamus amphibius. African Zoology* 37: 127-130.

Bennett D, Green N, Basuglo B. 2000. The abundance of *Hippopotamus amphibius* in the Black Volta River at Bui National Park, Ghana. *African Journal of Ecology* 38: 372-373.

Bennett AF, Saunders DA. 2010. Chapter 5: Habitat fragmentation and landscape change. In: Conservation Biology for All. Sodhi and Ehrlich (eds). Oxford University Press. pp. 88-106. <http://ukcatalogue.oup.com/product/9780199554249.do>

Betts BJ. 2010. Activity budgets of Townsend's big-eared bats at a maternity colony in Northeastern Oregon. *Northwestern Naturalist* 91: 13-22.

Blake S. 2002. The ecology of forest elephant distribution and its implications for conservation. Ph.D. thesis, University of Edinburgh.

Blowers TE, Waterman JM, Kuhar CW, Bettinger TL. 2010. Social behaviors within a group of captive female *Hippopotamus amphibius*. *Journal of Ethology* 28: 287-294.

Blowers TE, Waterman JM, Kuhar CW, Bettinger TL. 2012. Female Nile hippopotamus (*Hippopotamus amphibius*) space use in a naturalistic exhibit. *Zoo Biology* 31:129-136.

Boisserie JR, Eltringham SK. 2013. Genus *Choeropsis* Pygmy Hippopotamus. In: Mammals of Africa: Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Kingdon J, Hoffmann M (eds). Bloomsbury Publishing, London. pp. 78-79.

Boisserie JR, Fisher RE, Lihoreau F, Weston EM. 2011. Evolving between land and water: key questions on the emergence and history of the Hippopotamidae (Hippopotamoidea, Cetancodonta, Cetartiodactyla). *Biological Reviews* 86: 601-625.

Boisserie JR, Zazzo A, Merceron G, Blondel C, Vignaud P, Likius A, Mackave HT, Brunet M. 2005. Diets of modern and late Miocene hippopotamids: evidence from carbon isotope composition and micro-wear of tooth enamel. *Palaeogeography, Palaeoclimatology, Palaeoecology* 221: 153–174.

Börger L, Franconi N, Ferretti F, Meschi F, De Michele G, Gantz A, Coulson T. 2006. An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist* 168: 471-485.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: weather patterns and the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* 39: 11-25.

Burnham KP, Anderson DR. 2004. Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* 33: 261-304.

Cerling TE, Harris JM, Hart JA, Kaleme P, Klingel H, Leakey MG, Levin NE, Lewison RL, Passey BH. 2008. Stable isotope ecology of the common hippopotamus. *Journal of Zoology* 276: 204-212.

Chamaillé-Jammes S, Valeix M, Fritz H. 2007. Managing heterogeneity in elephant distribution: Interactions between elephant population density and surface-water availability. *Journal of Applied Ecology* 44: 625-633.

Chansa W, Milanzi J, Sichone P. 2011b. Influence of river geomorphologic features on hippopotamus density distribution along the Luangwa River, Zambia. *African Journal of Ecology* 49: 221-226.

Chansa W, Senzota R, Chabwela H, Nyirenda V. 2011a. The influence of grass biomass production on hippopotamus population density distribution along the Luangwa River in Zambia. *Journal of Ecology and the Natural Environment* 3: 186-194.

Chettibi F, Khelifa R, Aberkane M, Bouslama Z, Houhamdi M. 2013. Diurnal activity budget and breeding ecology of the White-headed duck *Oxyura leucocephala* at Lake Tonga (North-east Algeria). *Zoology and Ecology* 23: 183-190.

Chomba C. 2013. Factors affecting the Luangwa (Zambia) hippo population dynamics within its carrying capacity band – Insights for better management. *International Journal of Biodiversity and Conservation* 5: 109-121.

Chomba C, Senzota R, Chabwela H, Nyirenda V. 2012. Population status of the common hippopotamus (*Hippopotamus amphibius*) in Luangwa River, Zambia. *Journal of Ecology and the Natural Environment* 4: 247-257.

Chomba C, Senzota R, Chabwela H, Nyirenda V. 2013. Does shore length influence population size and density distribution of hippopotamus? *Journal of Ecology and the Natural Environment* 4: 56-63.

Chrystal RA, Scharler UM. 2014. Network analysis indices reflect extreme hydrodynamic conditions in a shallow estuarine lake (Lake St Lucia), South Africa. *Ecological Indicators* 38: 130-140.

CITES Scientific Authority of South Africa. 2011. Non-detrimental finding for *Hippopotamus amphibius* (Hippopotamus). Reference number: Hip_amp_Apr2011.

Clauss M, Streich WJ, Schwarm A, Ortmann S, Hummel J. 2007. The relationship of food intake and ingesta passage predicts feeding ecology in two different megaherbivore groups. *Oikos 116: 209-216.*

Coughlin BL, Fish FE. 2009. Hippopotamus underwater locomotion: Reduced gravity movements for a massive mammal. *Journal of Mammalogy*, 90: 675-679.

Cyrus DP. 1989. The Lake St Lucia System – A research assessment. *Southern African Journal of Aquatic Science* 15: 3-27.

Cyrus D, Jerling H, MacKay F, Vivier L. 2011. Lake St Lucia, Africa's largest estuarine lake in crisis: Combined effects of mouth closure, low levels and hypersalinity. *South African Journal of Science* 107: 13 pages. DOI 10.4102/sajs.v107i3/4.291.

Cyrus D, Vivier L. 2006. Status of the estuarine fish fauna in the St Lucia Estuarine System, South Africa, after 30 months of mouth closure. *African Journal of Aquatic Science* 13:71-81.

de Azevedo CS, Ferraz JB, Tinoco HP, Young RJ, Rodrigues M. 2010. Time-activity budget of greater rheas (*Rhea American*, Aves) on human-distributed area: the role of habitat, time of day, season and group size. *Acta Ethologica* 13: 109-117.

de Beer Y, van Aarde RJ. 2008. Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environments* 72: 2017-2025.

Dittrich L. 1976. Age of sexual maturity in the hippopotamus *Hippopotamus amphibius. International Zoo Yearbook* 16: 171-173.
Doenier PB, DelGiudice GD, Riggs MR. 1997. Effects of winter supplemental feeding on browse consumption by white-tailed deer. *Wildlife Society Bulletin* 25:235-243.

Dudley JP. 1997. Reports of carnivory by the common hippo *Hippopotamus amphibius. South African Journal of Wildlife Research* 28: 58-59.

Ellery WN, Grenfell SE, Grenfell MC, Humphries MS, Barnes KB. 2013. Chapter 6: The Wetlands. In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a global model. Perissinotto R, Stretch DD, Taylor RH. (eds). Cambridge University Press. pp. 95-111.

Eltringham SK. 1993. The Common Hippopotamus, (*Hippopotamus amphibius*). In: Status survey and conservation action plan: Pigs, Peccaries and Hippos. Oliver WLR. (ed). IUCN, Gland, Switzerland. pp. 43-55.

Eltringham SK. 1999. The Hippos natural history and conservation. Text by: T &AD Poyser Ltd. Academic Press. London. Printed by: University Press, Cambridge. ISBN 0-85661-131-X.

Eltringham SK, Kingdon J, Boisserie JR. 2013. Genus *Hippopotamus* Common Hippopotamus. In: Mammals of Africa: Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Kingdon J, Hoffmann M (eds). Bloomsbury Publishing, London. pp. 64-67.

ESRI (Environmental Systems Resource Institute) 2012. ArcMAP 10.0. ESRI, Redlands, California.

ESRI (Environmental Systems Resource Institute) 2012. ArcMAP 10.1. ESRI, Redlands, California.

Fausch KD, Torgersen CE, Baxter CV, Li HW. 2002. Landscapes to Riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* 52: 483-498.

Feore S, Montgomery WI. 1999. Habitat effects on the spatial ecology of the European badger (*Meles meles*). *Journal of Zoology London* 247: 537-549.

Fernandez-Duque E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of Owl Monkeys (*Aotus azarai*). *Behavioral Ecology and Sociobiology* 54: 431-440.

Field CR. 1970. A study of the feeding habits of the hippopotamus (*Hippopotamus amphibius*) in the Queen Elizabeth National Park, Uganda, with some management implications. *Zoologica Africana* 5: 71-86.

Field CR, Laws RM. 1974. The distribution of the larger herbivores in the Queen Elizabeth National Park, Uganda. 273-294.

Galasso V, Pichierri F. 2009. Probing the molecular and electronic structure of norhipposurdoric and hipposudoric acids from the red sweat of *Hippopotamus amphibius*: a DFT investigation. *The Journal of Physical Chemistry A* 113: 2534-2543.

Gatesy J. 2009. Whales and even-toed ungulates (Cetartiodactyla). In: The Timetree of Life. Hedges SB, Kumar S (eds). Oxford University Press, Oxford. p. 511-515.

Gent A. 2013. Family Hippopotamidae Hippopotamuses. In: Mammals of Africa: Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Kingdon J, Hoffmann M (eds). Bloomsbury Publishing, London. p. 63-64.

Gordon JCD, Gillespie D, Potter J, Frantzis A, Simmonds MP, Swift R, Thompson D. 2004. A review of the effects of seismic survey on marine mammals. *Marine Technology Society Journal* 37: 14-32.

Green RA, Bear GD. 1990. Seasonal cycles and daily activity patterns of Rocky Mountain elk. *The Journal of Wildlife Management* 54: 272-279.

Grubb P. 1993. Taxonomy and description. In: Status survey and conservation action plan: Pigs, Peccaries and Hippos. Oliver WLR. (ed). IUCN, Gland, Switzerland. pp. 41-43.

Guisan A, Zimmermann NE. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.

Guo S, Li B, Watanabe K. 2007. Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. *Primates* 48: 268-276.

Harrison ME, Kalindekafe MP, Banda B. 2007. The ecology of hippopotamus in Liwonde National Park, Malawi: implications for management. *African Journal of Ecology* 46: 507-514.

Hashimoto K, Saikawa Y, Nakata M. 2007. Studies on the red sweat of *Hippopotamus amphibius. Pure and Applied Chemistry* 79: 507-517.

Hatfield JR, Samuelson DA, Lewis PA, Chisholm M. 2003. Structure and presumptive function of the iridocorneal angle of the West Indian manatee (*Trichechus manatus*), short-finned pilot whale (*Globicephala macrorhynchus*), hippopotamus (*Hippopotamus amphibius*), and African elephant (*Loxodonta africana*). *Veterinary Ophthalmology* 6: 35-43.

Hill RA, Barrett L, Gaynor D, Weingrill T, Dixon P, Payne H, Henzi SP. 2003. Day length, latitude and behavioural (in)flexibility in baboons (*Papio cynocephalus ursinus*). *Behavioral Ecology and Sociobiology* 53: 278-286.

Hoffman TS, O'Riain MJ. 2011. The spatial ecology of Chacma baboons (*Papio ursinus*) in a human-modified environment. *International Journal of Primatology* 32: 308-328.

Hoffman TS, O'Riain MJ. 2012. Landscape requirements of a primate population in a human-dominated environment. *Frontiers in Zoology* 9: 17 pages <http://www.frontiersinzoology.com/content/9/1/1>

Horikoshi-Beckett C, Schulte BA. 2006. Activity patterns and spatial use of facility by a group of captive female manatees (*Trichechus manatus latirostris*). *Zoo Biology* 25: 285-301.

IBM Corp. Released 2013. SPSS Statistics for Windows, Version 22.0. Armonk, New York: IBM Corp.

IUCN Red List of Threatened Species. 2014. Version 2014.2. <http://www.iucnredlist.org>. Downloaded on 24 July 2014.

Kanga EM, Ogutu JO, Olff H, Santema P. 2011. Population trend and distribution of the Vulnerable common hippopotamus *Hippopotamus amphibius* in the Mara Region of Kenya. *Oryx* 45: 20-27.

Karczmarski L, Cockcroft VG, McLachlan A. 2000. Habitat use and preferences of Indo-Pacific Humpback dolphins *Sous chinensis* in Algoa Bay, South Africa. *Marine Mammal Science* 16: 65-79.

Karstad EL, Hudson RJ. 1986. Social organization and communication of riverine hippopotami in southwestern Kenya. *Mammalia* 50: 153-164.

Kelbe BE, Taylor RH, Haldorsen S. 2013. Chapter 8: Groundwater hydrology. In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a global model. Perissinotto R, Stretch DD, Taylor RH. (eds). Cambridge University Press. pp. 151-167.

Kendall CJ. 2011. The spatial and agricultural basis of crop raiding by the Vulnerable common hippopotamus *Hippopotamus amphibius* around Ruaha National Park, Tanzania. *Oryx* 45: 28-34.

Kingdon J. 1979. East African mammals; an atlas of evolution in Africa. Vol III, part B. Academic Press, London. p. 250-277.

Kingdon J, Hoffmann M. (eds). 2013. Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. In: Mammals of Africa. Volume VI. Bloomsbury Publishing, London.

Klingel H. 1991. The social organization and behaviour of *Hippopotamus amphibius*. In: African Wildlife: Research and Management. Kayanja FIB, Edroma EL (Eds). International Council of Scientific Unions, Paris. pp. 72-75.

Klingel H. 2013. *Hippopotamus amphibius* Common Hippopotamus; In: Mammals of Africa: Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids. Kingdon J, Hoffmann M. (eds). Bloomsbury Publishing, London. p. 68-77.

Kolowski JM, Katan D, Theis KR, Holekamp KE. 2007. Daily patterns of activity in the spotted hyena. *Journal of Mammalogy* 88: 1017-1028.

Kosheleff VP, Anderson CNK. 2009. Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. *American Journal of Physical Anthropology* 139: 172-181.

Krausman PR. 1999. Some basic principles of habitat use. In: Grazing Behavior of Livestock and Wildlife. Idaho Forest, Wildlife & Range Expedition Station Bulletin #70, University of Idaho, Moscow, Idaho. Launchbaugh KL, Sanders KD, Mosley JC. pp. 85-90.

Kujirakwinja D. 2010. The status and conservation of common hippopotamuses in Virunga National Park, Democratic Republic of Congo. M.Sc. thesis, University of Cape Town, South Africa.

Laidre KL, Heide-Jørgensen MP, Logdson ML, Hobbs RC, Heagerty P, Dietz R, Jørgensen OA, Treble MA. 2004. Seasonal narwhal habitat associations in the high Arctic. *Marine Biology* 145: 821-831.

Lawrie RA, Stretch DD. 2011. Occurrence and persistence of water level/salinity states and the ecological impacts for St Lucia estuarine lake, South Africa. *Estuarine, Coastal and Shelf Science* 95: 67-76.

Laws RM, Clough G. 1966. Observations on reproduction in the hippopotamus, *Hippopotamus amphibius*. *Symposium of the Zoological Society of London* 15: 117–140.

Lewison R, Oliver W. (IUCN SSC Hippo Specialist Subgroup) 2008. *Hippopotamus amphibius.* The IUCN Red List of Threatened Species. Version 2014.2 <www.iucnredlist.org>. Downloaded on 07 August 2014.

Lewison R. 1998. Infanticide in the hippopotamus: evidence for polygynous ungulate. *Ethology, Ecology and Evolution* 10: 277-286.

Lewison R. 2007. Population responses to natural and human-mediated disturbances: assessing the vulnerability of the common hippopotamus (*Hippopotamus amphibius*). *African Journal of Ecology* (9 pages). doi: 10.1111/j.1365-2028.2006.00747.x

Lewison RL, Carter J. 2004. Exploring behaviour of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus. *Ecological Modelling* 171: 127-138.

Luck CP, Wright PG. 1964. Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). *Quarterly Journal of Experimental Physiology and Cognate Medical Sciences* 49: 1-17. Downloaded from Experimental Physiology (ep.physoc.org) on 11 July 2013.

Luís AR, Couchinho MN, dos Santos ME. 2014. Changes in the acoustic behavior of resident bottlenose dolphins near operating vessels. *Marine Mammal Science* DOI: 10.1111/mms.12125.

Lusseau D, Williams R, Wilson B, Grellier K, Barton TR, Hammond PS, Thompson PM. 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters* 7: 1068-1076.

Mackie CS, Dunham KM, Ghiurghi A. 2012. Current status and distribution of the Vulnerable common hippopotamus *Hippopotamus amphibius* in Mozambique. *Oryx* 47: 70-76.

Marker LL, Dickman AJ. 2005. Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research* 35: 105-115.

Marshall PJ, Sayer JA. 1976. Population Ecology and response to cropping of a hippopotamus population in eastern Zambia. *Journal of Applied Ecology* 13: 391-403.

McCarthy TS, Ellery WN, Bloem A. 1998. Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius L.*) in the Okavango Delta, Botswana. *African Journal of Ecology* 36: 44-56.

Miksis-Olds JL, Donaghay PL, Miller JH, Tyack PL, Reynolds JE. 2007. Simulated vessel approaches elicit differential responses from manatees. *Marine Mammal Science* 23: 629-649.

Miksis-Olds JL, Wagner T. 2011. Behavioral response of manatees to variations in environmental sound levels. *Marine Mammal Science* 27: 130-148.

Naylor LM, Wisdom MJ, Anthony RG. 2009. Behavioural responses of North American elk to recreational activity. *The Journal of Wildlife Management* 73: 328-338.

Neumann DR. 2001. The activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwerstern Bay of Plenty, New Zealand. *Aquatic Mammals* 27: 121-136.

Noirard C, La Berre M, Ramousse R, Lena JP. 2008. Seasonal variation of thermoregulatory behaviour in Hippopotamus (*Hippopotamus amphibius*). *Journal of Ethology* 26: 191-193.

Nowak RM. 1999. Walker's mammals of the world. 6th ed. Johns Hopkins University Press, Baltimore, Maryland.

O'Connor TG, Campbell BM. 1986. Hippopotamus habitat relationships on the Lundi River, Ghonarezhou National Park, Zimbabwe. *African Journal of Ecology* 24: 7-26.

Okello JBA, Nyakaana S, Masembe C, Siegismund HR, Arctander P. 2005. Mitochondrial DNA variation of the common hippopotamus: evidence for a recent population expansion. *Heredity* 95: 206-215.

Oliver WLR. (ed). 1993. Status survey and conservation action plan: Pigs, Peccaries and Hippos. IUCN, Gland, Switzerland. pp. 1-219.

Olivier RCD, Laurie WA. 1974. Habitat utilization by hippopotamus in the Mara River. *East African Wildlife Journal* 12: 249-271.

Onyeanusi AE. 2004. Some behavioural characteristics of common hippopotamus (*H. amphibius* Linn. 1758) in Nigeria's Kainji Lake National Park. *International Journal of Agriculture and Rural Development* 5: 27-35.

Orians GH, Wittenberger JF. 1991. Spatial and temporal scales in habitat selection. *The American Naturalist* 137: 529-549.

Ottaviani D, Panzacchi M, Lasinio GJ, Genovesi P, Boitani L. 2009. Modelling semi-aquatic vertebrates’ distribution at the drainage basin scale: The case of the otter *Lutra lutra* in Italy. *Ecological Modelling* 220: 111-121.

Pearce J, Ferrier S. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling 133: 225-245.*

Perissinotto R, Miranda NAF, Raw JL, Peer N. 2014. Biodiversity census of Lake St Lucia, iSimangaliso Wetland Park (South Africa): Gastropod molluscs. *ZooKeys* 440: 1-43.

Perissinotto R, Pillay D, Bate G. 2010. Microalgal biomass in the St Lucia Estuary during the 2004 to 2007 drought period. *Marine Ecology Progress Series.* 405: 147-161.

Pluháček J, Bartošová J. 2011. A case of suckling and allosuckling behaviour in captive common hippopotamus. *Mammalian Biology* 76: 380-383.

Potts JM, Elith J. 2006. Comparing species abundance models. *Ecological Modelling* 199: 153-163.

Presley SJ, Willig MR, Castro-Arellano I, Weaver SC. 2009. Effects of habitat conversion on temporal activity patterns of Phyllostomid bats in lowland Amazonian rain forest. *Journal of Mammalogy* 90: 210-221.

Richardson WJ, Würsig B. 1997. Influences of man-made noise and other human actions on cetacean behaviour. *Marine and Freshwater Behaviour and Physiology* 29: 183-209.

Roberts NB, Curtis SA, Milan AM, Ranganath LR. 2015. A pigment in alkaptonuria relationship to melanin and other coloured substances: a review of metabolism, composition and chemical analysis. *Journal of Inherited Metabolic Disease Reports* 51-66.

Saikawa Y, Moriya K, Hashimoto K, Nakata M. 2006. Synthesis of hipposudoric and norhipposurdoric acids: the pigments responsible for the color reaction of the red sweat of *Hippopotamus amphibius*. *Tetrahedron Letters* 47: 2535-2538.

Scott-Shaw CR, Escott BJ (Eds). 2011. KwaZulu-Natal Provincial Pre-Transformation Vegetation Type Map – 2011. Unpublished GIS Coverage [kznveg05v2_1_11_wll.zip], Biodiversity Conservation Planning Division, Ezemvelo KZN Wildlife, P. O. Box 13053, Cascades, Pietermaritzburg, 3202.

Seiffert ER, Kingdon J. 2013. Suborder Whippomorpha –Hippopotamuses, Cetaceans. In: Mammals of Africa: Volume VI: Pigs, Hippopotamuses, Chevrotain, Giraffes, Deer and Bovids*.* Kingdon J, Hoffmann M. (eds). Bloomsbury Publishing, London. p. 61.

Sidney J. 1965. The past and present distribution of some African ungulates. Transactions of the Zoological Society of London 30: 1-397.
Sims DW. 2003. Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology* 63: 53-73.

Skinner DJ, Scorer JA, Millar RP. 1975. Observations on the reproductive physiological status of mature herd bulls, and young bulls in the hippopotamus *Hippopotamus amphibius* Linnaeus. *General and Comparative Endocrinology* 26: 92-95.

Smuts GL, Whyte IJ. 1981. Relationships between reproductive and environment in hippopotamus *Hippopotamus amphibius* in the Kruger National Park. *Koedoe 24: 169-185.*

Sönnichsen L, Bokje M, Marchal J, Hofer H, Jędrzejewska B, Kramer-Schadt S, Ortmann S. 2013. Behavioural responses of European Roe deer to temporal variations in predation risk. *Ethology* 119: 233-243.

Stock M, Hofeditz F. 1996. Time-activity-budgets of Brent Geese (*Branta bernicla bernicla*) on saltmarshes in the Wadden Sea: The impact of human disturbance. *Vogelwarte* 38: 121–145.

Stoffel C, Dufresnes C, Okello JBA, Noirard C, Joly P, Nyakaana S, Muwanika VB, Alcala N, Vuilleumier S, Siegismund HR, Fumagalli L. 2015. Genetic consequences of population expansions and contractions in the common hippopotamus (*Hippopotamus amphibius*) since the Late Pleistocene. *Molecular Ecology* 24: 2507-2520.

Stretch DD, Maro AZ. 2013. Chapter 7: Catchment Hydrology. In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a global model. Perissinotto R, Stretch DD, Taylor RH. (eds). Cambridge University Press. pp. 77-93.

Taylor RH. 1980. A land capability study for hippopotamuses at Lake St Lucia, Zululand. M.Sc. thesis, University of Natal, Pietermaritzburg, South Africa.

Taylor RH. 2013. Chapter18: Hippopotamuses. In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a global model. Perissinotto R, Stretch DD, Taylor RH. (eds). Cambridge University Press. pp. 354-365.

Taylor R, Adams JB, Haldorsen S. 2006a. Primary habitats of the St Lucia Estuarine System, South Africa, and their responses to management. *African Journal of Aquatic Science* 31: 31-41.

Taylor R, Fox C, Mfeka S. 2013a. Monitoring the St Lucia Estuarine System: A synthesis and interpretation of the monitoring data for March-April 2013. Unpublished Ezemvelo KZN Wildlife report. 19 pages.

Taylor R, Fox C, Mfeka S. 2013b. Monitoring the St Lucia Estuarine System: A synthesis and interpretation of the monitoring data for June 2013. Unpublished Ezemvelo KZN Wildlife report. 24 pages.

Taylor R, Fox C, Mfeka S. 2013c. Monitoring the St Lucia Estuarine System: A synthesis and interpretation of the monitoring data for February-March 2013. Unpublished Ezemvelo KZN Wildlife report. 18 pages.

Taylor R, Fox C, Mfeka S. 2013d. Monitoring the St Lucia Estuarine System: A synthesis and interpretation of the monitoring data for May 2013. Unpublished Ezemvelo KZN Wildlife report. 16 pages.

Taylor R, Fox C, Mfeka S. 2015. St Lucia Estuarine System: A synthesis and interpretation of monitoring data for March 2014 to March 2015. Unpublished Ezemvelo KZN Wildlife report. 27 pages, plus 6 appendices.

Taylor R, Kelbe BE, Haldorsen S, Botha GA, Wejden B, Været L. 2006b. Groundwater-dependent ecology of the shoreline of the subtropical Lake St Lucia estuary. Environmental Geology 49: 586–600.

Timbuka CD. 2012. The ecology and behaviour of common hippopotamus *Hippopotamus amphibius* L. in Katavi National Park, Tanzania: Responses to varying water resources. Unpublished PhD, University of East Anglia, School of Environmental Sciences.

Ursing BM, Arnason U. 1998. Analyses of mitochondrial genomes strongly support hippopotamus-whale clade. *Proceedings of the Royal Society London B* 265: 2251-2255.

Váczi O, Koósz B, Altbäcker V. 2006. Modified ambient temperature perception affects daily activity patterns in the European ground squirrel (*Spermophilus citellus*). *Journal of Mammalogy* 87: 54-59.

Været L. 2008. Responses to global change and management actions in coastal groundwater resources, Maputaland, southeast Africa. Ph.D. thesis, Norwegian University of Life Sciences.

Været L, Kelbe B, Haldorsen S, Taylor RH. 2009. A modelling study of the effects of land management and climate variations on groundwater inflow to Lake St Lucia, South Africa. *Hydrogeology Journal* 17: 1949-1967.

van Beest FM, Uzal A, Vander Wal E, Laforge MP, Contasti AL, Colville D, McLoughlin PD. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *Journal of Animal Ecology* 83: 147-156.

van Doorn AC, O'Riain MJ, Swedell L. 2010. The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal Chacma baboons (*Papio ursinus*) in the Cape Peninsula of South Africa. *American Journal of Primatology* 72: 104-112.

Verweij RJT, Verrelst J, Loth PE, Heitkönig IMA, Brunsting AMH. 2006. Grazing lawns contribute to the subsistence of mesoherbivores on dystrophic savannas. *Oikos 114: 108-116.*

Viljoen PC. 1995. Changes in number and distribution of hippopotamus (*Hippopotamus amphibius*) in the Sabie River, Kruger National Park, during the 1992 drought. *Koedoe* 38: 115-121.

Viljoen PC, Biggs HC. 1998. Population trends of hippopotami in the rivers of the Kruger National Park, South Africa. In: Behaviour and ecology of riparian mammals (Dunstone N, Gorman M. (eds). Cambridge University Press, Cambridge, United Kingdom. p. 251–279.

Weilgart LS. 2007. A brief review of known effects of noise on marine mammals. *International Journal of Comparative Psychology* 20: 159-168.

Wengström A. 2009. How Maasai settlements affect the grazing habits of the Common Hippopotamus (*Hippopotamus amphibius*) in the Maasai Mara National Reserve, Kenya. Unpublished Student report 255, Swedish University of Agricultural Sciences. ISSN 1652-280X.

Whitfield AK. 2013. Foreword. In: Ecology and Conservation of Estuarine Ecosystems: Lake St Lucia as a global model. Perissinotto R, Stretch DD, Taylor RH. (Eds). Cambridge University Press.

Whitfield AK, Bate GC, Forbes T, Taylor RH. 2013. Relinkage of the Mfolozi River to the St Lucia estuarine system – urgent imperative for long-term management of a Ramsar and World Heritage Site. *Aquatic Ecosystem Health and Management* 16: 104-110.

Whitfield AK, Taylor RH. 2009. A review of the importance of freshwater inflow to the future conservation of Lake St Lucia. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 838-848.

Wiesner H, von den Driesch A. 1996. Altersrekord bei einem FluBpferd (*Hippopotamus amphibius* L.). *Der Zoologische Garten* 66: 195-196.

Wittemyer G, Douglas-Hamilton I, Gets WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* 69: 1357-1371.

Wright PG. 1964. Wild animals in the tropics. *Symposium of the Zoological Society of London* 13:17–28.

List of figures

Note: The nomenclature expresses both the chapter and associated figure or table number (e.g. Fig. 1.1 is the first figure in Chapter 1.)

List of tables

Note: The nomenclature expresses both the chapter and associated figure or table number (e.g. Table 1.1 is the first table in Chapter 1.)

List of appendices

Appendices

Appendix 1: Exploration of data dispersion and zero-inflation within broad- and fine-scale data sets.

Data set	**Mean**	**Variance**	**% zero**
Broad-scale occurrence	0.09	0.08	91
Fine-scale occurrence	0.40	0.24	60
Fine-scale frequency of occurrence	0.98	2.99	60

Appendix 2: Spearman rank order correlations for the broad-scale hippo occurrence data (presence/absence) and the continuous variables (Natural log (distance to humans)=ln(D_Human) and Natural log (distance to inlet)=ln(D_Inlet); n=419) with significant ρ-values in bold.

	Occurrence		**ln(D_Human)**		**ln(D_Inlet)**	
	Correlation coefficient	**ρ-value**	**Correlation coefficient**	**ρ-value**	**Correlation coefficient**	**ρ-value**
Occurrence			0.046	0.349	-0.131	**0.007**
ln(D_Human)	0.046	0.349			0.521	**<0.001**
ln(D_Inlet)	-0.131	**0.007**	0.521	**<0.001**		

For the broad-scale data set the occurrence data were significantly negatively correlated to the natural logarithm of distance to inlets [ln(distance to inlet)] data. ln(distance to human settlements) showed no significant correlations with hippo occurrence, but did exhibit a strongly positive correlation to the In(distance to inlet) variable. This may be because human settlements are typically built in close proximity to fresh water, thus settlements close to the estuary are often close to river inlets as well.

Appendix 3: Spearman's ranked correlation coefficients (R) for the dependent variables (Occurrence and Frequency of use) and continuous parameters within the Fine-scale data set of hippo occurrence and frequency of cell use within the St Lucia Estuary. (Significant p-values are in bold, α<0.05).

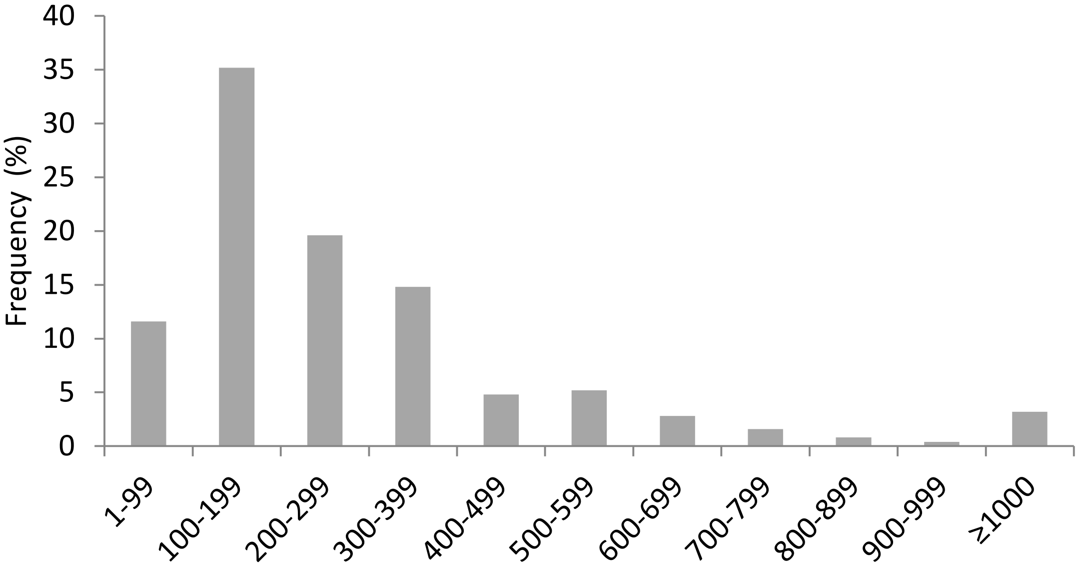
	ln(D_Humans)		**ln(D_Inlet)**		**ln(D_NN)**	
	R	**ρ-value**	**R**	**ρ-value**	**R**	**ρ-value**
Occurrence	0.088	0.166	-0.147	**0.02**	-0.128	**0.04**
Frequency of use	0.082	0.195	-0.132	**0.037**	-0.157	**0.012**

Both the occurrence and frequency of use data were negatively correlated to the distance to inlet and distance to nearest neighbour predictor variables.

Appendix 4: Spearman’s ranked correlation coefficients (R) among the continuous parameters within the Fine-scale data set (Significant p-values are in bold, α<0.05).

	ln(D_Humans)		**ln(D_Inlet)**		**ln(D_NN)**	
	R	**ρ-value**	**R**	**ρ-value**	**R**	**ρ-value**
ln(D_Humans)			-0.440	**<0.001**	-0.144	**0.042**
ln(D_Inlet)	-0.440	**<0.001**			0.164	**0.022**
ln(D_NN)	-0.144	**0.022**	0.164	**0.009**		

The ln(Distance to inlet) and ln(Distance to nearest neighbour) predictor variables were also significantly correlated to one another, suggesting that as the distance to nearest neighbours increased so too did the distance to the nearest inlet. The fine-scale data also exhibited a strong negative correlation between the ln(Distance to humans) and ln(Distance to inlet) variables. All other predictor variables weakly, but significantly, correlated to one another.



Appendix 5: The cumulative frequency (%) histogram of the distance between nearest neighbouring hippo groups within the Narrows of the St Lucia Estuary.

The above figure (Appendix 5) illustrates that the majority of hippo groups (81.2%) settled within 1 - 399m of neighbouring groups, preferentially settling within 100 -199m of neighbouring groups (35.2%).

All three data sets tested positive for spatial autocorrelation (Appendix 6), which lead me to sub-sampling the data sets in order to eliminate spatial autocorrelation prior to modelling (Appendix 7).

Appendix 6: Spatial autocorrelation test statistics (Moran's I and z-scores) for broad- and fine-scale occurrence and the fine-scale frequency of use data sets (N= the total number of cells within the data set; significant values (ρ < 0.05) are marked in bold).

Data set	N	Presence	Absence	Moran's I	z-score	ρ-value
Broad-scale occurrence	419	36	383	0.295	7.11	**<0.001**
Fine-scale occurrence	252	100	152	0.218	4.269	**<0.001**
Fine-scale frequency of use	252	-	-	0.117	2.354	**0.019**

Appendix 7: Spatial autocorrelation test statistics (Moran's I and z-scores) for broad- and fine-scale occurrence and the fine-scale frequency of use sub-sampled data sets (N= total number of cells within the sub-sampled data set; significant values (ρ > 0.05) illustrate that all data sets tested negative for spatial autocorrelation).

Data set	N	Presence	Absence	Moran's I	z-score	ρ-value
Broad-scale occurrence	186	17	169	0.078	1.227	0.22
Fine-scale occurrence	151	60	91	0.134	1.86	0.063
Fine-scale frequency of use	151	-	-	0.025	0.428	0.669

The Relative Operating Characteristic (ROC) curve explained

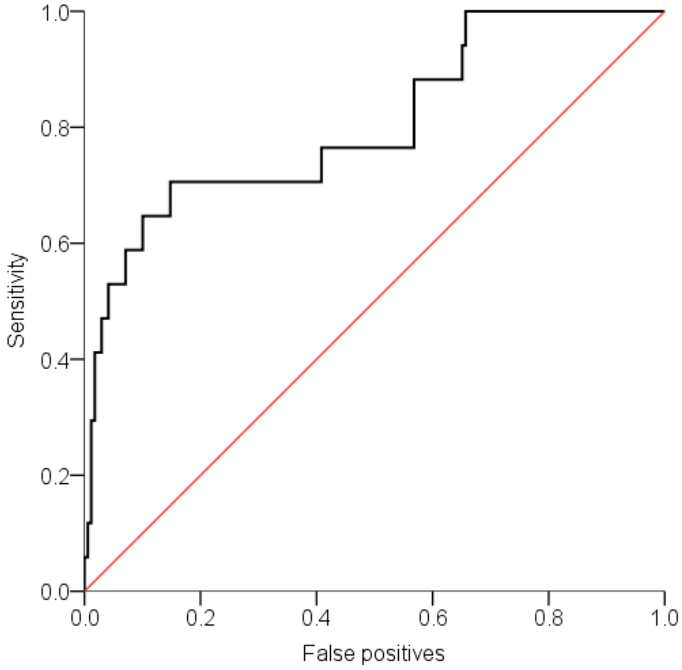
The ROC curve used the predicted probability of occurrence values generated by the model, for each of the cells in the dataset, as the decision threshold at which sites were deemed either occupied or unoccupied. Using these values as cut-offs you are able to calculate the coordinate points used to generate the ROC curve, plotting Sensitivity (the proportion of observed positives; Appendix 8) on the y-axis and False positive fraction (the probability of a false positive; Appendix 9) on the x-axis. Sensitivity and false positive fractions are proportions of all sites with a given observed state (presence/absence) and both are thus independent of hippo prevalence (the proportion of hippos observed in the data set, e.g. 17/186). As the ROC curve uses these values as coordinate points it is independent of both hippo prevalence and the decision- threshold, thereby meeting the requirements of an unbiased discrimination index (Pearce & Ferrier, 2000).

Appendix 8: The equations used to calculate the Sensitivity values used as the y-axis coordinate points on the Relative Operating Characteristic (ROC) curve.

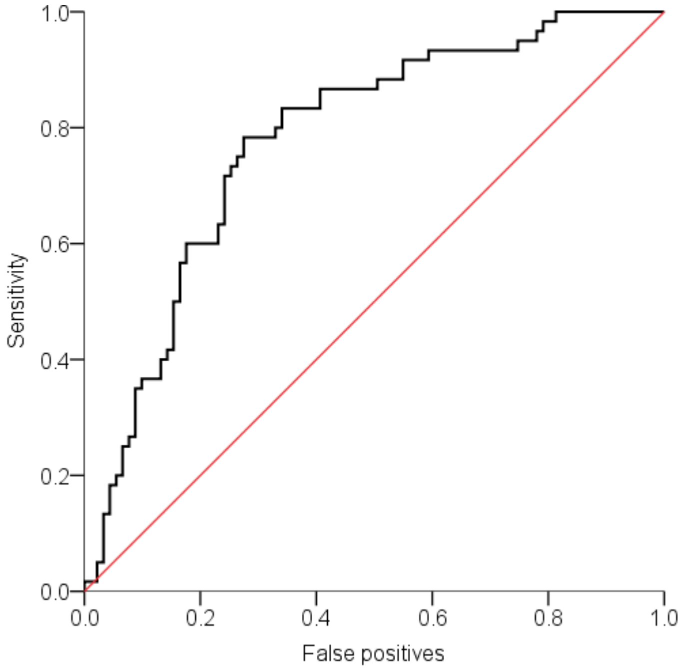
$$\text{Sensitivity} = \frac{\text{Number of occurrences correctly predicted}}{\text{Total number of observed occurrences in the sample}}$$

Appendix 9: The equations used to calculate the False positive fraction values used as the x-axis coordinate points on the Relative Operating Characteristic (ROC) curve.

$$\text{False positive fraction} = \frac{\text{Number of occurrences incorrectly predicted}}{\text{Total number of observed absences in the sample}}$$



Appendix 10: The Relative Operating Characteristic (ROC) curve used to evaluate the broad-scale occurrence model. Red line indicates the Null hypothesis that the area under the curve equals 0.5.



Appendix 11: The Relative Operating Characteristic (ROC) curve used to evaluate the fine-scale occurrence model. Null hypothesis: area under the curve equals 0.5(Red line).