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Sexual Dimorphism in the Common Hippopotamus

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Award date:
2020

Awarding institution:
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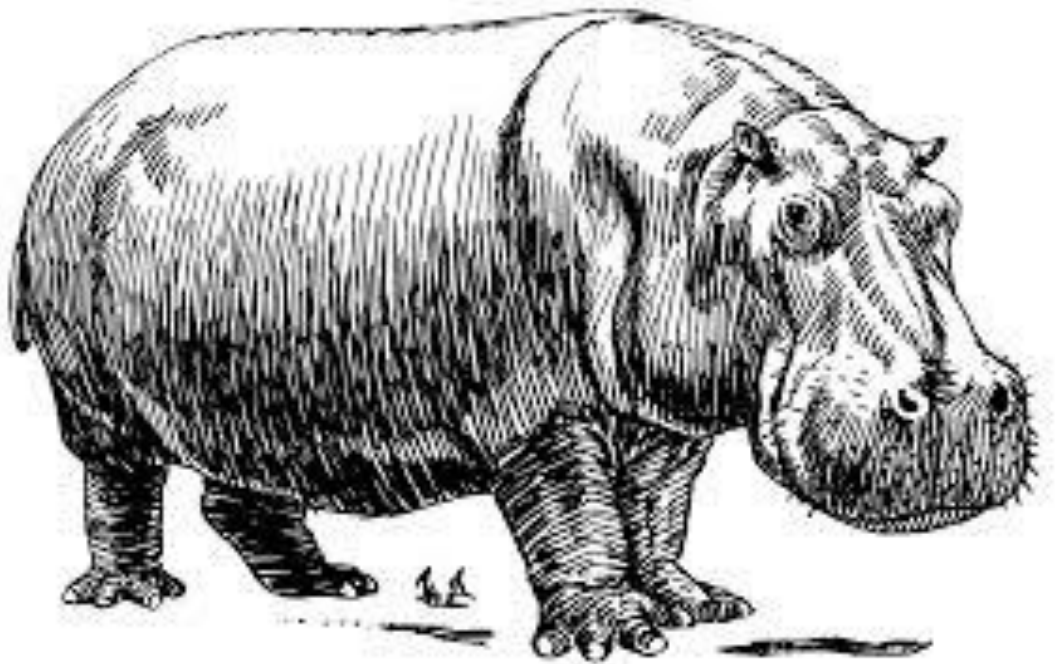
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“Sexual Dimorphism in the Common
Hippopotamus
(*Hippopotamus amphibius*)”



Master of Science Research (MSciRes)

By Phoebe Sadler

For the School of Biological Science

Bangor University

(September 2019)

Acknowledgements

I am not the sole contributor to this thesis and wish to take this opportunity to thank those involved in its creation; both directly and through personal support.

The advice gained from my supervisor Dr Graeme Shannon and co-supervisor Dr Jo Smith was imperative in the success of this thesis. Their knowledge of the study area allowed me to discuss and explore multiple directions of focus with support and guidance. Not only this, their reassurance and feedback allowed me to persevere through setbacks in my analysis. It has been an honour working alongside Graeme and Jo, and I am grateful for their participation and support. I would also like to thank Ellie Royance-Casson for her help in the early stages of data organisation, helping digitalise the vast amount of data collected in Laws' handwritten journals. Tom Brekke was also very supportive while I was learning R-Studio, and for that I am very grateful.

I would like to thank my friends who have endured my ongoing stressful rants about hippos and coding. I owe a lot of people drinks! Their support and friendships have been vital to my progress and has allowed me to forget about hippos and laugh when I was particularly overcome with stress. Without my friends, these past 5 years would not have been as special.

Lastly, I would like to thank my family for their support over the past five years. To my father – Peter Sadler, you encourage me to be as successful and intelligent as you think I am, and I am grateful for all you have done for me throughout my life. I would also like to thank Sareth Stanley for her emotional support, and impeccable proof-reading skills! To my grandparents; Irene Oates and Keith Ridgway. Although you still tell people I work with rhinos, I am eternally grateful for your love and support. My sister Ashleigh Gleave; you have been the best big sister anyone could wish for. Thank-you for everything you have done for me; including coming to McDonald's at midnight because I'm hungry and stressed. Finally, I would like to thank my mother – Samantha Oates. You set an example of strength and kindness and have always been there for me when I needed you. I apologise for being a moody teenager well into my twenties and hope to one day be half as brilliant as you are. To all my family; I am eternally grateful for your financial, physical and emotional support. Without you, none of my achievements would have been possible and I hope to make you proud.

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Abstract

Sexual dimorphism is the difference exhibited between the sexes of a species, often in the form of a larger size, colouration or weaponry in one sex. Commonly associated with polygamous mating systems and greater sociality; many species of ungulates show high levels of sexual dimorphism due to the benefits gained during sexual selection. The hippopotamus (*Hippopotamus amphibius*) is an African megaherbivore which shows highly competitive and aggressive social behaviours. Their polygamous and social nature predicts high levels of sexual size dimorphism (SSD), with males being substantially larger than females. However, there has been a significant lack of research conducted into the sexual dimorphism of this species. This study suggested there is not a large difference between adult male and female mean body masses that you would expect from this species. However; there was a significant difference found in the mass of the lower jaws, with males having on average 42% heavier lower jaws than females. These results imply hippopotamus do not show a large extend of SSD, regardless of their similarity to species who exhibit large differences in body size between the sexes. Instead it is suggested male hippopotamus invest more into developing larger jaws, possibly to increase success in sexual selection. This is could be related to this species' semi-aquatic nature as well as their vulnerability to periods of drought. Further study into this species could help examine the drivers involved in the evolution of sexual dimorphism, and the effects niche and environment may have on its presence.

Introduction

Males and females often show a large level of variation within a species other than basic genital differences; this is called sexual dimorphism (Lammers *et al.*, 2001). Dimorphism literally translates to two forms, exhibited via differences in, weaponry, (e.g. antlers, teeth and tusks), displays (e.g. colours and feathers) and overall body size (Lammers *et al.*, 2001). These variations between the sexes can be both obvious and discrete. For example, the male and female magpies (*Pica pica*) only show a small colour difference in their head feathers (Toon *et al.*, 2003), while other species like elephant seals (*Mirounga*), have males which can grow 10 times larger than females (Haley *et al.*, 1994). Charles Darwin (1885) first noted chickens (*Gallus gallus domesticus*) feathers varied between the sexes, with some males having different colourations or elaborate neck feathers. Here Darwin began to develop a hypothesis for these differences, suggesting these traits evolved from sexual selection and only become pronounced

within one sex if it brings specific advantages, for example successfully competing for mating rights or the attraction of a mate.

The theory that differences in morphology bring an overall advantage to one sex is still the umbrella explanation for these differences, with sexually selective traits being the most common advantage used to explain sexual dimorphism. However, other factors such as competition for food and divergent reproductive roles are also believed to be involved in the acquisition of these variations. If one sex of a species has a different food source (Shine *et al.*, 2002), niche (Thom *et al.*, 2004) or role to fulfil during reproduction (Slagsvold and Sonerud, 2007), the pressures implemented on this sex would be different. In these theories a trait such as a different sized beak may exclusively benefit a sex with a different role or niche rather than the species as a whole, resulting in sexual dimorphism. Essentially every trait established is an allocation of energy to increase overall fitness through reproductive success or resource gain (Harrison *et al.*, 2011). For one sex to evolve bright colours or a larger body mass, it must provide a benefit for them to counteract the survival risks and energetic costs which may accompany these adaptations (Sokolovska *et al.*, 2000). For example, being brightly coloured is dangerous for a prey species, making them more easily spotted (Promislow *et al.*, 1992). This assumption is supported within the sex-specific colouration differences of damselflies and some *Lepidoptera* species with the more conspicuous males having a higher mortality rate through increased predation (Van Gossum *et al.*, 2004).

Not only do colourations and flashy appearances increase detection by a predator, any pigmented elaborate feathers or increase in body mass requires a large amount of energy to develop and maintain (Blankenhorn, 1995). Since these traits are so prevalent within nature, there must be an extraordinary benefit to the sex (and specifically the individual) who exhibits these traits to warrant the risks associated. This theory doesn't just stand for prey species, traits found among any organism must result in an increased overall fitness. Predators have specific traits which benefit them while stalking, chasing and attacking their prey (Curio, 2012). For example, the streamlined physique and elongated legs of the cheetah (*Acinonyx jubatus*) allows them to reach high speed when chasing prey (Hudson *et al.*, 2011, Hildebrand and Hurley, 1985). A higher body mass or different physical appearance within one sex could lower the kill rate and therefore cause detrimental damage to their energy supplies which are so vital. Therefore, to truly understand the differences exhibited between the sexes of a species, we must first fully understand the different pressures they face within their reproductive roles or during resource acquisition. The major theories discussed in the following section explore the

alternative pressures placed on sexes, thus allowing an understanding of the benefits any sexual dimorphisms may bring.

Sexual Selection

The premise of sexual selection is based around the choice or competition for mates, where mating success is widely affected by phenotypic variation amongst individuals (Coltman *et al.*, 2002). Males will often compete in numerous ways in order to ‘win’ mating rights for one or multiple females. This is a form of intraspecific competition, where males with certain traits; such as a larger body size or bigger horns, have a greater competitive advantage and therefore reproduce more often, passing their genes on to their offspring (Tidière *et al.*, 2017). A well-known example of this type of behaviour is shown in many species of deer and other ungulates. Deer species often partake in rutting season, which involves fierce battles where the males of the species fight using their large antlers, often leading to injury or even death. The purpose of these battles is to establish dominance within a herd and therefore gain access to mate with one or more females (Bergerud, 1974). There is no increase in reproductive success linked to antler growth in females, which explains why only males develop antlers in many species of deer (Stewart *et al.*, 2000). Many species of ungulates also adapt to the large weight of antlers in males with increasing body size and neck girth (Kitchener, 1985). This is related to increasing strength in rutting season (Jennings *et al.*, 2004) and sustaining the larger mass of the antlers (Solberg and Saether, 1994). Some species who have grown larger in body size to accommodate huge weighty antlers have become extinct due to their excessive size. For example; the Irish elk (*Megaloceros giganteus*), although not exclusive to Ireland nor an elk. The male of this species grew to a magnificent size of 2.1 meters tall to the shoulder with antlers that could span up to 3.5 meters in width tip to tip and weighed up to 40kg (Gould, 1974). Scientists have hypothesised that their extinction was related to their inability to adapt their feeding habits successfully enough to maintain their large body size and antlers in the colder conditions brought about in times of changing environments (Simpson, 1955). This outlines the limitations and potential costs of increasing weapon size as a function of sexual selection. However, this specific example has more commonly been explained by the species inability to survive a climate change event which occurred 600 years ago (Kokko and Brooks, 2003) as they were unable to reduce their antler size quick enough (Moen *et al.*, 1999)

The other side of sexual selection is choice, where typically a female ‘chooses’ the males who get to mate with her through attractive qualities or behaviours (Andersson and

99 Simmons, 2006). A prime example of female choice is in the peahen (*Pavo cristatus*). The
100 male of this species – the peacock, displays an elaborate tail with colourful patterned feathers,
101 while the peahen remains brown in colour, with a shorter much duller tail. The peacock's
102 extravagant tail feathers are used as a display to advertise their worth as a mate, with the most
103 elaborate male being chosen by the females (Petrie *et al.*, 1991). Peahens are suggested to
104 prefer males with more elaborate tails as it signifies the quality of the potential mate. To survive
105 as a prey species with such large colourful tail feathers, suggests they have a higher fitness than
106 other duller males, as well as showing they are strong enough to acquire the amount of energy
107 required to maintain this type of plumage (MacDougall and Montgomerie, 2003). Another
108 implication of this type of mating system is something known as the 'sexy son' hypothesis
109 (Weatherhead and Robertson, 1979). As this choice of an elaborate male is a popular option
110 among females of the species due to symbolism of superiority, mating with an elaborate male
111 increases the chances that the female's offspring will also show these elaborate traits. This
112 means the offspring are also more likely to be chosen to mate with, which in turn increases the
113 presence of the original female's genetic material within the gene pool. Essentially, this argues
114 that the popularity of the trait creates more preference in itself. From a peacock's perspective,
115 although the elaborate colorations and tail feathers create massive risks through energy
116 expenditure and increased risk of predation, the benefits of improved mating chances outweigh
117 the risks taken. Alternatively, for peahens; who do not need to compete in order to attract males,
118 this attention seeking plumage does not increase their mating chances but does increase
119 predation and other negative implications (Götmark, 1997). This explains why elaborate tail
120 feathers are only found in the male of the species.

121 As stated previously, sexual selection is often the most widely accepted explanation of
122 sexual dimorphism, however, Issac (2005) noted some issues with this generalisation. If sexual
123 selection was the only driver behind sexual dimorphism, polygamous species would have the
124 largest degree of variation between the sexes, with monogamous species having significantly
125 less sexual dimorphism present (Boonstra *et al.*, 1993). However, this is not the case for many
126 species who have high levels of sexual dimorphism throughout monogamous pairings.
127 Similarly, many species who participate in polygamous mating show little to no sexual
128 dimorphism (Heske and Ostfeld, 1990). This suggests there are other drivers in the acquisition
129 of sexually dimorphic traits.

Reproductive Roles

The difference in the roles fulfilled by the sexes could also influence the sexual dimorphism found within certain species. Some of the sex variations among our own species are down to these differences in the sexes' roles. For example, the reproductive role of females includes carrying and historically caring for the young in early stages. The larger mammary glands and wider set pelvis found within females benefits their reproductive role and is therefore not found within the anatomy of males (Singh and Young, 1995). The feature of widened hips also plays into sexual selection, as wider hips can be subconsciously viewed as a sign of fertility and therefore seen as more attractive (Platek and Singh, 2010). Many species have specific traits in females due to their role in carrying the offspring. The huge amount of energy involved in carrying offspring can require females to be significantly larger than males in general (Butte and King, 2005). An example includes the pipefish (*N. ophidion*) where a larger size in females results in a higher fecundity (Jones and Avise, 2001). Some examples of different reproductive roles lead to an extreme extent of male dwarfism, for example the anglerfish (Yoneda, 1998). The male anglerfish's entire life purpose is to fuse to a female's skin and provide sperm whenever necessary. These extremely different roles result in much smaller males who lack many features including feeding apparatus. Another similar extreme example can be found within the giant orb weaver (*Nephila plumipes*), where males of the species are sometimes 10% of the female's size. Males rely on this large size difference to participate in 'sneaky mating', which allows them to avoid cannibalism during copulation (Elgar and Fahey, 1996). These examples of varied reproductive roles explain how a specific trait may benefit one sex rather than the species in general, resulting in a different characteristic or size in one sex.

Ecological Niches

Competition for food and resources is high in the wild. Certain species have sexes who rely on different diets in order to decrease intraspecific food competition with the opposite sex. Some species are even suggested to develop different features which benefit a sex in these different resource opportunities. For example, some species such as the middle-spotted woodpecker (*Dendrocoptes medius*) show differences in their foraging behaviour and bill size, with males having a larger bill length than females on average (Pasinelli, 2000). Similarly, it has been discussed that hummingbird species (family: *Trochillidae*) differentiate on preferred flowers by sex, with each sex having a different bill shape to accommodate specific species of

plants (Tremeles *et al.*, 2000). Another example includes mustelids such as weasels (family: *Mustela*), who have significantly larger males than females. Moors (1980) suggested a clear difference in the diet between the two sexes, with females favouring smaller rodents such as mice, while males consumed significantly more larger rodents and lagomorphs. The difference in the size of the meals preferred by this species could explain why females are not required to be as large as the males, as they do not need the larger size to attack a larger prey. However, it is suggested trophic structures and feeding habits are not likely to be the major driving factor in sexual size dimorphism (often referred to as SSD) within mustelid species but may play a major role in its maintenance. This was concluded by assessing other similar carnivore species in their phylogenetic tree. These similar species also show male orientated sexual dimorphism regardless of feeding differences, suggesting ecological niches may not be the most likely cause of SSD, and instead they are merely a supporting factor or even a reaction to SSD itself (Thom *et al.*, 2004).

Although there are many theories on the drivers of sexual dimorphism, much like within the Thom *et al.*, (2004) discussion, it's difficult to differentiate with high levels of confidence which pressures are the cause of sexual dimorphism rather than simply a correlation. This is because the different drivers of divergence found within the animal kingdom may all interact to result in sexual dimorphism (Ruckstuhl, 2007).

Forms of Sexual Dimorphism

When examining sexual dimorphism, it is important to understand the full range of sexually dimorphic traits which can present themselves. Here the main categories of sexual dimorphism are classified as; sexual size dimorphism, colouration, weaponry and other secondary sexual characteristics (Ralls and Mesnick, 2009)

Sexual Size Dimorphism

Sexual size dimorphism (SSD) was one of the first forms of sexual dimorphism studied, when Charles Darwin (1885) attributed the larger size of one sex to a sexually selective pressure rather than a direct result of natural selection. Species may exhibit sexual size dimorphism for multiple reasons; the main gain being reproductive success (Fairbairn *et al.*, 2007). Individuals who are larger may increase their dominance or rank within a group (Pelletier and Festa-Bianchet, 2006), their ability to stay dominant (Anderson and Fedak, 1985, Setchell *et al.*, 2001), territory gain and defence (Magnhagen and Kvarnemo, 1989, Guillermo-

Ferreira and Del-Claro, 2012) and even the increased attention from available mates (McElligott *et al.*, 2001).

Elephant seals are a perfect example of the advantages of sexual size dimorphism. In both species of the elephant seal; northern (*M. angustirostris*) and southern (*M. leonine*), males can grow up to seven times the weight of the average female (Haley *et al.*, 1994) which live in a ‘harem’ social group. A harem social structure means the females group together in large numbers with males fighting to become the dominant of the group (Hofmeyr, 2000). Dominant males reside within the group of females, with the alpha male achieving higher copulatory success (Fabiani *et al.*, 2004) and usually a higher reproductive success rate (Le Boeuf, 1974). The large body size of the male elephant seals, large canines and proboscis (elongated nose) give an advantage during their vicious fights to become or remain the dominant male of the harem (Modig, 1996). The large body mass and teeth of the bulls are also an advertisement of aggression and dominance to other males in the area (La Boeuf and Laws, 1994). As females do not engage in these fights for dominance, the advantages gained by having a substantially larger body size are not present. This difference in pressures and sexual behaviour has therefore led to the extensive deviation of body mass between the sexes of this species.

Another example of sexual size dimorphism is in the African elephant (*Loxodonta africana*). Male bull elephants can be much larger than females, growing to 3-4 metres at the shoulder; significantly larger than females who grow to approximately 2-3 metres (Poole, 1989). The height difference not only makes mounting the female easier, it also physically contributes an advantage during the competition for mating rights. Males often use their height and weight to push and intimidate other bull elephants who are also chasing an oestrus female, with the larger stronger individuals usually chasing the competing males away (Hollister-Smith *et al.*, 2007). A larger male within a group not only is more likely to be victorious in battles of strength and dominance, but also could be seen to suggest a superiority through their size, by advertising their ability to grow large and survive (Wong and Candolin, 2005). These large sizes in males and the increased superiority, increase their chances of mating and in most cases does increase reproductive payoffs (Haley, 1994). This explains the large differences in sizes between the sexes of these species, as the benefits SSD brings to one sex; in many cases the males, justifies the energy required to grow and maintain a larger body size. Whereas the other sex does not require such a larger stature to increase mating chances or dominance within the group, thus the increase in body size would not be productive and therefore a potential waste of valuable energy.

Rensch's rule is a biological rule used to predict the extent of sexual size dimorphism (Rensch, 1950). Rensch's rule states that when SSD favours a larger female, size difference decreases with increasing body size, i.e. Giant orb weavers (*Nephila*) are small arachnids who have much larger females - up to 10x larger than the males (Elgar and Fahey, 1996), whereas in a larger species such as hawks (family: *Accipitridae*) and other birds of prey, the female is larger but only by a small amount (Snyder and Wiley, 1976). Alternatively, when SSD favours a larger male, size difference increases with increasing body size, i.e. male rats (*Neotoma*) tend to be larger than females but not by a substantial amount (Krasnov *et al.*, 2005), whereas male elephant seals as stated previously are significantly larger than females (Poole, 1989).

To demonstrate Rensch's rule, a graph was formed with a linear equation to represent the relationship between the size of males, and the extent of SSD in ungulates (specifically focusing on male based sexual size dimorphism) (Figure 1). A common index for the extent of sexual size dimorphism was first chosen using Lovich and Gibbons (1992) method of quantifying SSD as SDI (Sexual Dimorphism Index). Lovich and Gibbons calculations for SDI follows:

$$SDI = (Mass\ of\ Larger\ Sex / Mass\ of\ Smaller\ Sex) + 1 *$$

* + if male larger like in this instance, however the calculation changes to -1 if females larger in the species

A group of 24 species was chosen which were herbivorous, terrestrial quadrupeds, and similar either behaviourally or ecologically to hippos. The SDI was then calculated for each of the 24 species using the above equation and the mean adult male and female body masses. The log transformation of the data was carried out to allow a linear regression to be formed from non-linear data (Figure 1). The logarithmic regression $y = 0.03x + 0.33$, (shown in red) shows the relationship between SDI and the weight of the male of certain species who show sexual size dimorphism (Figure 1). This equation represents Rensch's biological rule which predicts that a larger species will show a greater difference between the mass of the sexes when the male is larger and therefore a higher SDI value. However, although figure 1 helps illustrate Rensch's biological rule, it does not take into consideration the phylogeny of each species. If this were to also be taken into account through an PGLS or other phylogenetic comparison method, the results would be much more indicative of the relationship between male weight and sexual size dimorphisms, as it would account for any similarities attributed to the species phylogenetic relationship rather than sexual size dimorphism.

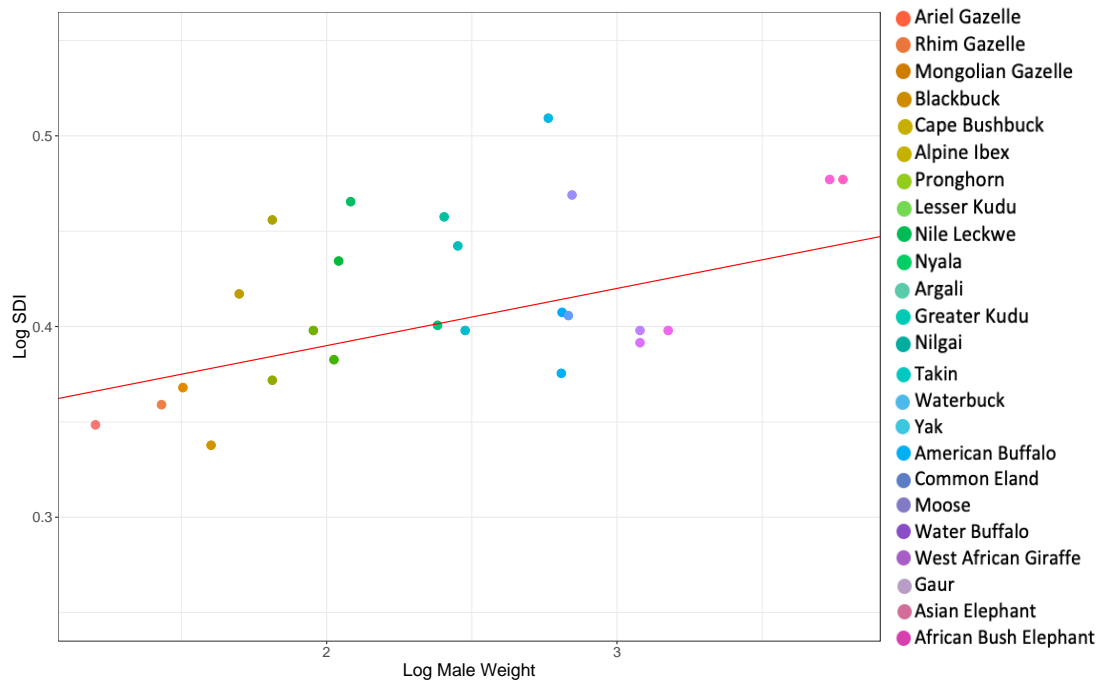


Figure 1: Logarithmic regression of SDI's against the average male weight of 24 species. Species data involved was taken from a number of sources including Jarman (1983), Abouheif and Fairbairne (1997) and Bro-Jørgensen (2007). These individual species chosen were limited to ungulates with similar ecologies and behaviours to hippos. The regression equation was formed using ggplot2 function on R-Studio and showed the equation $y = 0.03x + 0.33$. The equation represents Rensch's biological rule.

Colouration

Some examples of colouration differences; such as the peacock (previously discussed), are extremely striking, whereas others are a specific shade difference in a small area of the body. Much like other forms of sexual dimorphism, it is apparent that these colourations are used to stand out and advertise to other individuals. A well-known example of colouration is found within the family *Paradisaeidae*, better known as birds of paradise. This family of extravagantly beautiful birds have extremely flamboyant males, whose plumage is wild in colour and shape, and who sometimes 'dance' in order to prove their worth within a group of other competing males (Scholes, 2008). These species of birds gather in 'lekking' settings, where males of the species group and compete for the attention of a female in order to win mating rights (Irestedt, 2009). The most attractive male is the individual whose colourations and 'dancing' is the most flamboyant, and therefore these attractive males are chosen more often by the females to copulate. Much like within the peacock, it is suggested these flashy appearances and attention seeking behaviours signify fitness within the individual. Only the

fittest males are able to maintain the beautiful colouration and long tail feathers, and therefore are suggested to be the best mate choice within the group (Arnold and Wade, 1984). Developing extravagant tail feathers in the male of this species, is suggested to be driven by the need to out compete other males for the female's attention. By advertising their superior worth to the choosy female, they are internally increasing their chances of copulation, and therefore reproductive success (DuVal and Kempenaers, 2008).

Another example of less extreme colour differences can be found within the Eurasian blue tit (*Cyanistes caeruleus*). This small bird shows minimal differences between the colourations of the sexes, with males displaying a slightly darker, thicker blue line around the crown of the animal (Mainwaring *et al.*, 2011). However, recent studies have found that under UV light conditions there is a significant difference in the head plumage of this species, showing strong blue chroma colouration which cannot be seen by the human eye (Andersson *et al.*, 1998). It is also suggested that the level of ultraviolet colour is related to male attractiveness and increased parental effort, making it a much more desirable characteristic within the competition for mates (Johnsen *et al.*, 2005). This suggests that these birds, although once thought to be only slightly dimorphic due to our visual abilities, are in fact largely sexually dimorphic when viewed with the visual abilities of the blue tit. Overall colouration is used widely among species to advertise fitness within sexual selection, with bird species commonly having a more flamboyant male, using colours to compete for a female's attention in lekking groups.

Weaponry

Many sexually dimorphic species develop large antlers or tusks within one sex, these are examples of weaponry (Emlen, 2008) and are very common among species of ungulates. Larger more powerful weapons benefit those species who partake in aggressive competition and are therefore favoured among sexually selected males (Bro-Jørgensen, 2007). An example of sexually selected weaponry is found in the African bush elephant (*Loxodonta africana*). Male elephants have much larger tusks than the females with the average tusk weight being 55kg in males and 7kg in females (Poole, 1987). Males in musth use these tusks and intimidating size difference to advertise their availability and worth to the female, as well as competing to prove superiority with other males (Wittermyer and Getz, 2007). Aggression is common within species who exhibit intraspecific competition, as it is a way of competing with other individuals for the right to mate (Tidière *et al.*, 2017). Aggressive use of larger weapons

is also often associated with greater sociality (Plard *et al.*, 2011), which explains why many ungulate species which engage in aggressive activities usually live in large groups, such as the red deer (*Cervus elaphus*). This species partakes in fierce rutting seasons (discussed previously). Rutting season is used to identify the dominant males in the herd in order for them to ‘win’ mating rights. The males with the larger body size and large antlers are at an advantage in rutting (Bergeron *et al.*, 2010), which explains the presence of weaponry in these social and aggressive male ungulates. Rutting season takes an extreme toll on the male deer’s body, with some estimates showing individuals can lose on average 63kg over the period of rutting season (Bobek *et al.*, 1990), while also facing the risk of being severely injured and even killed. However, weaponry and aggressive competitions are still very common within ungulates and other species. This suggests the risk of deterioration and injury is outweighed by the possible benefits associated with victory, such as increased mating chances and social status.

Other non-ungulate species also show sexually dimorphic weaponry. Primates often exhibit pronounced sexual dimorphism with complex social systems, for example mandrills (*Mandrillus sphinx*) not only show large amount of sexual size and colouration dimorphisms, but also show some sexually dimorphic weaponry. Males possess large canines with an average of 45mm in length, while females rarely exceed 20mm. Research has suggested that males who sire more offspring have significantly larger canines, not only this, the males with canines larger than 30mm exclusively sired the offspring of a troop (Leigh *et al.*, 2008). This direct effect of weaponry on sexual success allows an understanding on the importance of these weapons to the males. Not only do the canines benefit the individual when fighting for social rank or when catching prey, they directly affect the ability for the individual to pass down their genetic material to the next generations. These examples of weaponry and ornaments in multiple species all suggest how characteristics which are often advertisements of strength, aggression and dominance can enhance a male’s copulation success and are therefore favoured in males of a species.

Other Secondary Sexual Characteristics

Although weapons are an example of secondary characteristics, there are other characteristics found among species which are not categorised as weaponry, i.e. ornaments. Weapons are often thought to be a tool for aggression within physical fights while ornamental features are used to attract the opposite sex or to signal their worth without physical interactions (McCullough *et al.*, 2016). These traits are specific to the species and often seem without use

to an uneducated eye. Traits which are used solely for the advertisement of social rank or fitness and used within sexual selection are referred to as secondary sexual characteristics. Much like the other features previously discussed, these secondary characteristics are specifically designed to increase the chances of mating or increase the social rank of the individuals who acquire them. An example of a secondary sexual characteristic is a male orangutan's (Genus: *Pongo*) facial plates. Adult male orangutans can display two morphs; unflanged or flanged. This is a type of bimaturism. Flanged males are considerably larger than females (sometimes twice the size), with fatty tissue sacks on the sides of their faces which give them their name, while unflanged males, although still slightly larger on average, are inconspicuous among females (Delgado and Van schaik, 2000). The flanges on the large males are thought to be used to increase call distance when attracting or displaying availability to the females (Utami-Atmoko *et al.*, 2009). Although unflanged males do produce a very small percentage of the sired young in a group, this is usually through sneaky opportunistic mating while flanged males have a higher copulation and reproductive success rate (Utami-Atmoko *et al.*, 2002). Although there are minimal direct fights or competitions between male orangutans which require weaponry or flashy appearances, these secondary sexual characteristics do have a direct effect on the social rank and attraction of mates. The increased siring potential in flanged males and increased attractiveness therefore suggests that the presence of these ornamental facial plates is driven by the result of inter-sexual selection in males, explaining why flanges are only found within males.

Understanding the mechanisms driving sexual dimorphism within a species that is well studied can be challenging due to the many influences involved. It is therefore not surprising that species which are relatively under studied, are often not adequately examined for sexual dimorphism. One such species is the hippopotamus, which the following study focuses on.

The Study Species

The Common hippopotamus (*Hippopotamus amphibius*) is an African megaherbivore; a herbivore species weighing more than 1000kg (Owen-Smith, 1992), and the largest living member of the order artiodactyl (Even toed ungulates). Often referred to as hippos, they are one of the only two extant members of the *Hippopotamidae* family, the other being the much smaller pygmy hippo (*Choeropsis liberiensis*) (Boisserie, 2005). These animals are semi-aquatic creatures, spending the majority of the day cooling down in lakes and other water sources only venturing on land at night to graze (Lewison and Carter, 2004). Although it is

often thought that hippos are related to pigs due to their physical appearance, which has been described as clumsy, with large heads and larger stomachs which sometimes 'hang just above the ground' (Du Chailu, 1868), they are actually closer taxonomically to *Cetaceans* (Boissarie, 2005). Hippos are recognisable for their pig-like shape, large heads with wide opening mouths and big tusk like canines and incisors. Although not predatory, hippos have an extremely territorial nature causing a high number of human fatalities each year. These fatalities almost always involve a hippo defending their territory, especially in response to boats in the water (Treves and Naughton-Treves, 1999). They also have ferocious canines and incisors, reaching up to 50cm in length (Estes, 1991) which can produce a bite force of 2,000 pounds per square inch (psi); which is equal to a jaguar (*Panthera onca*) (Anderson, *et al.*, 2008). There is not a huge array of semi-aquatic large herbivores comparable to this species, as their niche and behaviour is relatively unique for a herbivore. Species such as tapirs; who also live in semi-amphibious environments are similar in ecology (Jarman, 1983), however their solitary and passive behaviour is very different to the hippo.

General Ecology

The hippo is widespread across most of Africa with a small invasive population in South America, but they are more commonly found in sub-Saharan Africa (Lewison, 2007). Their population has mostly been stable; however, it has been reported their population has decreased by 7-20% over the past two decades (Lewison and Oliver, 2008). As discussed previously, hippos only venture onto land at night to graze, where they can travel miles feeding on grass and shrubbery until dawn when they return to wallow in the water sources such as rivers and lakes to escape the heat (Owen-Smith, 1992). Much like African elephants, hippos can be classified as ecological engineers, as their foraging habits and defecation into water sources helps sustain the ecology in sub-Saharan Africa, so much so that their population directly effects the health of the environment (Stears *et al.*, 2018). Groups often stay within relatively close proximity to water sources and will alter their feeding sites in response to variables such as vegetation density and competition (Lewison and Carter, 2004). It was often thought their food source was predominantly grasses (Eltringham, 1999), however it has recently been suggested that as this species is a 'pseudo-ruminant'(i.e. having chambered stomachs) their diet will be much more varied in other lower quality vegetation which can be fermented in the stomach (Boissarie *et al.*, 2005). Hippos wallow within lakes, rivers and mangrove swamps in the day, where they walk on the waterbed showing only the top of their

back, head and nostrils (*Eltringham, 1999*). During the day the species rarely leaves the water sources they inhabit to aid thermoregulation and energy conservation. They also defecate substantially onto the banks of the rivers and pools; this is part of their social behaviour as they use their tails to spread the dung across the area as a sign of territoriality.

Size

Although the hippo is known for being large-bodied, the average size of the species holds a broad range of estimates from different sources and there is little agreement on whether this species exhibits sexual size dimorphism at all (*Owen-Smith, 1992*). Other large herbivores with similar ecologies do show high levels of sexual size dimorphism (see Figure 1), therefore it is expected there will be significant differences in mass between the sexes of hippos. Dr Richard Laws spent a number of years working on the aging and dentition of hippos (*Laws, 1968*) and summarised within his unpublished notes that no sexual dimorphism was present in the overall body size of this species. Similarly, early anatomical studies concluded an average of both sexes to be 1500kg (*Luck and Wright, 1964*). Although Laws provided no evidence for sexual dimorphism of overall body size in his 1968 work; a later paper stated that males were approximately 5 inches longer than females, and up to 400 pounds heavier (*Field and Laws, 1970*). Other literature resources also claim to show a differentiation among the sexes weight. *Van Niekerk et al., (1963)* concluded that males have an average weight range of 1590 – 2050kg, and females 1360 – 1730kg, although no statistical analysis is provided to conclude any significant difference between the sexes. *Du Chailu (1868)* also states that during his hunting adventures males were significantly larger than the females, however once again this is merely anecdotal evidence and provides no clear statistical conclusion. *Owen-Smith (1992)* summarises the clear inconsistencies in the literature within his work ‘Megaherbivores: The influence of very large body size on ecology’. *Owen-Smith* states that the heaviest recorded weight was 2660kg for a male and 2025kg for a female in Uganda. However, he acknowledged that these showed extreme individuals and other areas; such as Kruger national park in South Africa, showed a maximum male weight of 2005kg. Studies in Zambia provide an average weight of 1600kg for males and 1565kg for females, although a larger sample size in Uganda showed averages of 1480kg for males and 1365kg for females. It could be suggested that these variations in estimates come from the range of habitat where the hippo is found in sub-Saharan Africa. Drought periods are common in these environments and can affect the growth and mass of hippos due to lack of both water sources and food (*Dunham, 1994*). Therefore, any of the

groups analysed in these studies could have been recovering from a drought period, which may have affected the results dramatically. The lack of an adequate sample size or statistical analysis of the data also reduces the reliability of these body size estimates.

Although the hippo is a large African herbivore, they are less studied than one might imagine. To be close enough to safely take measurements from an individual, they must be tranquilized due to their aggressive nature. Early studies have shown that to successfully tranquilize a hippo without fatality, the animal must be out of the water to avoid drowning (Pienaar *et al.*, 1966). Hippos only venture onto land during the night, where they can travel up to 3-5km to graze (Owen-Smith, 1992) adding to the issue of obtaining reliable observations and measurements. Thus, the majority of morphology data available at present comes from culled groups much like the data used in Laws (1968) study.

Captive studies into this species behaviour are problematic due to the different group sizes and sex ratios found in captivity. In many cases the group sizes can be fewer than three individuals, with a completely female group (Blowers, 2008). This is due to the issues with housing and controlling large groups of individuals. As well as male hippos being extremely territorial of the water resources (Estes, 1991). Therefore, the majority of studies focused on are smaller wild population studies.

Social Behaviour

Group sizes among hippos tend to vary according to rainfall in the area; in areas of higher water levels hippos' gather in numbers of 10-30, which includes several females and young, a dominant bull and two to six lower ranking males (Owen-Smith, 1992) (Skinner *et al.*, 1975). Small bachelor groups have also been recorded, although as a general rule there is usually only one dominant male in one territory. However, in times of drought, groups of up to 150 individuals have been witnessed gathering around one water source (Olivier and Laurie, 1974), which can lead to aggressive competitions over territory (Stommel, 2016). If neighbouring dominant bulls happen to meet, each will attempt to out rank the other by yawning, presenting their rear ends and defecating while scattering the faeces with their moving tails (Kingdon, 2013). When fights break out, individuals can be seen breaching the water and opening their mouths to the widest angle (Estes, 1991); exposing their large canines and incisors and often clashing teeth (Zoric *et al.*, 2018), sometimes even causing fatal wounds (Eltringham, 1993). The mouth gape of a hippo can almost reach 180 degrees, with a bite width of almost 0.5m (Owen-Smith, 1992, Herring, 1975), making them formidable during these

large aggressive competitions. The social behaviour of hippos has many similarities to that of species with competitive polygamous social structures and harems. Within a competitive polygamous social setting, fights are commonly used to determine dominance and territory (Haley *et al.*, 1994), and are often an indication of high levels of sexual dimorphism (Weckerly, 1998). Therefore, it is acceptable to assume a similar extent of sexual dimorphism within the hippo to that of other species with similar social behaviours.

Reproductive Behaviour

A singular dominant bull will attempt to mate with as many available females within his territory as possible, although it is expected that some sub-dominant males will also sire offspring (Laws and Clough, 1966). The gestation period of the hippo is eight months, with a peak in births during the wet season (January - February), this suggests a peak in conception around May to June (Smuts and Whyte, 1981). As peak mating season falls in a time of low rainfall in some areas of Africa, a dominant male mating with a large number of females will require a huge amount of energy (Eltringham, 1993). This massive energy requirement may be difficult to maintain, as these grazers will be forced to travel further for food in times of drought (Jennings *et al.*, 2010). In most wild groups, 40% - 80% of the females can be pregnant at any point (Smuts and Whyte, 1981), with a reduction to almost 5% in times of drought (Laws and Clough, 1966). The dominant bull of a group will consistently investigate any females in oestrus, those pursued often clash jaws with the male; who then will initiate pushing behaviour until the female concedes to the males attempts by lying on the waterbed and allowing him to mount her (Verheyen, 1954). The chasing and courting behaviour documented in the hippos suggests a possible level of female choice during copulation attempts. This could suggest that a dominant male must not only protect his territory and dominance through aggressive behaviour with other males, but also impress choosy females. Similarly, the aggressive nature of mating and courtship could signify male intimidation through reproduction, which could require males to be larger in order to overpower the females. In both scenario's, traits such as size and weaponry could influence the male's chance of copulation, which may explain the development of male specific traits.

Although there is a clear lack of research into the morphological difference between the sexes, the hippos' behaviour and mating system mirrors those often associated with high levels of sexual dimorphism (Weckerly, 1998). This leads to the hypothesis that there will be a high level of sexual size dimorphism present in this species, with a significantly larger body size

found within males. Although this is the major hypothesis to be examined in the coming investigations, it is also expected males may have other pronounced secondary sexual characteristics such as larger canines and incisors which may be used during sexual selection. The overall aim of this study is to evaluate if any sexual dimorphism is present within hippos, and if so, delve deeper into the possible mechanisms that are driving these differences, such as sexual selection of body size.

Methods

Data Collection

The data used within this study has been taken from the dataset collected by Dr Richard Laws in the late 1950's from a large population of culled hippos throughout Eastern Africa. In 1958, the Ugandan National Park trustees set out to control the population of hippos in the Queen Elizabeth Park through culling. This was due to the extent of ecological damage their rapid population growth had caused (Bere, 1959). Dr Laws joined the group to collect high quantities of biological measurements on the species, which was a continuation of W. M Longhurst's work who aimed to accurately document African wildlife. The raw data collected during this time was used by Laws to create a method of aging hippos using their dentition (Laws, 1968). Laws aging methodology allows an estimated age category to be identified and is particularly useful in estimating the ages of individuals within wild populations. This is because hippos are notoriously difficult to get close to but are often viewed from afar with their mouths open wide enough to inspect the majority of their teeth. The Queen Elizabeth national park is located in the Western Region of Uganda and extends over approximately 2,000 km², with many excellent hippo habitats including Lake George and Lake Edward. The notes found within Laws unpublished work, and the information within his published 1968 work indicate at least three geographical locations throughout the park were used during the culling expedition. Between 1961 and 1966, over 3,000 individuals of different ages were culled and measured, individuals were shot in Lake Edward where they wallowed, allowed to sink and then pulled out of the water to be measured while buyers purchased the meat. This is without doubt one of the largest recorded collections of morphological data of hippos ever taken, making it a vital resource in the research of this species.

Data was recorded in notebooks, and the measurements taken were inconsistent in format fluctuating from imperial to metric throughout. Measurements taken included; sex, age group, body girth, shoulder height, multiple head measurements (eye and mouth width, lower

jaw mass and length, width of canines and condyles, and height of the coronoid), neck girth, total body length (as well as nose to tail base length), the mass of multiple organs (mammary glands, uterus, testes and epidermis), overall body mass, acknowledgements of parasites, embryos and lactation, as well as a notation for any scars and general condition of the animal (marked 1-4). Each individual was noted with a tag number (if applicable – some were not tagged), and a code relating to the area, date and number culled that day. Individuals were sexed and given an age category based on the results from Laws' findings. These age categories give an age range where the individual can be estimated with fair accuracy (Table 1).

Table 1: Age categories from Laws (1968) work: age categories and the mean age estimated of the individuals placed in each category. Results were concluded from some 3,000 individuals. Individuals are placed into age categories with varying ranges.

Age Category	Mean Age (years)	Age Range (+-) (years)
1	0	<i>na</i>
2	0.5	<i>na</i>
3	1	<i>na</i>
4	3	0.5
5	4	1
6	7	1
7	8	2
8	11	2
9	15	2
10	17	3
11	20	3
12	22	3
13	24	3
14	27	3
15	30	3
16	33	3
17	35	4
18	38	4
19	40	4
20	43	5

Although the main outcome of this data collection was to identify markers in the dental makeup of the animal, the vast variety of morphological measurements taken throughout the development of a hippos allows us to identify development of many features of this species throughout their life and specifically as they become fully developed and sexually mature.

Data Organisation

Firstly, the data were entered into excel to allow statistical analysis to be carried out in R-Studio (R Core Team, 2018). Next, it was essential to assess what variables were most valuable within this dataset. It was suggested that dry weights of intestines, specific gland weights, uterus and other specific organ measurements could be removed for this study, however they could be useful in future research. The choices for preliminary analysis were: body mass (kg), total body length – from nose to tail end (cm), height to the shoulder (cm), neck girth (cm), the width between the canines (mm), lower mandible length (mm) and lower mandible mass (kg).

Data Analysis

As sexual dimorphism is often defined as differences between adult individuals, for the purposes of a clear investigation a definition and specific age for adulthood must be identified. Literature based on captive hippos classified adulthood as sexual maturity - approximately three years old (Dittrich, 1976). However, sexual maturity only refers to the ability to reproduce not the overall growth of individuals. Not only this, in populations where males often compete for access to females, males often continue to grow substantially after sexual maturity. Studies of culled animals from wild hippo populations suggest maturity occurs from 7-8 years old in males and 9-10 years in females (Laws and Clough, 1966). Behavioural studies in the wild also support this claim, stating that males tend to leave their original group at the age of 7-8 years old – suggesting they have become a competitive threat to the dominant bull of the group (Fazal *et al.*, 2014), and perhaps are therefore becoming fully developed in any sexually selective trait. It was suggested that to fully identify the age of maturity, the dataset should be evaluated graphically to plot where individuals are fully developed and identify whether this supports or contradicts other wild-based population studies. Using R studio, a graph showing the mean body mass at each age group was plotted for males and females, using the mean age of the age category (figure 2).

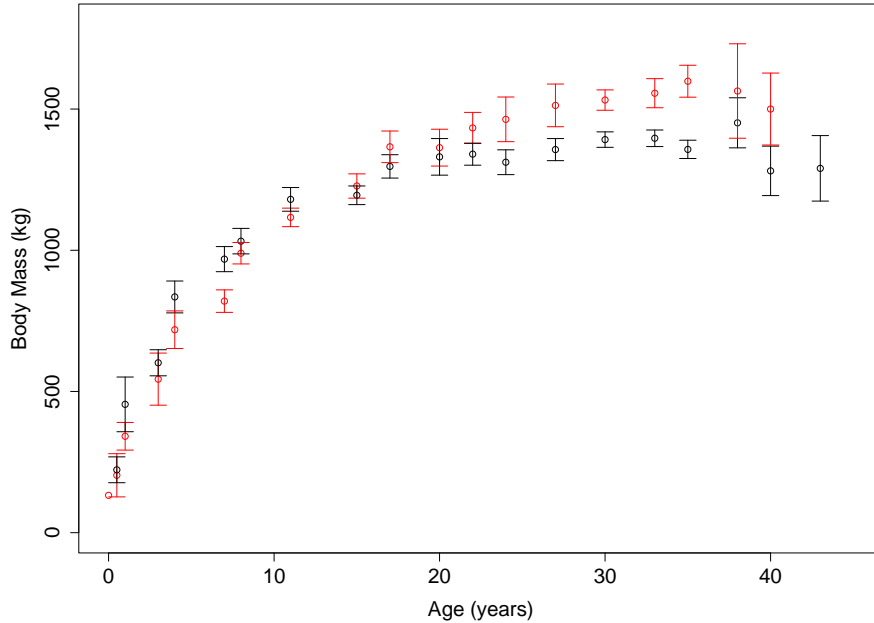


Figure 2: Plot comparing the mean body mass in kilograms (kg) of male and female hippopotamus in each of the age groups (shown in mean age of the group). Data used from Laws (1968) work on dentition and aging in hippopotamus, using 1,251 individuals whose mass and age were collected. Ages were categorised into age groups which were described with a mean age. Mean body mass (kg) for males (shown in red) and females (shown in black) with standard error shown (95% CI) fitted using R

This suggests the increase in mean mass over development in both male and female hippos, the results suggest both males and females increase until the approximate age of eleven years old where females (shown in black) can be seen to plateau while males (shown in red) continue to gradually increase at a lower rate than before this age (Figure 2). From this graph it was concluded that adulthood was classified as individuals within the age category 8 or over (mean age eleven), which supports the work published by Fazal *et al.*, (2014). Pregnant females were removed from the dataset to reduce any effect on body mass or other measurements which pregnancy may cause. However, some fetuses measured in this investigation were not marked to a female in the data set, suggesting that not all the pregnant females are identified precisely.

Statistical Analysis

During preliminary analysis, all variables showed a normal distribution in the Shapiro-Wilk test for normality. The mean adult female and male measurements of each characteristic was first calculated using R allowing us to give a quantitative difference between the sexes at adulthood. However, it was suggested that because the effect of age on the morphological measurements is not linear (see scatterplots), the most effective way of identifying potential

differences between the sexes morphological traits is to conduct a generalised linear model - gaussian (GLM), with a quadratic term on age and an interaction factor between age and sex. A GLM was chosen due to the continuous data type, and the violation of homogeneity of variance. This model would allow us to see if the difference in gradients for each sex is significantly different throughout full development and growth. Before each GLM was conducted Q-Q plots were formed to check was a normal distribution for the residuals, and therefore ensure the assumptions required for this statistical test were met.

To evaluate fully the differences between the two sexes, secondary characteristics such as neck girth (cm), width between the canines (mm), lower mandible length (cm) and lower mandible mass (kg) were compared to overall body size throughout adulthood by conducting another GLM. The variables were log transformed to ensure linearity (Xiao *et al.*, 2011) just like within Weston's (2003) study into scaling of hippo skulls. Similarly to the earlier GLM's conducted, there was a normal distribution for the residuals when plotted on Q-Q plots, which met the assumptions required for this statistical test.

This type of GLM analysis allows specific morphology such as jaw length to be evaluated between the two sexes while taking scaling issues into consideration. For example, it is important to consider whether a larger hippo will also likely have a larger jaw length regardless of sex. Isometric scaling would suggest the jaw length is indicative of the size of the hippo, as the jaw length grows at the same rate as overall body size. If the scaling of the jaw length is not isometric, the jaw length grows at a different rate to overall body size. This is called allometric scaling and can suggest other pressures are influencing the growth of the jaw length. If a male hippo that weighs 1700 kg has a significantly longer jaw length than a 1700 kg female, it is clear that overall body size is not the only influence in the development of the length of the jaw, and other pressures are influencing longer jaws in males. A scaling factor (x axis variable) is required for a regression of this nature, to allow the variable tested to be compared to 'overall body size'. Body mass is the usual choice for this type of evaluation as it encompasses the whole-body size. However, only a comparatively small number of individuals within the dataset have data for both body mass and other variable such as jaw length, jaw weight, and neck girth. This along with the known effect of drought on hippo's body mass, led to body length to be chosen as the constant scaling factor for the regression analysis. Along with simple GLM analysis, GLM with interaction factors were also employed to examine if sex has an effect on the relationship between these specific secondary characteristics and overall body size.

Results

Scatterplots of mean body mass (Figure 2), body length (Figure 3a) and shoulder height (Figure 3b) throughout development, show the differences between the sex's growth. Both sexes can be seen to increase in mass, length and height until adulthood where female hippos (shown in black) can be seen to plateau while males (shown in red) continue to increase.

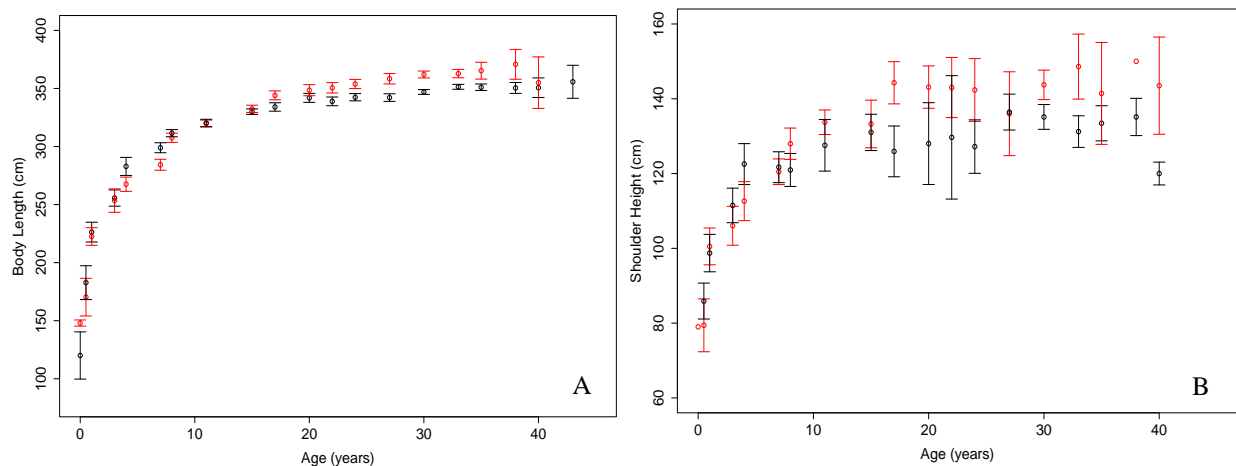


Figure 3a-b: (A) body length (cm) and (C) shoulder height (cm) differences between male and female hippos throughout development. Data was adapted from Law's (1969) work, body length $n = 2790$ and height $n = 506$. Data for males (shown in red) and females (shown in black), with CI of 95%.

Mean measurements indicated that overall adult male hippos are taller at the shoulder (135 cm compared to 130 cm for females), longer in body length (339 cm compared to 337cm compared to females) and heavier in mass (1314kg compared to 1300kg in females)

Although mean body length, shoulder height and body mass of this species does show some differences between the sexes, there seems to be only marginal differences in some cases (a matter of 2 cm).

GLM analysis suggest all three characteristics are significantly affected by the interaction of sex and age (table 2). This suggests males are significantly larger throughout development in body mass, length and height.

Table 2: Results of three generalised linear models with quadratic terms for age and interaction factor analysis of sex and age on body mass (kg), body length (cm) and shoulder height (cm). The linear equations for both sexes are shown, with the f values, df values and R^2 values also stated. The significant level for the interaction between sex and age was set as 0.05 and significant results marked with *

	Male Equation	Female Equation	$f(df)$	R^2	Sex and Age Interaction P Value
Body Mass (kg)	$y = 0.369x + 1007.4$	$y = 0.6337x + 963.4$	$f(3,1247) = 355.1$	0.459	$<2^{-16} (P<0.05)^*$
Body Length (cm)	$y = 0.044x + 305.1$	$y = 0.069x + 300.5$	$f(3,2716) = 175.6$	0.472	$<2^{-16} (P<0.05)^*$
Shoulder Height (cm)	$y = 0.016x + 116.6$	$y = 0.027x + 121.1$	$f(3,502) = 73.34$	0.301	$0.000238 (P<0.05)^*$

To fully evaluate sexual dimorphism among this species, more morphological elements were considered such as neck girth and the width between the canines (figure 4a-b). These elements among others, are analysed to explore the possibility of secondary sexual characteristics being the main form of sexual dimorphism in this species rather than overall sexual size dimorphism.

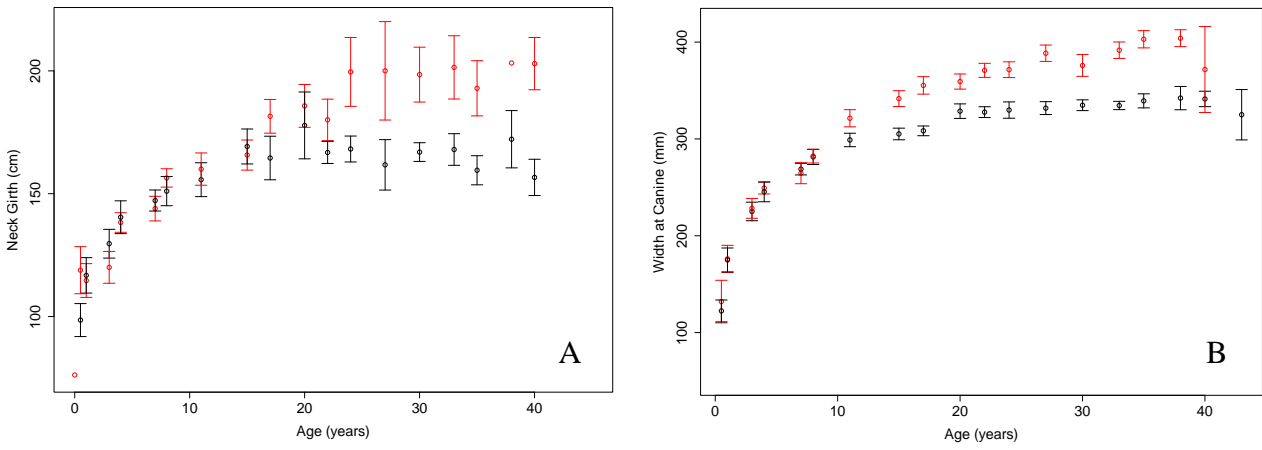


Figure 4a-b: (A) neck girth (cm) and (b) width between the canines (mm) differences between male and female hippos throughout development. Data was adapted from Law's (1969) work, neck girth $n = 410$ and width between the canines $n = 792$. Data for males (shown in red) and females (shown in black), with CI of 95%.

The development of both the neck girth and canine width suggest a difference between male and female hippos, with males continuing to increase their neck girth and canine width throughout adulthood (Figure 4a and 4b).

In both neck girth and canine width, males have a larger mean size with the mean adult male neck girth being 170cm in comparison to 163cm in adult females and mean adult male canine width being 357mm in comparison to 321mm in adult females. Adult males have on average a 7cm larger neck circumference than females in adulthood, while also having a larger average canine width by 35mm.

Table 3: Results of two generalised linear models with quadratic terms for age and interaction factor analysis of sex and age on neck girth (cm) and width between the canines (mm) The linear equations for both sexes are shown, with the f values, df values and R^2 values also stated. The significant level for the interaction between sex and age was set as 0.05 and significant results marked with *

	Male Equation	Female Equation	$f(df)$	R^2	Sex and Age Interaction P Value
Neck Girth (cm)	$y = 0.058x + 144.7$	$y = 0.025x + 140.1$	$f(3,406) = 122.3$	0.471	7.68×10^{-13} ($P < 0.05$)*
Width Between Canines (mm)	$y = 12.59x + 271.3$	$y = 12.54x + 271.2$	$f(3,788) = 175.6$	0.523	1.04×10^{-13} ($P < 0.05$)*

A GLM was then conducted to analyse the interaction between age and sex on these measurements (see table 3). This analysis suggests both neck girth and the width between the canines are significantly affected by the interaction of sex and age. This suggests males are significantly larger throughout development in neck girth and canine width.

Although these results show different mean measurements between male and female morphology, it is important to take into account body size when analysing specific morphological differences between the two groups. To account for scaling issues, a generalised linear model was produced to compare these secondary characteristics with total body length (figure 5a-b).

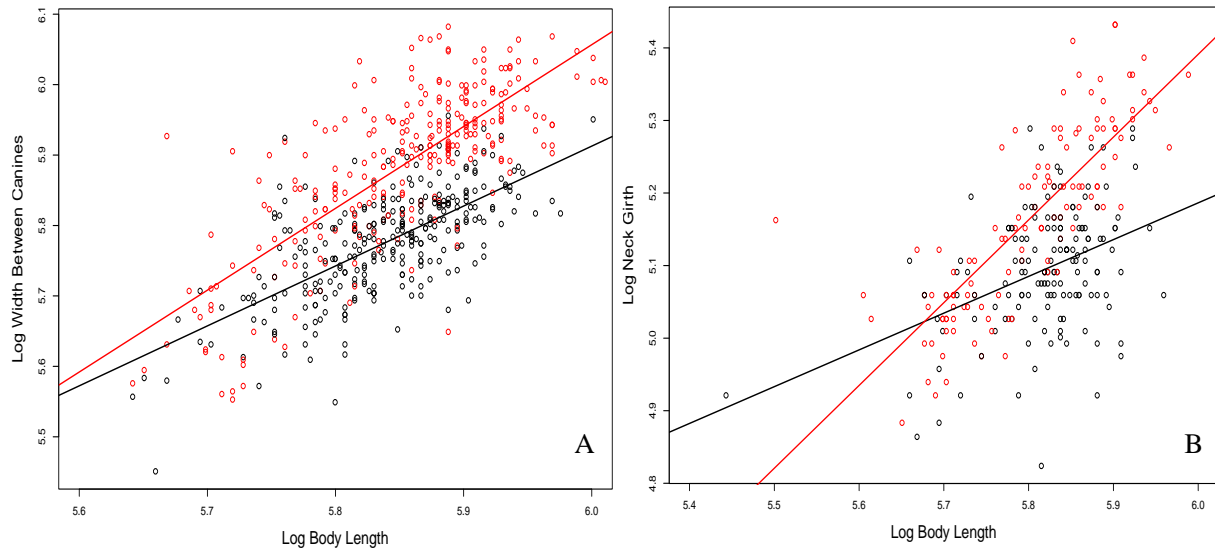


Figure 5a-b: Generalised linear models (GLM) of male and female hippos comparing log neck girth (a) and log width between the canines (b) with log body length of adults. Calculated in order to analysis the growth of neck girth and width between the canines in males and females when controlling for body length. Adults classified as individuals aged 11 or over. Female neck girth regression (shown in black): $y = 0.51x + 2.15$, $F(1,147) = 29.22$, $p < 0.001$, $R^2 = 0.25$. Male neck girth regression (shown in red): $y = 1.14x - 1.45$, $F(1,119) = 212.9$, $p < 0.001$, $R^2 = 0.63$. Female canine width regression (shown in black): $y = 0.85x + 0.81$, $F(1,285) = 231.5$, $p < 0.001$, $R^2 = 0.45$. Male canine width regression (shown in red): $y = 1.16x - 0.91$ ($F(1, 271) = 364.8$ $p < 0.001$), $R^2 = 0.57$

The GLM for the width between the canines and body length determined body length and sex individually both had a statistically significant effect on the width between the canines. The interaction of body length and sex (0.37 ± 0.08) also showed a statistically significant effect on canine width (figure 5a). This suggests that the effect of body length on the development of the width between the canines, is significantly different between the sexes, with males having a large width between the canines regardless of overall body size.

Similarly, a GLM determined both body length and sex individually had a statistically significant effect on neck girth. The interaction of body length and sex (0.63 ± 0.12) also showed a statistically significant effect on neck girth (figure 5b). This suggests that the effect of body length on the development of neck girth, is significantly different between the sexes, with males having a larger neck girth regardless of overall body size.

Table 4: Results of two logarithmic generalised linear models with interaction factor analysis of sex and body length on neck girth (cm) and width between the canines (mm) The linear equations for both sexes and the interaction of body length and sex are shown, as well as the P-values. The significant level for the interaction between sex and age was set as 0.05 and significant results marked with *

	Male Equation	Female Equation	Log body length P value	Sex P value	Interaction of log body length and sex +SE (P value)
Neck girth (cm)	$y = 1.14x - 1.45$	$y = 0.51x + 2.15$	$P < 0.05^*$	$P < 0.05^*$	0.63 ± 0.12 ($P < 0.05$) [*]
Width between the canines (cm)	$y = 1.16x - 0.91$	$y = 0.85x + 0.81$	$P < 0.05^*$	$P < 0.05^*$	0.37 ± 0.08 ($P < 0.05$) [*]

There is a slight difference in the development of jaw length between male and female hippos (Figure 6a). The mean measurement for this data supports this suggestion as the mean adult male jaw length is 514 mm which is larger than the female's length of 493 mm.

There is also a visible difference between male and females jaw masses throughout development, with males continuing to increase in jaw mass throughout adulthood (Figure 6b). This is supported by mean measurements which show lower jaw mass of adult males as 12.1 kg and 8.5 kg in adult females. The results for jaw mass exhibited the most profound difference, with mean male jaw mass being 3.6kg greater than females, which equates to male jaws being on average just over 42% larger than the female jaw mass.

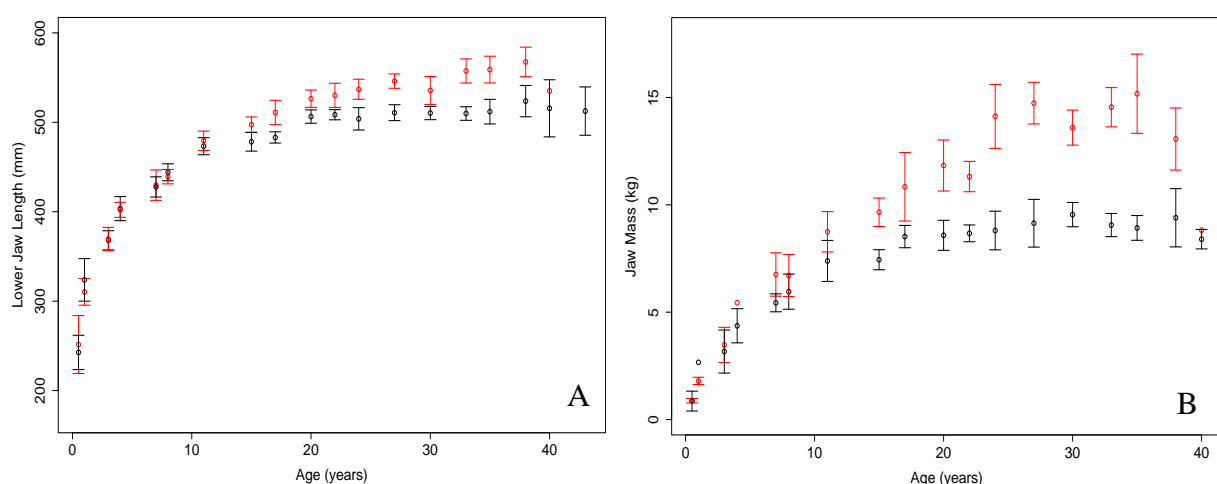


Figure 6a-b: Assessment of the difference between the sexes of hippopotamus in Jaw Length (mm) and the Jaw Mass (kg). Data was adapted from Law's (1969) work and measurements taken of the lower mandibular only. Jaw length $n = 587$ and jaw mass $n = 245$. Data for males (shown in red) and females

GLM analysis showed both lower jaw length and mass are significantly affected by the interaction of sex and age (table 5). This suggests males have significantly longer and heavier jaws throughout development.

Table 5: Results of three generalised linear models with quadratic terms for age and interaction factor analysis of sex and age on lower manible length (cm) and lower mandible mass (kg) The linear equations for both sexes are shown, with the f values, df values and R^2 values also stated. The significant level for the interaction between sex and age was set as 0.05

	Male Equation	Female Equation	$f(df)$	R^2	Sex and Age Interaction P Value
Lower Jaw Length (mm)	$y = 0.134x + 430.35$	$y = 0.081x + 430.35$	$f(3,583) = 175.6$	0.473	$5.47e^{-08}$ ($P < 0.05$)*
Lower Jaw Mass (kg)	$y = 0.007x + 7.011$	$y = 0.003x + 6.127$	$f(3,241) = 120.6$	0.5953	$2.59e^{-10}$ ($P < 0.05$)*

A logarithmic GLM analysis (figure 7a) determined both body length and sex individually had a statistically significant effect on jaw length and the interaction of body length and sex also showed a statistically significant effect on jaw length (table 6). This suggests that the effect of body length on the development of jaw length, is significantly different between the sexes.

Similarly, the logarithmic GLM analysis (figure 7b) on body length and sex individually showed a statistically significant effect on jaw mass. The interaction of body length and sex also showed a statistically significant effect on jaw mass (table 6). This suggests that the effect of body length on the development of jaw mass, is significantly different between the sexes.

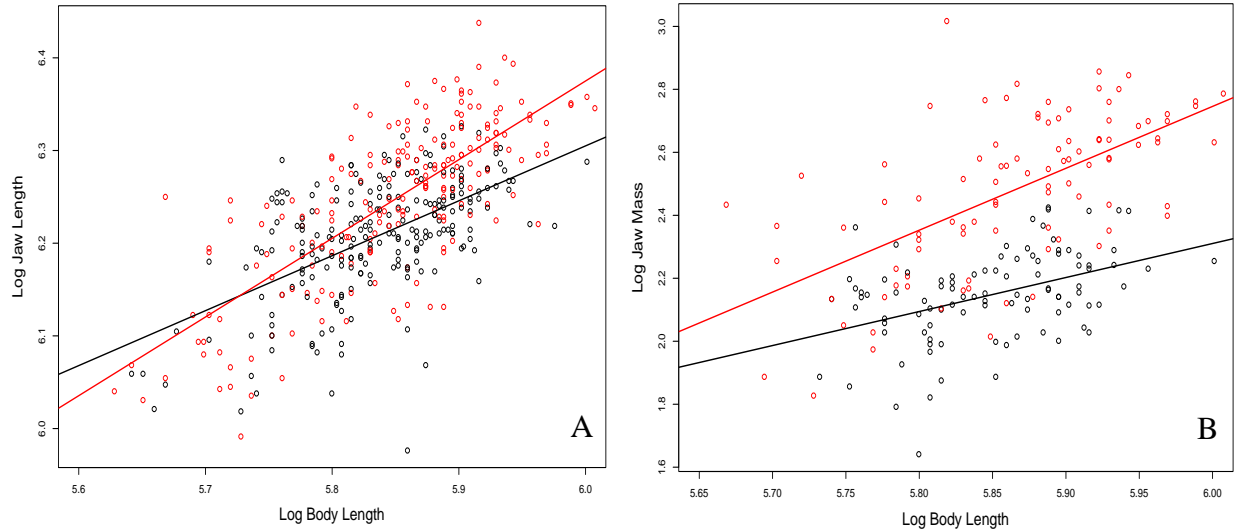


Figure 7a-b: Generalised linear models of male and female hippos comparing both the log lower jaw length and log lower jaw mass with log body length (cm) of adult Individuals. calculated in order to compare the jaw length and mass growth in males and females when controlling for body length. Adults classified as individuals aged 11 or over. Female jaw length regression (shown in black): $y = 0.59x + 2.75$, ($F(1, 219) = 104.2$, $p < 0.001$), $R^2 = 0.32$. Male jaw length regression (shown in red): $y = 0.85x + 1.28$ ($F(1, 201) = 251.4$, $p < 0.001$), $R^2 = 0.55$. Female jaw mass regression (shown in black): $y = 1.08x - 4.17$, ($F(1, 95) = 21.6$, $p < 0.001$), $R^2 = 0.21$. Male jaw mass regression (shown in red): $y = 1.97x - 9.05$, ($F(1, 94) = 54.96$, $p < 0.001$), $R^2 = 0.36$.

Table 6: Results of two logarithmic generalised linear models with interaction factor analysis of sex and body length on lower jaw length (cm) and mass (kg) The linear equations for both sexes and the interaction of body length and sex are shown, as well as the P-values. The significant level for the interaction between sex and age was set as 0.05 and significant results marked with *

	Male Equation	Female Equation	Log body length P value	Sex P value	Interaction of log body length and sex +SE (P value)
Jaw length (cm)	$y = 0.85x + 1.28$	$y = 0.59x + 2.75$	$P < 0.05^*$	$P < 0.05^*$	0.26 ± 0.079 ($P < 0.05$)*
Jaw mass (kg)	$y = 1.97x - 9.05$	$y = 1.08x - 4.17$	$P < 0.05^*$	$P = 0.03^*$	0.89 ± 0.37 ($P = 0.02$)*

Discussion

When first analysing the difference in overall body size among hippos, it is apparent there is not a huge difference between the sexes, especially between adult individuals. Although there was a significant difference found within the mass, length and height of this species, the minimal difference between the means of the sexes forces us to view a suggestion of a significantly heavier, longer and taller male hippo with uncertainty. This is due to the original data collection being measured in feet and inches; resulting in a low level of accuracy. Therefore, the differences of 2-5cm between the sexes are unlikely to be reliable measurements. Other papers tend to acknowledge sexual size dimorphism when the percentage difference is approximately 10% upwards (Lindenfors *et al.*, 2007). In this analysis adult males had an average height difference of only 5cm larger than females, which is only a 3.7% difference, and more notably the percentage difference between male and female body mass is a mere 1.09%. However, percentage difference is not always the most accurate form of analysis due to scaling (Smith, 1999).

The sexual size dimorphism results found within this study are surprising considering preliminary research into the reproductive strategy and social structure of this species. Some studies into ungulate species suggest a positive relationship between increasing group size and an increase in the extent of SSD (Loison *et al.*, 1999). As hippos are known to group in large herds, the lack of a large level of sexual dimorphism present suggests a deviation from other species with high levels of sociality. It was also expected hippos may follow the extent of sexually dimorphic exhibited in other large herbivore species, whose courtship behaviours are similar to theirs, e.g. elephants (Owen-Smith, 1992). Elephant males partake in polygamous mating systems, using their larger size to benefit reproductive efforts through intimidation in competition and mate guarding. Male hippos are also a very polygamous species, who use territorial aggression in order to monopolise females in their area (Kingdon *et al.*, 2013). The fierce territoriality and mate guarding techniques used by the hippo, are also very similar to the harem social systems of the elephant seal (Stommel, 2016). Male elephant seals use pupping beaches to monopolise on a large source of females who congregate for shelter. This produces intense territorial behaviour and competition among the male elephant seals, who are benefitted through a much larger body size i.e. sexual selection (Fabiani *et al.*, 2004). The spatial restriction of hippos to water sources allows males to have equal opportunity to monopolize large aggregations of females. These similarities to sexually dimorphic species behaviours, suggest hippos could use a larger body size to intimidate competing males when fighting for

dominance in a territory. Thus, producing selective pressures on male hippos to be larger in body size in order to gain the physical benefits during their aggressive competition for territory, oppose to the species in general. This potential for sexual selection encouraging the development of sexual size dimorphism makes the lack of extensive sexual size dimorphism in hippos even more interesting.

Another reason for expecting a high level of size dimorphism among hippos is Rensch's biological rule (Rensch, 1950, Abouheif and Fairbairne, 1997). This biological rule suggests that when sexual size dimorphism favours the male of a large species, it is expected that the degree of sexual dimorphism will be higher than that of a smaller species (Polák and Frynta, 2010). Considering the hippo is a very large species, growing upwards of 1,300kg, the lower level of SSD found within these results indicates a pronounced difference from the expected extent of sexual size dimorphism, and therefore it is suggested hippos do not follow Rensch's rule.

There are many examples of ungulates species who strongly support Rensch's rule (Silby *et al.*, 2011, Polák and Frynta, 2010). However, there are also many examples of ungulate species who do not show any dimorphism regardless of social-sexual behaviour (Ruckstuhl and Neuhaus, 2009). Similarly, many species deviate from the expected level of sexual dimorphism (Martinez and Bidau, 2016). An example of this can be found in another African megaherbivore - the white rhino (*Ceratotherium simum*), whose males are slightly larger in comparison to females. The size difference however is not as high as expected when considering the species size and Rensch's rule (Jarman, 1983). White rhinos and hippos have a similar grazing ecology (Waldrem *et al.*, 2008), and both have been suggested to often supplement low energy intake in times of food shortage with fat reserves (Shrader *et al.*, 2006). Therefore, it could be suggested both species have deviated from Rensch's rule due to dietary constraints, as large species may not be able to maintain a larger mass in one sex through grazing feeding habits, especially in areas often effected by food shortage. Rachlow *et al.*, (1998) suggested the white rhino's degree of sexual dimorphism could be related to their semi-solitary nature rather than diet. This is because males only come into contact with females during the oestrus period and therefore do not follow the trends which occur with species who exhibit greater sociality and larger degrees of sexual size dimorphism (Plard *et al.*, 2011). However, hippos are shown to be a widely social species (Barklow, 2004) and therefore if sexual size dimorphism is strongly correlated with sociality, we would expect to see sexual size dimorphism in this species. Similarly, male African elephants also show low levels of

sociality similar to the white rhino, only socialising with females during courtship and mating (Woolley *et al.*, 2009). As elephants have a large difference in height and mass between males and females, this could suggest the sociality of the species is not always the primary driver for sexual size dimorphism.

Some species are believed to have deviated from Rensch's rule due to factors such as intersexual food competition and interspecific competition (Casanova, 2013). It is reasonable to consider if drought periods and other environmental factors which can affect the hippo's development, may have contributed to the deviation from what is expected from them in regard to SSD. If during drought periods these grazing animals are constrained on food availability and territory, growing significantly larger males for the purposes of sexual attraction may be difficult and have a huge negative impact on the individual's ability to survive. However, these studies focus on domesticated species and are therefore different to the wild species used in this investigation.

Studies have noted that the large size in male kudus made them significantly more susceptible to an early mortality, suggesting larger body size decreased agility during predation while also increasing nutritional requirements (Owen-Smith, 1993). Illius and Gordon (1987) support this suggestion, outlining the vulnerability an increased body size has on a species, due to the increased nutritional requirements. Along with the overall increase in nutritional needs associated with a larger body size in herbivores, a link has also been made between a larger body size and an earlier mortality due to increased teeth wear (Owen-Smith, 1993). This is because larger individuals must eat more to maintain their size, increasing the rate of tooth wear resulting in early malnutrition in the individual. This could outline a direct cost with developing a larger body mass in male hippos, as the increase in malnutrition needs may produce an early mortality due to starvation and increase tooth wear. However, male kudus still show a high level of sexual size dimorphism, and if drought were to inhibit SSD there would not be so many examples found in sub-Saharan Africa (Lindenfors *et al.*, 2007).

It could be suggested that the hippo's environmental settings; such as their semi-aquatic nature, may increase the negative impacts of food unavailability. This is because the only foraging areas available to the hippos are those in proximity to water, which are in high competition in times of drought when hippos congregate in large numbers. Whereas other species such as Kudus have a far greater territory range (Nersting and Arctander, 2001). In serious drought periods, hippos may have to congregate in groups of 150-200 individuals and share limited vegetation (Viljoen, 1995 and Zisadza *et al.*, 2010). This grazing species relies

heavily on low energy food sources such as vegetation and other grasses, and the frequent negative impacts of drought will reduce these resources and increase competition within large groups of individuals (Koerner and Collins, 2014). This could majorly impact the health of hippos and may affect their ability to grow one sex substantially heavier. Adaptations in changing environments can be risky in general to species vulnerable to lack of food resources or habitat, and sexually selective traits may not withstand the pressures placed in these delicate environments (Badyaev, 2002). Traits which reduce overall fitness of individuals in times of hardship such as winter periods are uncommon, however extinction due to sexually dimorphic traits have been examined for species who encounter unforeseen environmental changes like ice-ages (Kokko and Brookes, 2003). If hippos have common environmental hardship in drought periods its acceptable to suggest massive increase in body size within one sex may not be sustainable within this species. As this could otherwise cause potential extinction if all valued males die from starvation or are unable to prepare for the huge energetic costs involved in mating, especially in drought periods (Lane *et al.*, 2010). However, this species weighs over 1,000kg and therefore it is unlikely that drought periods have such a huge impact on the species overall size; as if this was the case, the species would be considerably smaller.

Another explanation is rooted in their semi-aquatic nature. Although the mating behaviour and social structure of the hippo parallels other species who rely on extreme male based sexual size dimorphism to increase mating chances, these species social interactions are done out of the water where physical appearance is evident (Blankenhorn, 2005). In these social systems physical size benefits males through preference by females and physical dominance when competing for access to mates (Baniel *et al.*, 2017). Hippos spend most of their days almost fully submerged in water with little showing except their eyes, snout and ears (Owen-Smith, 1992). This poses an important evolutionary question: is body size beneficial in the displays and competition for dominance within this species? if not, what specific traits (if any) are beneficial? Physical fights which are observed, generally only required the clashing of large heads and teeth (Laws and Clough, 1966). Although body size will benefit males during these fights, larger weaponry is likely to be much more effective.

The neck girth of adult males is significantly larger on average than females. This is supported by analysis that takes scaling into account, suggesting that the effect of body length on neck girth is significantly different between the sexes. Male hippos neck girth therefore develops at a higher rate than females throughout adulthood, regardless of overall body size. It could be suggested that neck girth has a positive benefit for male hippos, such as within social

standing and fighting power within aggressive acts. During physically aggressive interactions, larger neck girth gives increased strength in headbutting and pushing of competing males. For example, male fallow deer who have larger necks have prolonged rutting sessions and are therefore more likely to be victorious in comparison to males with smaller necks (Jennings *et al.*, 2010). Significantly larger neck muscles in fallow deer are also valuable in supporting the seasonal growth of antlers (Alvarez, 1990 and Alvarez, 1995). In this case the larger neck girth in male hippos could be a correlation with other added characteristics which require muscular support - for example, larger teeth (Laws, 1968). Analysis of the width between the canines and jaw length suggest adult males have a statistically significantly wider and longer lower jaw compared to females, with males having longer and wider jaws throughout development regardless of overall body size. However, once again these mean dimensions for males and females are separated by 2-3 cm, and therefore more detailed study should be done to validate these findings and confirm early data collection techniques have not influenced these results.

This difference in canine width and jaw length between males and females could suggest that male hippos are using the width of their snouts and possibly their entire skulls to signify dominance and fitness within their social groups. This would mirror the strategies employed by male African elephants with their height (Rasmussen *et al.*, 2007) or an elephant seal with their larger size and elongated proboscis (McCann, 1981). Larger facial features may be more beneficial to this species due to their semi-aquatic nature. As previously discussed, the head and top of the body of hippos are sometimes the only areas visible during the day. If female choice is implemented at all in the reproductive behaviour of this species, a wider head or snout may be perceived as more attractive and symbolic of dominance and greater fitness. Similarly, as hippos often open their mouth to a wide angle and clash their open jaws in fights for dominance. A larger lower jaw length and wider canine width is likely to be more intimidating and benefit the individual when it comes to competing for access to females. Male badgers (*Meles meles*) are said to have a significantly different jaw size and shape (Wiig, 1986) which is suggested to be beneficial during their intraspecific competitions to gain access to females (Peter and Roper, 1988). Similarly, female grey mouse lemurs have a significantly wider and taller head morphology, used during their predation of larger prey species due to their increased bite force (Thomas *et al.*, 2015). Although male hippos do not seem to have a different diet to females, an increased jaw width and length may increase bite force. Thus, providing an advantage during intraspecific competition; much like within badgers.

Average lower jaw mass is significantly different between the sexes with male lower jaws being on average 3.6kg heavier. This difference equates to adult males on average having 42% heavier lower jaws than females. Once again, as we have no data collected on the size of the canines and incisors of this species, it is therefore suggested this higher mass in male lower jaws is correlated to larger weapons such as canines and incisors. The results of the GLM also suggested that the effect of overall body size on the development of jaw mass is significantly affected by sex, and that males are investing more energy into developing heavier lower jaws, and possibly larger canines and incisors. This suggestion is one of the most interesting results to come from this investigation, as it suggests there is some level of sexual dimorphism present within this species. These findings also support Law's (1968) work into the dentition and ageing of hippos, where it's stated the combined incisor and canine weights of adult females were significantly lower than males. In Law's findings males' canines were in most cases double the mass of females, which again supports the 42% higher jaw mass found in males within this analysis. The use of their canines and incisors within aggressive interactions, suggests a parallel to rutting behaviour in other ungulates (Yoccoz *et al.*, 2002). It's clear that much like other social species, the hippo uses aggression to compete for dominance and mate acquisition (Tsi *et al.*, 2011). As large weapons are beneficial to achieving victory in these social behaviours, the enlarged canines and incisors could have developed within the males to enhance their chances of reaching dominant and powerful positions within a herd (Perry, 2015). As females have less use for elongated canines and incisors, except for small fights with neighbouring females and to reject a male's advances (Blowers, 2008), they may not acquire the same benefits associated with developing much larger teeth.

Although sexual size dimorphism analysis of body mass did not produce the extensively large difference expected from the initial literature study, it is pertinent to this analysis to theorise why males may have chosen to invest in larger weaponry instead of larger body size. Looking at the suggestions formed from the results and the literature of similar species used in our preliminary hypothesis, it could be argued that the pressures for larger body size in males is found primarily in species who partake in social/sexual behaviour out of the water (Bonnet *et al.*, 2010). In these species, social interactions use body mass tactically through intimidation and/or mounting (Lindenfors and Tullberg, 2011). However, many marine species show high levels of sexual size dimorphism, such as Chinese river dolphins (*Inia geoffrensis*) and sperm whales (*Physeter macrocephalus*) (Martin and Da Silva, 2006). The high level of sexual size dimorphism found within these species, is said to be driven by intense male-male competitions

for mating rights (Connor *et al.*, 2000). This suggests the benefits of sexual size dimorphism can be translated to aquatic animals. Although sexual selection is noted in species who are fully marine, the hippos underwater social communication is predominantly vocal (Barklow, 2004), this may be due to a lack of clear vision in muddy water. Similarly, hippos spend the majority of their time with their heads out of the water, unlike marine mammals who are completely submerged. Therefore, any hippo characteristics covered by the water may not be as easily seen by other individuals in the area, thus making them less effective in sexual selection. Although aggressive acts such as breaching and leaping toward each other may be effective and intimidating with a large body mass, it is not the main form of aggression used in mating and territorial displays (Eltringham, 1993). The clashing of their large heads and mouths, and specifically ferocious and large canines and incisors, is often the major use for intimidations and sexual coercion (Fazal *et al.*, 2014). Females irregularly partake in these teeth clashes, while males use these behaviours for important territory defence and within courtship. Its perhaps possible that the hippos sexually dimorphic traits are more similar to species who also use their large weapons to establish dominance, such as other smaller ungulates like deer (Bro-Jørgensen, 2007 and Janis, 1982). Comparison with other ungulate species who use weapons, such as deer species (Alvarez, 1990) suggests male hippos may have developed the larger necks, jaws and teeth to benefit them through aggressive interactions, while females lack these behavioural pressures, resulting in sexual dimorphism found within secondary sexual characteristics.

The dataset does have some limitations which should be taken into account when interpreting the results. Firstly, a link between jaw mass and the canines and incisors has been made in order to interpret the investment into weapons within this species. Ideally, further analysis would be made with a more thorough and complete dataset, using measurements such as canine and incisor length. Similarly, not all the important measurements were taken for every individual, and gaps lead to a substantially smaller dataset when individuals without specified measurements were removed. Secondly, the data which was taken by Dr Laws and his team over five years does have some precision issues. Not all measurements will have been precisely taken within such a large data collection operation. Within environments where the carcasses were being chopped up quickly and efficiently for meat to be sold, imprecision with taking measurements is to be expected (Laws, 1968). Only 207 of the individuals had their jaws cleaned and dried to be analysed in more detail. In a perfect scenario, each individual would be assessed with the same precision. This limitation however is counteracted by the scale of

data laws was able to achieve in his collection, as not many other studies have over 3,000 hippos to analyse. In further studies, an improvement could be made by finding a medium of both quantity and quality to produce the most reliable results. As well as more precision throughout data collection, other important notations should be valued such as marking pregnancy or nursing. This would allow the data to be altered to produce a dataset without misleading measurements which may come from pregnancy or illnesses. Thirdly, the individuals sampled who have the largest collection of measurements are more commonly found within the age range of 10-30, leaving the youngest and oldest populations under-represented. To give an accurate analysis of the development of this species, more thorough analysis should be taken into all age groups. Lastly and possibly most importantly, to complete a thorough investigation behavioural data should be gathered to identify if the sexual dimorphisms found benefit the individuals. This would allow more information to be gained into the benefits of specific morphological differences between the sexes and allow better insight into the drivers behind the species sexual dimorphism. Along with behavioural data, phylogenetic mapping and PGLS analysis should also be implemented when analysing the trends in sexual size dimorphism within similar species. This type of analysis would allow the presence or absence of sexual size dimorphism to be studied while controlling for the phylogeny of the study species, and how phylogenetic relationships have contributed to the physical appearance of this species rather than sexual dimorphism related pressures.

Conclusion

To conclude, the hypothesis of a much larger body mass within male hippos has to be rejected as there seems to be little significant difference between the sexes mean adult body masses. Although there is some difference in the mass, height and body length of the adult hippos, the differences found are substantially smaller than initially predicted, particularly when compared with other large herbivores. This is because Rensch's rule and the similarities to other dimorphic species, suggested a high level of sexual size dimorphism in hippos; especially within body mass. The hippos highly polygamous and territorial nature parallels species who exhibit huge differences between the sexes, such as elephants and many *pinnipeds*. The males of these species exhibit characteristics beneficial to their competitive interactions; such as increased body mass, in order to achieve reproductive success.

It is theorised that these deviations from the expected trends in sexual size dimorphism are related to the hippo's semi-aquatic nature. This is due to body size being less important in

the success of competitions and not visually evident to other members of the herd when wallowing in water sources. Other secondary sexual characteristics such as jaw and head size may be more effective in displaying aggression or dominance even when submerged in water. The results support this suggestion, showing a significant difference between the sexes in the jaw and neck of hippos. With males having 42% heavier jaws on average to females, it's clear there are separate pressures implemented on the sexes causing such a large diversion in jaw and neck development. Considering the polygamous and social behaviour of this species, it's suggested these larger jaws in male hippos are developed due to the benefit of increased aggressive ability, which in turn leads to improved social dominance and reproductive opportunities much like within rutting deer.

With a larger scope of research into this species, more detail should be uncovered into the extent of sexual dimorphism and its related benefits. Behavioural data should uncover the effect of larger canines and incisors within males of this species and help identify any direct costs associated. As this species has a specialized niche i.e. their semi-aquatic nature, any sexual dimorphisms present may help identify the drivers involved in the evolution of sexual dimorphism. Possibly even allowing the cause of sexual dimorphic traits in other species to be more easily identified.

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