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Rensch's Rule and the Drivers of Sexual Dimorphism in Ungulates

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Award date: 2021

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# Rensch's Rule and the Drivers of Sexual Dimorphism in Ungulates

Eleanor Roylance-Casson

A thesis submitted for the degree of Master of Science by Research (MScRes) in Biological Sciences

Bangor University



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# Acknowledgements

Firstly, I would like to thank Dr Graeme Shannon for their invaluable guidance and support throughout the project.

I would also like to thank my family and friends for their encouragement, support and help with proof reading.

Many thanks go to Leo Coucher for their continual enthusiasm and providing much needed reassurances and coffee whenever I hit a mental block.

I would like to extend my gratitude to my examiners, both Dr Joanna Smith and Dr Alan McElligott, for their invaluable and insightful comments and feedback.

# Abstract

Rensch's rule states that in species with male-biased sexual dimorphism the differences in body size will be most pronounced in larger species, while the opposite is true in species with female-biased sexual dimorphism. There is conflicting evidence in the current literature concerning whether ungulates (hoofed mammals) follow Rensch's rule. There are two primary forms of sexual dimorphism in ungulates, sexual size dimorphism (SSD) in body mass, and secondary sexual characteristics (SSC) in their weaponry. In this study, data were extracted from the literature for 334 species of ungulates to determine whether they follow Rensch's rule, either in terms of their SSD or SSC. The magnitude of sexual dimorphism was measured and represented by a sexual dimorphism index (SDI). While consistency with Rensch's rule was determined by whether the slope of the allometric relationship between male and female body size exceeded one.

The results from this study demonstrated that ungulates follow Rensch's rule for body mass but not weaponry length. Different ecological variables; habitat type, foraging strategy and social grouping, were shown to have a significant effect on the SSD exhibited by ungulates, but only habitat type and social grouping had a significant influence on SSC. When groups of ungulate species defined by their ecological variables were tested for allometry to Rensch's rule independently, the body mass of grazing and omnivorous species along with gregarious and sexually segregated species were found to be inconsistent with Rensch's rule. Although they are sexually dimorphic groups of ungulates, the cost of increased SSD with species mass outweighed any benefits to their reproductive success. When the weaponry length of ungulate groups was tested independently, they were still found to be inconsistent with Rensch's rule. These dimorphic weapons are multipurpose and so there are different selection pressures beyond reproductive success influencing the relationship between species mass and sexual dimorphism. It is the finding of this study that the SSD of ungulate species exhibiting male-biased sexual dimorphism are greater in larger species and those with female-biased SSD express greater dimorphism in smaller species. Furthermore, that this trend is driven by the social structure, habitat type and foraging strategy of the species.

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# **Chapter 1: A Review of the Current Literature**

# Ungulates

An ungulate has classically been defined as a "hoofed" mammal (Groves & Grubb, 2011). A hoof is considered to be a hard keratin structure at the end of a toe, it differs from a nail or claw as it supports the weight of the animal during locomotion (Chapman, 2013; Hamrick, 2001). Ungulates are often referred to as a clade, Ungulata, with the species falling within two orders. The order Perissodactyla contains the odd-toed species and the order Artiodactyla contains the even-toed species. The orders Hydracoidea, Proboscidae and Tubulidentata are referred to as near-ungulates or paeungulates (Estes, 2012; Janis, *et al*, 1998). The paeungulates hoofs are "poorly defined" (Sale, 1960) and considered to be more like nails rather than hoofs, hence these orders are not included in the clade Ungulata (Groves & Grubb, 2011).

The phylogenetic definition of an ungulate is not clear-cut, for example the order Artiodactyla contains the family Cetacea, which are generally not considered to be ungulates. More recent studies into their evolutionary and genetic composition have shown that the cetaceans are in fact evolved from Artiodactyls (Gatesy, *et al*, 1999; Shimamura, *et al*, 1997), with many referring to this new order as Cetartiodactyla (Asher & Helgen, 2010). For the purposes of this review (which focuses on terrestrial species), the hybridised name will not be used, and they shall be referred to as their original separate orders, Artiodactyla and Cetacea.

### The Re-classification of Ungulate Taxonomy

In the last 20 years, a number of studies have developed lists of ungulate species using different types of classification methods. This process of re-classification has caused considerable debate about an ungulate species list with a wide range of proposed taxonomic rankings. Wilson and Reeder (2005), quoted 252 extant species whereas a more recent study Ungulate Taxonomy, Groves and Grubb (2011), list 477 extant species. This near doubling of species caused a taxonomic debate on what is considered an ungulate, and the best method for species determination (Cotterill, *et al*, 2014; Groves, 2013; Heller, *et al*, 2013; Zachos, *et al*, 2013). When determining taxonomy, it is crucial to consider both the morphological and ecological characteristics of clades (Bibi, 2013). The majority of the classification debate can be split into two distinct groups. Those who tend to "lump"

subspecies together as one species and those who have a tendency to "split" species by elevating subspecies to the rank of species (Zachos, 2018). The use of different classification concepts leads to different definitions of species with different taxonomists championing the use of their preferred concept. Studies warn that the phylogenetic species concept, used in Ungulate Taxonomy, leads to more "splitting" than is accurate (Zachos, 2015). Vilstrup, *et al*, (2013) used mitochondrial phylogenetics to confirm many of the newly classified subspecies of equids proposed in Ungulate Taxonomy. The most widely accepted species lists are those that use conciliant classification, which use both morphological and molecular evidence (Cotterill, *et al*, 2014).

Generating a species list is an important process for many different reasons, one being that if a group of animals are defined as a species they become affected by legislation (Isaac, et al, 2004). With more species across the globe becoming endangered, threatened and extinct in the wild, it is now more important to conserve vulnerable species and re-classifying a subspecies as a species is one way to access more protection (Morrison, et al, 2009). Having a consistent species list across different orders enables wider comparisons between species, as a species is a fundamental unit for macroevolution (Aldhebiani, 2018; Isaac, et al, 2004). Unfortunately, the re-classification process of different species lists can lead to taxonomic inflation (Alroy, 2003; Isaac, et al, 2005). Taxonomic inflation is often biased towards the ease of studying the populations along with their charisma (Isaac, et al, 2004). This means it can mislead biodiversity hotspots when subspecies are defined as species, it makes well studied areas appear "hotter", this can lead to a masking of extinction events in other locations (Karl & Bowen, 1999; Myers, et al, 2000). It has been argued that the taxonomic inflation on ungulates isn't evenly distributed as a majority of the new species are within the family Bovidae (Heller, et al, 2013). With many ungulate genera now significantly smaller than others, they may miss out on being studied & protected.

#### The Importance of Ungulates

Ungulates are widely dispersed geographically and are morphologically diverse, providing some of the most recognisable species in the world. Many have been domesticated or selectively bred and used for human benefit (Bökönyi, 1989). Due to their variety, when ungulate species are discussed and studied they are often grouped together by their diet, habitat, social structure, seasonal variation and predator responses (Jarman, 1974).

The varying diets and foraging strategies of ungulates has led to different dentition and cranial morphology. For example, wider muzzles have evolved for grazing in open and mixed

habitats; however, this is not an exclusive trait to these species alone (Mendoza & Palmqvist, 2008). The hypsodonty index along with the length of the jaw and muzzle width can be used to shed light on the feeding preferences of extinct ungulates (Mendoza & Palmqvist, 2008). The primary constraints on forage intake of ungulates are forage quality and availability (Bergman, *et al*, 2001). Ungulates are commonly grazers and browsers, and have an important impact on their ecosystems as they affect nutrient availability and vegetation structure. These herbivores modify primary production, nutrient cycling, patch dynamics and abiotic disturbance (Augustine & McNaughton, 1998; Hobbs, 1996; Sinclair, 2003). Vegetation communities can be significantly altered by ungulates when their top predators are removed from the ecosystem (Laliberte & Ripple, 2004). Due to their effect on their environment, both as herbivores and as prey for larger species, ungulates are often considered keystones species (Sinclair, 2003). This can be seen with the wildebeest in the Serengeti, as their removal from the environment has been shown to have a direct impact on the grass density and lion populations (Sinclair, 2003).

Migration is often used to maximise resource availability and to avoid seasonal resource scarcity (Hebblewhite & Merrill, 2009). Many ungulates are migratory, for example the blue wildebeest, meaning that the ecosystems affected by an ungulate can be considerably large. Many ungulates have a seasonal migration pattern whether it is for feeding or breeding purposes, being a migratory ungulate increases the efficiency of resource use and it means that they are less vulnerable to regular predation (Fryxell, et al, 1988). Migrating ungulates reduce exposure to predation by 70% compared to non-migratory ungulates (Hebblewhite & Merrill, 2009). Areas foraged in by migratory elk contained higher quality food. As a counterstrategy to migration, non-migratory elk lowered their predation risk by foraging in areas closer to humans that predators avoid, they traded off lower food quality for lower predation risks (Hebblewhite & Merrill, 2009). Many non-migratory ungulates exhibit morphological seasonal changes, Northern American ungulates show seasonal differences depending on their location. Mainland populations have a reduced body size and increased fecundity with winter warming whereas maritime region populations have an increased body size and reduced fecundity with winter warming. In these species their phenotype and demographic variables are tied to the North Atlantic Oscillation (Post & Stenseth, 1999).

Ungulate population numbers have yearly fluctuations, caused by environmental variability that influences food supply and animal condition, changing annual fecundity and mortality numbers (Caughley, 1970). A steady increase in population number for two generations followed by a sudden decline is called eruptive fluctuation, these are well known in well-

established populations and in populations caused by recent liberation. These eruptive fluctuations are common in ungulate populations. An example of this is in the Himalayan thar, *Hemitragus jemlahicus*, their populations numbers swelled due to an increase in food availability, however with increased population sizes the populations increased foraging caused food scarcity, increasing the mortality rates (Caughley, 1970).

### **Ungulate Threats and Conservation**

Many species of ungulate are classified as endangered, with some now extinct in the wild, most notably the recent wild extinction of the Northern White Rhino (Fletcher, 2020). Ungulates have lost a large portion of their population range, which has been caused by human settlement and development (Laliberte & Ripple, 2004). Trophy hunting and game ranching of ungulates is often proposed as a means of conservation in Africa. However, the trophies desired are mainly male, this will lead to populations with lower female fecundity (Ginsberg & Milner-Gulland, 1994).

The expansion of highways and roads can fragment natural habitats and thus decrease the viability of ungulate subpopulations, and impact migration paths (Bruinderink & Hazebroek, 1996). Wild ungulate ranges are likely to contract in areas of higher human influence (Laliberte & Ripple, 2004). This is reflected in Northern American biomes, the temperate grasslands and broad-leaf mixed forest, which have a higher human population, have lost the highest number of ungulate species. Whereas, the boreal forests and tundra, that have a lower human population have lost fewer ungulate species (Laliberte & Ripple, 2004).

Interbreeding subspecies can be used as a genetic rescue to continue a viable population. This interbreeding can occur through relocation of wild animals or the reintroduction of captive individuals into a wild population. However, this is not always simple in ungulate species as their species definitions are oversimplified which can lead to genetic incompatibility. For translocations and genetic rescue programmes to be carried out there must be accurate taxonomy available (Gippoliti, *et al*, 2018). With these interbreeding and genetic rescue programmes using members of the same subspecies, how related individuals are should be a primary focus to prevent inbreeding. Inbreeding leads to high juvenile mortality, this has been tested thoroughly in captive populations (Ralls, *et al*, 1979). A species' chance of being successful once reintroduced into the wild after being bred in captivity is hindered by genetic chances that could occur within captive breeding. The best way to avoid this genetic adaptation is to reduce the number of generations the species spend in captivity (Williams & Hoffman, 2009).

# **Sexual Dimorphism**

Sexual dimorphism occurs when one sex expresses a trait differently to the other beyond their primary sexual characteristics (Jarman, 1983; McPherson & Chenoweth, 2012; Pérez-Barbería, et al, 2002). Sexual dimorphism can be morphological and/or behavioural (Kunz, et al, 1996). There are two common forms of sexual dimorphism in mammals; differences in body size, sexual size dimorphism (SSD), and differences in colouration or exaggerated weaponry, secondary sexual characteristics (SSC) (Jarman, 1983; Kunz, et al, 1996; McPherson & Chenoweth, 2012; Pérez-Barbería, et al, 2002). If the sexually dimorphic trait is exhibited or more developed primarily in males it is referred to as a male-biased sexual dimorphism. Whereas if the females of the species exhibit the dimorphism, for example if they are larger than the males, the dimorphism is referred to as female-biased sexual dimorphism. Many ungulates exhibit sexual dimorphism with a difference in body size, weaponry and colouration (Pérez-Barbería, et al, 2002). Horns, antlers, tusks and welldeveloped canines are present in many species of ungulate, either in one or both sexes (Bro-Jørgensen, 2007). These weapons are used in sexual selection as well as for defence against predators and for non-aggressive behaviours, e.g. the long incisors of the common hippopotamus are used for digging roots and tubers out of the ground (Caro, et al, 2003; Laws, 1968).

Sexual dimorphism is physiologically caused by the evolution of diverging growth patterns of the sexes (Isaac, 2005). Sexual dimorphism arises through competitive sexual selection, the selection pressure can be intrasexual and/or intersexual (Loyau, *et al*, 2005; Moore, 1990). When a certain trait aids in reproductive success, it is more likely to be passed on to the individual's offspring, who then in turn become more reproductively successful from the inherited trait. This process continues to a point where one of the sexes have developed a quantifiably different trait to the other.

Sexual dichromatism occurs within mammals, with males tending to be more colourful than females (Cooper & Hosey, 2003; McPherson & Chenoweth, 2012). There are multiple reasons for this dimorphism, primarily the more colourful males of the species are more likely to have a low parasite burden and be healthier (Hamilton & Zuk, 1982; McPherson & Chenoweth, 2012). Their vibrant pelage also acts as an indicator of fitness as they have evaded predation despite being more conspicuous than their duller male conspecifics (Zahavi, 1975). With less conspicuous females gaining an anti-predation advantage (Geist, 1977). An example of sexually dimorphic pelts can be seen the dark facemasks of the male eland (Bro-Jørgensen & Beeston, 2015; Caro, 2005). This dimorphism goes beyond presence and absence. The males with the darker facemasks and larger face brushes are selected by the females as it indicates a higher level of testosterone, and increased health compared to males with lighter facemasks (Bro-Jørgensen & Beeston, 2015).

#### The Drivers of Sexual Dimorphism

When investigating sexual dimorphism, it is crucial to understand what is driving its evolution within the species, this provides insight into how the dimorphism is aiding reproductive success. The drivers of variation within the sexes as well as between them should be considered for a full understanding of sexual dimorphism (Blanckenhorn, 2005). The evolution of sexual dimorphism can be explained by the selective pressures of; sexual selection, fecundity selection, parental role division, differential niche occupation between the sexes and interference competition, throughout the species life history (Plavcan, 2001; Rico-Guevara & Hurme, 2018). However, there are normally multiple drivers of sexual dimorphism in a natural population (Hedrick & Temeles, 1989; Isaac, 2005; McPherson & Chenoweth, 2012). Additionally, it isn't just the sex expressing the dimorphic trait that drives the evolution of sexual dimorphism within the species (Moore, 1990). This can be seen in the evolution of leks, where the sexual dimorphism is male-biased but the mate selection is female dependent (Bro-Jørgensen, 2003; Clutton-Brock, *et al*, 1992).

The primary drivers for the evolution of sexual dimorphism in mammals are oriented around their social structure. The intersexual and intrasexual selection pressures affecting mammals orient around attracting a mate, undergoing intrasexual competition for resources and maintaining dominance over conspecifics, even when members of the opposing sex are not present (McPherson & Chenoweth, 2012). Different social structures lead to different selection pressures and thus differing types and magnitudes of sexual dimorphism. It is suggested that sexual dimorphism evolved in ungulates when they moved from occupying closed habitats to more open ones due to food availability (Pérez-Barbería, *et al*, 2002). This increased the average group size and caused a shift in mating system from monogamous to polygynous raising the selection pressures for reproductive success (Pérez-Barbería, *et al*, 2002). Polák and Frynta, (2009), found that species of ungulate inhabiting closed forest environments are generally monogamous and less dimorphic than those in open landscapes.

Intrasexual selection commonly arises when a species is polygynous, because within this reproductive strategy there is a hierarchy that leads to only the most dominant individuals

being reproductively successful. In a polygynous mating system - common in mammal species - there is a higher selection pressure on males, as nearly all females will reproduce in these mating systems but not all males will (McPherson & Chenoweth, 2012). The hierarchies within polygynous mating systems tend to be determined through aggressive displays that can then lead to fights. So, most dimorphic features in these species are weaponry and sexual size dimorphism which both directly impact the success of aggressive intraspecific interactions.

Sexual segregation refers to when the sexes of a species separate into two distinct groups, one with the mature males and the other consisting of females and juveniles (Mysterud, 2000; Ruckstuhl & Neuhaus, 2000). One cause of sexual segregation is through the asynchronicity of activity time budgets (Isaac, 2005; Ruckstuhl & Neuhaus, 2000). As the sexes evolve different foraging specializations caused by sexual dimorphism, it causes intersexual niche divergence, leading to sexually segregated species (Shine, 1989). The different foraging strategies caused by sexual dimorphism are commonly driven by the difference in nutritional requirements between the sexes, often females require higher quality food for lactation whereas males require higher forage biomass for maintaining a larger size, this can be seen in oryx and ibex (Ruckstuhl & Neuhaus, 2000). This type of social structure is most commonly seen in herbivorous mammals, with the sexes coming together during the breeding season. The frequency of this ecological segregation is greater among more dimorphic species of herbivores (Mysterud, 2000). There is a specific window for reproduction so the selection pressure is greater for the males, which invest heavily in traits that will provide an advantage during intraspecific aggressive interactions leading to a male-biased sexual dimorphism. This selection pressure can be observed in bighorn sheep who are seasonal breeders and one of the most sexually dimorphic species of ungulate (Festa-Bianchet, et al, 1996).

In general, monogamous and solitary mammal species are less sexually dimorphic (Ruckstuhl & Neuhaus, 2002). In this social structure the sexual selection pressures are interspecific rather than intraspecific with one sex choosing their mate rather than one sex directly competing for access to the other. This leads to be behavioural dimorphism and ornamentation rather than investment in weaponry and large size (Björklund, 1990; Hooper & Miller, 2008).

In species with male-biased sexual dimorphism, it is important to also consider the selection pressures on the females. Females are more likely to reach a breeding age earlier in these species as males grow for longer (McPherson & Chenoweth, 2012). Fecundity is a crucial

selection pressure with a relationship between body mass and fecundity present in many mammal species (Lindenfors, *et al*, 2007). The litter size of large mammals is negatively associated with species mass, it is also negatively associated with sexual dimorphism across all mammal taxa with more dimorphic species having smaller litter sizes (Carranza, 1996). The gestation length and weaning age of many offspring is greater in species with more sexual selection pressures, with male offspring having an even longer gestation length than females in many species (Lindenfors, *et al*, 2007; McPherson & Chenoweth, 2012; Olson, *et al*, 2009). There is a relationship between female condition and the sex ratio of offspring in many species of ungulates, this relationship is stronger in more dimorphic species. Female embryos are more likely to come to term than male embryos in a mother that is in poorer condition, this is tied to the longer gestation period of the male offspring in species with male-biased SSD (Sheldon & West, 2004). Where males spend resources on developing larger body sizes, females use those resources on fecundity, gestation and lactation (McPherson & Chenoweth, 2012).

#### **Sexual Size Dimorphism**

Sexual size dimorphism (SSD) is one of the most common forms of sexual dimorphism. It is the easiest to quantify and compare between different species. Resource availability, specifically the availability of food is vital to development and growth. Due to this, latitude influences SSD through seasonal food availability (Isaac, 2005). Likewise, population density controls food availability, within larger populations there will be increased competition for resources (Isaac, 2005). A significant consideration of sexual size dimorphism is the cost of developing and maintaining a large body size. In both mammals and birds, the juvenile mortality rate is higher for males than females as they are more susceptible to resource scarcity, as they have greater nutrient requirements to maintain a greater growth rate (Clutton-Brock, *et al*, 1985). The biggest cost to a large body size in ungulates is the difficulty in maintaining condition in areas of food scarcity. Therefore, the limit of ungulate body size is determined by the species' ability to extract nutrients while feeding at the point of lowest resource availability within their seasonal cycle (Illius & Gordon, 1992).

In mammals SSD is most commonly male-biased and is greatest within polygynous mating systems and species with overlapping home ranges, as intrasexual selection pressures and territoriality are increased (Lindenfors, *et al*, 2007; McPherson & Chenoweth, 2012). It is suggested that female-biased SSD arises from a reduction in male-male competition that then leads to a reduction in male body size (Isaac, 2005). Most species of primate exhibit

male-biased SSD, there are multiple drivers influencing this pattern of evolution. The more dimorphic species are larger, terrestrial species, with a polygynous mating system and a browsing folivorous diet (Cheverud, *et al*, 1985; Clutton-Brock, *et al*, 1977). Cheverud, *et al*, (1985), determined that one primate species will be more dimorphic than others if its ancestors were more dimorphic and if it has a greater species size. Additionally, primates have a larger body size when there are fewer competing species in the area, as this enables the species to focus on intraspecific over interspecific competition (Clutton-Brock, *et al*, 1977). A driver of small female size is argued to be that in changeable environments the smaller females have a younger breeding age (Clutton-Brock, *et al*, 1977). Musteloidea show a different trend in sexual dimorphism to other mammals, they exhibit greater SSD in smaller species. This is influenced by their feeding ecology, as an omnivorous and insectivory diet means that a polygynous mating system where a dominant male defends females isn't viable (Noonan, *et al*, 2016). Musteloids that live in pairs or groups show the least SSD, the less dimorphic species also have the larger litter sizes.

Ungulates contain species that exhibit female-biased SSD such as Madoqua phillipsi, Phillip's dikdik and Rhinoceros sondaicus, Javan one- horned rhinoceros, but those with male-biased SSD are far more common (Pérez-Barbería, et al, 2002). In some species of ungulate, there is a direct corollary between the ratio of males to females within the area to the body size of the males. An example of this being moose, *Alces alces;* male body size is greater in areas with additional bulls, whereas in an area with majority females the SSD is reduced (Garel, et al, 2006; Gould & Gould, 1989; McPherson & Chenoweth, 2012). Weckerly, (1998), demonstrated the association between mating systems and SSD in Simian primates and ruminants. They found that the ruminants with monogamous and territorial polygynous mating systems were less dimorphic than species that used harems. The body size of the ruminants were found to be influenced by the mating system more than the other species tested (Weckerly, 1998). The drivers of sexual dimorphism differ between domesticated species and their wild counterparts. Many domesticated species of ungulates show more pronounced SSD, livestock species such as cattle are selectively bred so that the males are larger and the females have increased fecundity (McPherson & Chenoweth, 2012; Polák & Frynta, 2010). However, the removal of natural selection pressures can have the opposite effect. For instance, wild species of goats and sheep are more dimorphic than their domesticated counterparts, this is caused by the increased pressure of male-male combat in the wild (Polák & Frynta, 2009).

#### **Secondary Sexual Characteristics**

SSC's are exaggerated features that aid in mate selection, these features may have little or no apparent additional survival benefits (McPherson & Chenoweth, 2012). They include but are not limited to, differences in colouration, ornaments, dominance traits and combat traits. A dominance trait is used to maintain and increase the individual's position within a hierarchy (Rico-Guevara & Hurme, 2018). A combat trait is a type of dominance trait, these aren't exclusively weapons as this group includes traits such as neck girth, thickened skin and larger muscles that benefit combat (Kunz, et al, 1996; McPherson & Chenoweth, 2012; Rico-Guevara & Hurme, 2018). For example, the male giraffe has a longer more muscular neck which provide an advantage in intrasexual fights (McPherson & Chenoweth, 2012; Simmons and Scheepers, 1996). SSC's can be identified by the fact that their development is tied to puberty. How developed they are can therefore often be used to age individuals (Kunz, et al, 1996). In most species, SSC's show the greatest morphological variety within a species, often being representative of the individuals body size and condition, requiring adequate resource availability to fully develop (Cotton, et al, 2004; Emlen, 2008; Emlen, et al, 2012; McCullough, et al, 2016). There is a high metabolic cost for developing and maintaining SSC's and a more obvious cost to male-male competition as this can often lead to injuries. There is also a cost and a stress associated with maintaining a dominant position within a population (McPherson & Chenoweth, 2012). For example, Setchell, et al, (2010), while studying Mandrills, P. spinx, found that the glucocorticoid level of the dominant male Mandrill was raised when in the presence of receptive females. SSC's can often provide additional advantages to the individual, for instance weapons are commonly used for antipredation in many species of mammals (McPherson & Chenoweth, 2012).

It can be difficult to distinguish between animal weaponry and ornaments due to a human visual bias (McCullough, *et al*, 2016). Weapons are defined by their use for interspecific combat and intrasexual fighting as well as being used as signals in aggressive and dominance displays (McCullough, *et al*, 2016; Rico-Guevara & Hurme, 2018). Intrasexually selected weapons (ISW) are weapons that have evolved to fight those of the same sex and species, they are more commonly found in males but not restricted to one sex (Rico-Guevara & Hurme, 2018). Whereas ornaments are purely aesthetic signals, they are also used in dominance displays but not in combat (Berglund, *et al*, 1996; Hunt, *et al*, 2009; McCullough, *et al*, 2016; Rico-Guevara & Hurme, 2018). One of the primary drivers for the evolution of weaponry is to defend spatially restricted resources (Emlen, 2008). Ornaments evolve within a mating system where copulation is determined by female choice over malemale fighting. Ornaments are more likely to evolve quicker than male weaponry as there is a

positive feedback cycle, known as the Fisher process, between female preference and genetic variation of ornaments (Andersson, 1994; McCullough, *et al*, 2016). Male weapons that evolve through intrasexual competition aren't influenced at all by female selection or preference and so their evolution is slower (McCullough, *et al*, 2016). Female preference is an important driver of speciation, their mate choice can affect gene flow to such a degree that it can become a direct barrier (Kraaijeveld, *et al*, 2011; Lande, 1892; McCullough, *et al*, 2016; Rodriguez, *et al*, 2013; Schluter & Price, 1993).

As weaponry evolved in mammals as a result of conflict, it is more developed within the more combative and aggressive sex, this can be towards conspecifics or predators (McPherson & Chenoweth, 2012). Males often possess weapons that are larger or lacking in female mammals. Some weaponry, such as antlers in cervids, are lost after the breeding season as they are primarily a tool for sexual selection rather than anti-predator behaviour (McPherson & Chenoweth, 2012). The most common type of weaponry within ungulates are horns, antlers and tusks. Many species of ungulate, especially equids and camelids, have sexual dimorphic canines that are found only in mature males of the species, (McPherson & Chenoweth, 2012; Niehaus, 2009). Given the vast variety of weapon forms, different weaponry types are used for different fighting styles. Shorter smooth horns are used by species favouring a stabbing style of fighting, curved, sturdy horns are used by ramming species and long, more complex weapons are used for wrestling and fencing (Geist, 1966; Lundrigan 1996; McCullough, et al, 2016). The physical makeup of these weapons differs to reflect the fighting style used, for example weapons used for wrestling need to be more flexible than those used for ramming (McCullough, et al, 2014; McCullough, et al, 2016). Both the ornaments and weaponry of ungulates increase at a greater rate than body size, the scaling exponentials within a species are within the range 1.5-2.5 showing a strong positive allometric pattern (Kodric-Brown, et al, 2006).

The only cervids where both sexes grow antlers are reindeer, *Rangifer tarandus* (Jarman, 1983). Reindeer antlers are used for different purposes by the sexes; the males use them for dominance during the breeding season then shed them, whereas the females of the species do not lose their antlers after the breeding season like the males (Jarman, 1983; McPherson & Chenoweth, 2012; Rico-Guevara & Hurme, 2018; Shah, *et al*, 2008). This is thought to be so that females have an advantage competing with the males in a resource scarce environment during the winter reducing the chances of infant mortality (McPherson & Chenoweth, 2012; Shah, *et al*, 2008). Studies into antlers have shown there is no correlation

between the complexity of antlers, measured by number of tines per unit of absolute length, and body size (Jarman, 1983).

Bovidae is an ideal study group for sexual dimorphism as they have a range of habitats, diets, social systems and body masses. Horns in bovids, which are less developed in females, aren't used primarily for predator defence, they are instead for intrasexual sparring (Bro-Jørgensen, 2007; Jarman, 1983; McPherson & Chenoweth, 2012). In bovids male horn length is positively associated with harem size and negatively with territoriality (Lundrigan 1996; McPherson & Chenoweth, 2012). There is little evidence indicating that the shape of bovid horns is affected by environmental factors (Caro, *et al*, 2003). The horns of female bovids increase proportionally to the size of the species, their horns are thinner than the males and are primarily for predator defence and for fighting over resources (Lundrigan 1996; McPherson & Chenoweth, 2012). It has been found that female bovids in exposed habitats have larger horns for predator defence. Whereas, small bovid species that rely on crypsis and live in dense habitats, have small or no horns (Jarman, 1983; McPherson & Chenoweth, 2012). Furthermore, monogamous solitary bovids have more simplistic straight horns, with bovids in polygamous groups exhibiting a wider variety of horn shapes (Caro, *et al*, 2003).

#### **Sexual Monomorphism**

Sexual monomorphism is considered to be the opposite to sexual dimorphism. Dimorphism occurs when the morphology of the sexes diverge so that one sex can increase its reproductive success; whereas monomorphism is when the sexes hav e a very similar morphology (Geist, 1977; III, *et al,* 1986). Sexual monomorphism appears more frequently in ungulate species that are smaller in size, territorial and monogamous, as both sexes need to be equally successful at resource defence (Geist, 1977). An example of monomorphism in ungulates can be seen in the African oryx, *Oryx gazelle,* this species' similar size is attributed to the near identical time budgets between the sexes, the only difference is seen when lactating females spend more time foraging (Ruckstuhl & Neuhaus, 2002).

## **Rensch's Rule**

Rensch's rule is used to explain the relationship between sexual dimorphism and species mass (Rensch, 1959). For species where males are larger than females, i.e. the sexual dimorphism is male-biased, the magnitude of sexual size dimorphism will increase with body

size; whereas the opposite is true for species where the sexual dimorphism is female-biased with sexual size dimorphism decreasing as body sizes increases (Abouheif & Fairbairn, 1997; Johnson, *et al*, 2017).

When investigating Rensch's rule it is impossible to ignore the contributions made to the field by Abouheif and Fairbairn (1997). The means by which they tested for allometry to Rensch's rule in different animal groups has since been used for the basis of testing whether species follow Rensch's rule. They perform a regression of independent contrasts of log(female size) and log(male size), where "a slope <1 indicates allometry inconsistent with Rensch's rule, a slope >1 indicates allometry consistent with Rensch's rule, and a slope of 1 indicates isometry" (Abouheif & Fairbairn, 1997). They analysed 21 different taxa for allometry to Rensch's rule and found that 33% were significantly allometric to Rensch's rule. Within this study it was concluded that ungulates had a weak correlation with Rensch's rule but that their findings were statistically non-significant.

#### Mammals and Rensch's Rule

Despite Rensch's rule being a well-established biological rule, there are large discrepancies between the results of different studies that analyse which species follow it. Mammals following Rensch's rule suggests that there are parallel selection pressures on body size on different species (Lindenfors, et al, 2007). As with many other orders that have been tested for allometry with Rensch's rule mammals show inconsistencies, with some families and genera found to be following the rule and others showing trends inconsistent with it. A study testing whether mammalian orders followed Rensch's rule discovered that only primates and diprotodonts showed significant allometry consistent with the rule (Lindenfors, *et al*, 2007). A recent study found that felids followed Rensch's rule whereas canids did not (Bidau & Martinez, 2016; Johnson, et al, 2017). It is argued that diet and resource dispersion promote social and mating systems that diminish the advantage of large male size, as it reduces the extent to which competition contributes to male reproductive success. It was found that the SSD exhibited was inconsistent with Rensch's rule (Bidau & Martinez, 2016). Furthermore, that the SSD didn't correlate with life history traits, but that this can be simply explained by the monogamous breeding system exhibited by this family (Bidau & Martinez, 2016; Johnson, et al, 2017).

Ungulates are highly dimorphic so it is suggested that they should follow Rensch's rule, they are even mentioned as examples of species that follow the rule in its first explanation, yet there is contradictory literature regarding whether ungulates follow Rensch's rule (Rensch, 1959). The nature of Rensch's rule means that domesticated species such as those within Caprinae and Bovidae have been selectively bred in such a way that they show allometry with Rensch's rule (Polák & Frynta, 2009; Polák & Frynta, 2010). As the males of the species are often bred to obtain higher body masses for their meat and the females of the species are selectively bred to increase their breeding frequency, and offspring count with low infant mortality. The allometry to Rensch's rule becomes more prominent with domesticated cattle species when the shoulder height of the species is used instead of mass (Polák & Frynta, 2010). This brings into question whether Rensch's rule applies only to mass in all species and whether the type of sexual dimorphism exhibited should be considered more closely within these analyses. As it has previously been demonstrated that often body size over body mass is beneficial to reproductive success in fallow deer, Dama dama (McElligott, et al, 2001). Similarly, the different types of measurement for body size other than mass was taken into account by a study researching SSD in swine, they used mass along with the wither's height (Parés-Casanova, 2013). They found that unlike other domesticated species, swine do not follow Rensch's rule. This is most likely caused by the different types of pressures that drove selective breeding, including that larger sows are better mothers and so there is a need for larger females as well as larger males.

Some studies on wild ungulates have found that ungulates have a statistically nonsignificant allometry to Rensch's rule (Abouheif & Fairbairn, 1997; Amado, *et al*, 2019; Lindenfors, *et al*, 2007). Whereas other studies report that ungulates follow Rensch's rule (Sibly, *et al*, 2011). Models designed to study the relationship between life history and body size in large herbivorous mammals, including deer and antelope, showed that they followed Rensch's rule (Sibly, *et al*, 2011). This demonstrates that female body size increases with female herd size, which drives male body size as they compete to dominate a female herd and gain mating rights (Sibly, *et al*, 2011). Indicating that Rensch's rule is determined by the ecological factors that govern group size, including foraging strategy and anti-predator behaviour. Cervids are named as examples of mammals that exhibit Rensch's rule (Rensch, 1959). However, further research has indicated that this is not the case (Amado, *et al*, 2019). It would appear that there are drivers of body size external to sexual selection and reproductive strategies that hold more influence in a species' size, for example resource dispersal and use (Amado, *et al*, 2019; Olalla-Tarraga, *et al*, 2015).

Although Rensch's rule is given the status of a biological rule many taxa do not show allometric patterns consistent with Rensch's rule. The question then arises as to why some species are a perfect model for Rensch's rule and others within the same clade are not. These inconsistent findings commonly occur when investigating whether ungulates follow Rensch's rule (Abouheif & Fairbairn, 1997; Amado, et al, 2019; Lindenfors, et al, 2007; Polák & Frynta, 2009; Polák & Frynta, 2010; Sibly, et al, 2011). Webb and Freckleton, (2007) argue that if only some exceptions follow Rensch's rule, should it really be considered a "rule" if it does not apply to the majority. They further state that Rensch's rule alone does not provide an independent scaling guide as additional variables and life-histories need to be considered, further reducing the validity of Rensch's rule (Webb & Freckleton, 2007). Many drivers of body size and sexual dimorphism are suggested to have an impact on the allometry to Rensch's rule, with many studies expressing that the difference in ecological pressures governing why some species of ungulate do not follow Rensch's rule (Amado, et al, 2019; Olalla-Tarraga, et al, 2015). The diet of the species and their foraging strategy impact the resources available for developing SSD, they also provide an incentive for SSC's to defend those resources from members of their own species and conspecifics (Colwell 2000; Johnson, et al, 2017; Sibly, et al, 2011; Székely, et al, 2004). The foraging strategies of African antelope and how this drives different social dynamics is often attributed as the origin of their sexual dimorphism (Pérez-Barbería, et al, 2002). The social system and group size of ungulates has a direct effect on the sexual selection pressures and anti-predation strategies (Bidau & Martinez, 2016; Colwell, 2000; Dale, et al, 2007; Frýdlová & Frynta, 2010; Herczeg, et al, 2010; Serrano-Meneses, et al, 2008; Sibly, et al, 2011; Székely, et al, 2004). The habitat type and quality have an influence on diet and social structure, while also providing its own limitations and pressures for sexual dimorphism (Frýdlová & Frynta, 2010; Serrano-Meneses, et al, 2008; Székely, et al, 2004). The sexes of many dimorphic ungulate species select habitats based on different requirements, females choose habitats to maximise offspring survival and males select one that meets their energy requirements for developing dimorphic traits (Main, 2008). Female fecundity and the cost of sexual dimorphism act as counterbalances for the benefits of increased sexual dimorphism (Colwell, 2000; Dale, et al, 2007; Frýdlová & Frynta, 2010; Parés-Casanova, 2013). To fully understand why there are inconsistencies with whether ungulates follow Rensch's rule, it is necessary to fully investigate how the drivers of sexual dimorphism and the different aspects of a species' life history affect allometry with Rensch's rule.

# Chapter 2: Rensch's Rule and the Drivers of Sexual Dimorphism in Ungulates

# Introduction

#### What is sexual dimorphism?

Sexual dimorphism occurs where the sexes of a species express different traits to overcome a selection pressure and increase their reproductive success (Jarman, 1983; McPherson & Chenoweth, 2012; Pérez-Barbería, et al, 2002). These traits can be both morphological and/or behavioural and can be expressed by either sex (Kunz, et al, 1996). Sexual dimorphism is most commonly male-biased in mammals (McPherson & Chenoweth, 2012). There are two major forms of sexual selection pressures acting upon a species; intersexual selection pressures and intrasexual selection pressures (Loyau, et al, 2005; Moore, 1990). In mammals, intrasexual selection pressures lead to members of the same sex directly competing with each other for mating rights (Rico-Guevara & Hurme, 2018), this is seen in the dominance hierarchies of gregarious species and harems, for example Hylochoerus meinertzhageni, the giant forest hog and Syncerus caffer, cape buffalo (Bowyer, et al, 2020; Jarman, 1983; McPherson & Chenoweth, 2012). Intersexual selection pressures in mammals can often rely on an individual guarding a resource-rich territory that will attract members of the opposite sex, for instance Certotherium simum, the southern white rhinocerous. These territorial individuals try to keep possible mates within their territory and expel any members of their own sex (Bowyer, et al, 2020; Forsyth, et al, 2005; Jarman, 1983; McPherson & Chenoweth, 2012; Pelletier, et al, 2006). Another form of intersexual selection in mammals can be seen in the form of leks, where males will rely on displays to attract a female into their territory; this can be seen during the rutting season of the lechwe and kob (Buechner & Roth, 1974; Schuster, 1976). It is these selection pressures that are the primary drivers for sexual dimorphism within a species. An individual that is better adapted to overcoming these selection pressures, for example a male with larger body size, will likely have greater reproductive success and pass on these traits to their offspring. Sexual dimorphism has associated costs to the individual that exhibits the exaggerated trait. Not only an energetic cost in developing and maintaining these traits but these exaggerated traits can make them more conspicuous to predators (Clutton-Brock, et al, 1977; Illius & Gordon, 1992). Some species have overcome this cost as their sexually dimorphic trait can

also be utilised in other aspect of their lives, for instance, some sexually dimorphic weaponry is used in anti-predator behaviour and foraging while simultaneously increasing reproductive success, examples of this can be seen in *Rangifer tarandus*, reindeer (Caro, *et al*, 2003; Laws, 1968; McPherson & Chenoweth, 2012).

There are two main forms of sexual dimorphism exhibited by mammals; sexual size dimorphism (SSD) and secondary sexual characteristics (SSC). SSD refers to one sex having a larger body mass than the other. This type of sexual dimorphism is advantageous for displays of dominance and provides a benefit to the individual during combat (Lindenfors, et al, 2007; McPherson & Chenoweth, 2012). However, there is an associated cost to developing and maintaining a larger body size; these individuals require a different diet, a longer gestation period and are more conspicuous than their smaller counterparts (Sheldon & West, 2004). SSC's often take the form of weaponry in mammals, which arise in multiple forms such as horns, antlers, claws and tusks (Bro-Jørgensen, 2007). Each weaponry type is specialised towards a different purpose, some are used in dominance displays and conspecific fighting, others are used for anti-predation and aid in foraging (Geist, 1966; Lundrigan 1996; McCullough, et al, 2014; McCullough, et al, 2016). For instance, the incisors of hippos are used to attract females and intimidate rivals, to defend against predators and to aid in digging for roots (Caro, et al, 2003; Laws, 1968). The benefits to survival mean that weaponry is commonly present in both sexes, with females utilising them in the protection of their offspring (Berger, 1995; Stankowich & Caro, 2009). As with SSD's, there is an associated cost to investing in sexually dimorphic weaponry, the cost being an increased nutritional requirement and a greater risk of being hindered when moving though denser vegetation (Metz, et al, 2018). Some species – such as deer - overcome these obstacles by developing weaponry that they shed after the breeding season (Caro, et al, 2003).

#### **Rensch's rule**

Rensch's rule is a biological rule proposed by B. Rensch in 1959 to explain the relationship between sexual dimorphism and species size. Although this biological rule was developed using birds as the model species, it has also been applied to a wide range of organisms, including mammals and invertebrates (Rensch, 1959). Rensch's rule states that in species with male-biased sexual dimorphism, the differences in body size between the sexes will be greatest in the larger-bodied species. The rule states that the inverse is true for species with female-biased sexual dimorphism, with greater sexual dimorphism evident in smaller-bodied species (Abouheif & Fairbairn, 1997; Rensch, 1959). This relationship is related to the hypothesis that the evolution of male body size isn't as restricted as females; as females are under the stabilizing selection pressure of gestation and offspring survival (Fairbairn, 1997). Since this rule was established, there have been many studies that have produced conflicting results; with many claiming that the rule is male-biased, as taxon's with femalebiased sexual dimorphism rarely follow the rule (Webb & Freckleton, 2007).

Ungulates are commonly referred to as examples of species that follow Rensch's rule, however there is inconclusive and contradicting evidence for this in the literature (Abouheif & Fairbairn, 1997; Amado, et al, 2019; Lindenfors, et al, 2007; Polák & Frynta, 2009; Polák & Frynta, 2010; Sibly, et al, 2011). Some studies have found that ungulates show allometry to Rensch's rule but with there are discrepancies between papers about the statistical significance of these findings (Abouheif & Fairbairn, 1997; Sibly, et al, 2011). Whereas, others show groups of ungulates - such as cervids and swine - breaking from Rensch's rule (Amado, et al, 2019; Lindenfors, et al, 2007; Parés-Casanova, 2013). Many domesticated species of ungulate have been shown to consistently follow Rensch's rule, which is unsurprising given the desired results that selective breeding has, especially when these species are bred for meat production (Polák & Frynta, 2009; Polák & Frynta, 2010). In domesticated situations, multiple natural barriers of exaggerated SSD are removed, for instance, the nutritional cost to develop and maintain a larger size. Additionally, they are raised in an environment with fewer predators and where terrain and density of vegetation are less restrictive. This allows the survival of individuals with exaggerated dimorphism that would have been a hinderance in the wild.

#### What are ungulates?

Ungulates are hoofed mammals, which contain species from the orders Artiodactyla, the even-toed ungulates and Perissodactyla, the odd-toed ungulates (Groves & Grubb, 2011). A study published in 2011 proposed a new species list of ungulates (Groves & Grubb, 2011). It suggested the addition of hundreds of new species and subspecies collectively. This has since sparked much debate as to the taxonomic classification of ungulates, with many looking to evolutionary patterns to determine the divergence of species.

The majority of ungulate species are sexually dimorphic, the dimorphism is commonly malebiased but there are a number of species with female-biased sexual dimorphism, in many of the smaller bovid and cervid species the females have a larger body mass than the males, such as *Madoqua kirkii*, Kirk's dikdik. There are also species of ungulate that don't exhibit any sexual dimorphism, for example *Connochaetes johnstoni*, Jognston's wildebeest. SSD and SSC's in the form of weaponry are common among ungulates and have been studied extensively (Bro-Jørgensen 2007; Kruuk, *et al*, 2014; McCullough, *et al*, 2016). Different forms of weaponry are adapted to different styles of combat, for instance, rounded horns are used in head to head charges and the more elaborate antlers are used in a fencing and wrestling style of combat (Geist, 1966; Lundrigan 1996; McCullough, *et al*, 2016).

Ungulates are a widely dispersed group of animals with species found across all continents (excluding Antarctica), ranging in size from 2kg to over 2000kg (Groves & Grubb, 2011) and displaying a broad range of social systems across different habitat types. Ungulates are either herbivorous or in some cases omnivorous and are often the key prey species for many carnivores. Ungulates are often considered to be keystone species within an ecosystem as they have a direct impact on the structure and condition of their environments (Augustine & McNaughton, 1998; Bergman, *et al*, 2001; Hobbs, 1996; Laliberte & Ripple, 2004; Sinclair, 2003). The IUCN Red List currently classified a third of ungulate species as vulnerable, endangered or critically endangered, with some species being extinct in the wild (IUCN, 2020). There are multiple threats to ungulate species, the most common being habitat loss and fragmentation, poaching and hunting (Bruinderink & Hazebroek, 1996; Ghoddousi, *et al*, 2019; Ginsberg & Milner-Gulland, 1994; Ito, *et al*, 2013). Many species of ungulate are targeted by trophy hunters for their large size and weaponry (Ginsberg & Milner-Gulland, 1994). Many species of ungulate have been domesticated and selectively bred for human benefit (Polák & Frynta, 2009).

One of the causes of inconclusive and contradictory findings when it comes to looking at the relationship between ungulates and Rensch's rule is limited sample size. It is the aim of this study to determine whether ungulates follow Rensch's rule, both for body mass and weaponry size. To remove the issue of sample sizes, this study tests Rensch's rule across as many species with published body mass available within published literature. It was predicted that as ungulates are highly sexually dimorphic with different species under contrasting sexual selection pressures, they will follow Rensch's rule for both weaponry and body mass. Additionally, this study aims to determine the effect that the drivers of sexual dimorphism have on both SSD and SSC and how this affects their allometry to Rensch's rule. The drivers of sexual dimorphism that were considered are the social organisation, habitat type and foraging strategy of each ungulate species. Given that social structure and reproductive strategy of mammals has been shown to affect sexual dimorphism, it was predicted that solitary and monogamous species would not follow Rensch's rule, but the more gregarious species would.

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# Methods

## **Data Collection**

This project focuses on species and not subspecies, as the classification of subspecies is an ongoing discussion among taxonomists (Heller, et al, 2013; Zachos, 2015). Domesticated species, as specified in Ungulate Taxonomy (Groves & Grubb, 2011), were not included in this study. Domesticated ungulates have been selectively bred to benefit humans (i.e. for the food industry or for transportation) and are not exposed to natural reproductive selection pressures and are therefore not representative of other wild ungulate species (Bökönyi, 1989). Whether ungulates follow Rensch's rule and how the drivers of sexual dimorphism affect this relationship was investigated by analysing different behavioural, ecological and morphological characteristics. Data for the following variables were extracted for each species of ungulate where available: the total average adult species mass (kg), the average adult male and female body mass (kg), the length of any male and female tusks, horns and antlers (hereon referred to as weaponry) (cm), social grouping and organisation (Table 3), habitat type (Table 1) and foraging strategy (Table 2). Succinct definitions were created for categorical variables (Table 1, 2 & 3) based on previous studies (Hofmann, 1989; Loison, et al, 1999; Leuthold & Leuthold, 1975; Mendoza, et al, 2002; Mendoza & Palmqvist, 2008).

Category	Habitat Type
Open Habitat	Treeless or Scarcely Wooded Savannah,
	Grasslands, Desert, Semi-Desert, Steppes,
	Alpine Meadows, Arctic Tundra, Arid and Barren
	Ground, Arid Country, Grassy Plains, Larva
	Plains, Grass Covered Hills, Dunes, Pastureland
Mixed Habitat	Wooded Savannas, Bushland, Open Forest,
	Forested Valley, Thickets, Ravines, Bushveld,

**Table 1.** Categories for ungulate species habitat type. These categories represent the common species habitat type across the year, they do not indicate habitat changes due to migration or breeding seasons. (Mendoza & Palmqvist, 2008)

	Kopjes, Forest Edge, Shrub Woodlands, Scrub				
	Savanna				
Closed Habitat	Closed Woodlands, Riverine, Moist Deciduous				
	and Evergreen Forest, Rainforest, Dense Acacia,				
	Dense Bamboo Forests, Taiga				

**Table 2**. Categories for ungulate species feeding type. These categories represent the average yearly diet of the ungulate species and do not specify any possible dietary differences between the sexes. (Hofmann, 1989; Mendoza, *et al*, 2002; Mendoza & Palmqvist, 2008)

Category	Diet Composition
Grazer	Grass represents >75% of their diet throughout the year
Browser	Diet consists of <25% grass, mainly eating leaves, bushes and flowering plants, above the ground level including on trees
Mixed Feeder	Grass consumption is between 25% and 75%, they also eat leaves and other vegetal matter throughout the year
Omnivore	Their diet is mainly non-fibrous vegetal matter, fungi and animal matter
Frugivore	Diet mainly consists of fruits (>50%) and other non-fibrous soft matter

**Table 3.** Categories for ungulate species social grouping. These categories represent the common species herd composition throughout the year; they do not specify any migration or breeding season differences. (Leuthold & Leuthold, 1975)

Category	Social organisations				
Solitary	Solitary species, breeding pairs, mother and				
	offspring pairs, breeding pair with offspring				
Sexually Segregated	Species with sex specific groups for the majority of				
	the year, i.e. maternal herds and bachelor herds or				
	solitary males				
Harem	Year-round maternal herds with a male present,				
	often with other males forming bachelor herds or				
	becoming solitary				

Gregarious	Year-round mixed sex herds, includes family herds,
	occasional small bachelor herds

Data were extracted using a systematic search approach in Google Scholar, Science Direct and the Bangor University online library catalogue. The same search terms (Table 4) were used in these three different search engines. These sites were selected to provide a wide variety of sources. Science Direct provides open access papers from scientific journals and Google Scholar provides books, journals and citations from a variety of different online sources. The Bangor University online catalogue provides results not only from their online sources but physical copies of journals and books available within the University libraries and from other institutions. Data sources were searched until five consecutive search-related result pages yielded no relevant data sources. The data collected from these sources was compiled together into a single database. An average value was calculated if the results gave multiple estimates or ranges of measurements for body mass and weaponry length. If contradictory data were found the most common and supported result was used. Due to the lack of studies and data scarcity for some ungulate species, there was no minimum number of sources, however, most species had an average of 3 different sources. Once the raw data were collected and the source recorded, the results were standardised to make comparisons possible. The sizes were converted into kilograms and centimetres, and the range of values averaged. The data collected and used within this study can be found within the appendices, Table i.

Table 4. The different terms and phrases that were used in a systematic search for specific sexual and	b
reproductive behavioural data on the species in the sample group	

Terms Used for Collecting Data	
Exact Phrase	At Least One of The Words
"ungulate" AND/OR "ungulate" AND/OR	body, mass, size, weight, horn, antler, tusk, length,
"hoofed mammal" AND/OR "perissiodactyla"	weapon, sexual, dimorphism, male, female, group, herd,
AND/OR "artiodactyla"	mating, breeding, habitat, territory, diet, feeding

### **Comparative analysis**

Allometry with Rensch's rule was tested following the methods of Abouheif & Fairbairn, (1997), which used a regression of log (female mass) against log (male mass). In this model, a slope >1 shows allometry consistent with Rensch's rule, <1 shows allometry inconsistent with Rensch's rule and a slope = 1 shows isometry. The significance of the

allometry to Rensch's rule is tested by whether the 95% confidence intervals overlap the boundary of value of 1. The body mass of 334 species were regressed to test for allometry to Rensch's rule along with the weaponry of 163 species. Allometry to Rensch's rule by different ecological categories was tested by regressing the species from 12 specific categories independently from the other species. These categories explore habitat type, foraging strategy and social organisation (defined in Tables 1, 2 & 3).

When investigating the drivers of sexual dimorphism, a standardised unit for dimorphism was used in the form of a sexual dimorphism index (SDI). The SDI was calculated using (Larger Sex)/ (Smaller Sex), with species of equal body mass producing a value of 1 (Lovich & Gibbons, 1992). The influence of habitat type, social structure and foraging strategy on SSD and weaponry length were tested using generalised linear models (Kruuk, *et al*, 2003). Separate models were used to test the influence of each ecological variable on body mass SDI and weaponry SDI. SDI represents the magnitude of sexual dimorphism and was used as the dependent variable across the models. The independent variables for these GLM's were habitat type, social organisation and foraging strategy. Specific categories of these ecological variables (Tables ,1 2 & 3) were used as a baseline for these models to provide a point of comparison.

# Results

Ungulate body mass shows allometry consistent with Rensch's rule, the slope of the log-log regression models is >1 (Table 5, Figure 1 & 2). This result indicates that in species with male-biased sexual size dimorphism, the difference in body mass between the sexes will be greater in larger species. Furthermore, in species with female-biased sexual size dimorphism, the females will be larger in comparison to the males the smaller the species. However, ungulate weaponry does not follow Rensch's rule with the relationship between log male and female weaponry length being <1 (Table 5, Figure 1 & 3). Ungulate species with both male and female biased SSC show a reduction in sexual dimorphism as species increase in size, breaking from Rensch's rule.



**Figure 1.** Allometric relationship between log male size and log female size of ungulate species. Body mass (kg) and weaponry length (cm) are distinguished and the line of isometry (slope = 1) is represented by the dashed line.

Additionally, many of the different life-history categories exhibit different allometries to Rensch' rule when tested independently (Table 5, Figure 2 & 3). Gregarious and sexually segregated species do not follow Rensch's rule for body mass, however, the solitary species and those that form harems do (Table 5, Figure 2). The body mass of species in all habitat types are found to follow Rensch's rule. The body mass of all foraging types follow Rensch's

rule apart from omnivores and grazing species (Table 5, Figure 2). Gregarious, sexually segregated and grazing species do not follow Rensch's rule for a lack of sexual dimorphism (Table 6), it is instead that the ratio of dimorphism to species mass does not change in a way consistent with this rule.

When the weaponry of different categories of ungulate species was tested independently they still break from Rensch's rule (Table 5, Figure 3). The magnitude of sexual dimorphism present in ungulate weaponry doesn't change with species mass regardless of sex bias.



**Figure 2**. The allometric slopes and 95% confidence intervals determining Rensch's Rule for different groups of ungulate species when considering the body mass of male and females. The dashed line represents the line of isometry, any slopes that are above 1 and their 95% confidence intervals do not overlap 1 follow Rensch's rule. The number of species used in each regression is included in parentheses.



**Figure 3.** The allometric slopes and 95% confidence intervals determining Rensch's Rule for different groups of ungulate species when considering the weaponry of male and females. The dashed line represents the line of isometry, any slopes that are above 1 and their 95% confidence intervals do not overlap 1 follow Rensch's rule. The number of species used in each regression is included in parentheses.

**Table 5.** Slopes and intercepts with their corresponding 95% confidence interval of the male to female regression used to calculate allometry to Rensch's rule across ungulates. The p-value refers to the significance of the slope from 1.

Group	Body Mass					Weaponry				
	Number of Species	Intercept (95% CI)	Slope (95% Cl)	p - value	Follow Rensch's Rule	Number of Species	Intercept (95% CI)	Slope (95% CI)	p - value	Follow Rensch's Rule
Ungulates (all species)	334	-0.03 (- 0.04, -0.01)	1.06 (1.05, 1.07)	2.20E-16	Y	163	0.49 (0.44, 0.55)	0.80 (0.76, 0.83)	2.20E-16	Ν
Gregarious Species	76	0.06( 0.02, 0.09)	1.01( 0.99, 1.03)	2.20E-16	Ν	44	0.88 (0.74, 1.03)	0.53 ( 0.44, 0.63)	2.15E-06	Ν
Species That Form Harems	31	-0.05 (-0.09, -0.02)	1.07 (1.05, 1.08)	2.20E-16	Y	14	0.10 (-0.14, 0.34)	1 (0.85, 1.14)	1.72E-05	Ν
Sexually Segregated Species	98	0.22 (0.17, 0.28)	0.96 ( 0.93, 0.99)	2.20E-16	Ν	56	1.15 (1.00, 1.30)	0.44 (0.34, 0.53)	4.90E-05	Ν
Solitary Species	124	-0.06 (-0.07, -0.04)	1.06 (1.05, 1.07)	2.20E-16	Y	46	0.42 ( 0.38, 0.46)	0.74 (0.69, 0.78)	2.20E-16	Ν
Species in Closed Habitats	97	-0.05 (-0.07, -0.03)	1.05 (1.04, 1.06)	2.20E-16	Y	44	0.40 (0.36, 0.44)	0.74 (0.70, 0.78)	2.20E-16	Ν
Species in Open Habitats	133	0.00 (-0.03, 0.04)	1.06 (1.04, 1.08)	2.20E-16	Y	74	1.14 (1.01, 1.27)	0.42 (0.34, 0.51)	3.40E-06	Ν
Species in Mixed Habitats	102	-0.01 (-0.04, 0.03)	1.05 (1.04, 1.07)	2.20E-16	Y	43	0.70 (0.57, 0.83)	0.66 (0.57, 0.74)	1.61E-09	Ν
Browsers	87	-0.05 (-0.07, -0.03)	1.06 (1.05, 1.07)	2.20E-16	Y	28	0.39 (0.30, 0.48)	0.83 (0.75, 0.90)	6.01E-11	Ν
Frugivores	14	-0.13 (-0.16, -0.10)	1.08 (1.05, 1.10)	7.69E-15	Y	9	0.54 (0.45, 0.63)	0.59 (0.44, 0.74)	6.22E-03	Ν
Omnivores	20	0.03 (-0.04, 0.11)	0.97 (0.91, 1.02)	1.02E-12	Ν	12	0.32 (0.20, 0.45)	0.85 (0.71, 0.98)	1.05E-04	Ν
Grazers	103	0.14 (0.10, 0.18)	0.99 (0.97, 1.01)	2.20E-16	Ν	60	1.17 (1.03, 1.30)	0.39 (0.31, 0.47)	1.66E-05	Ν
Mixed Feeding Species	108	0.01 ( -0.03, 0.04)	1.06 (1.04, 1.08)	2.20E-16	Y	51	0.81 (0.62, 1.00)	0.62 (0.48, 0.75)	3.11E-05	Ν

Ungulate species exhibit a greater magnitude of sexual dimorphism through their weaponry than their body size, shown by their sexual dimorphism index (SDI) (Table 6).

Group	Body Mass		Weaponry			
	Number of		Number of			
	Species	SDI (±SE)	Species	SDI (±SE)		
Ungulates (all species)	334	1.27 (±0.02)	163	1.99 (±0.11)		
Gregarious Species	76	1.25 (±0.02)	44	1.89 (±0.25)		
Species That Form Harems	31	1.19 (±0.03)	14	1.32 (±0.13)		
Sexually Segregated Species	98	1.49 (±0.04)	56	2.51 (±0.22)		
Solitary Species	124	1.13 (±0.02)	46	1.70 (±0.13)		
Species in Closed Habitats	97	1.15 (±0.02)	44	1.61 (±0.10)		
Species in Open Habitats	133	1.32 (±0.03)	74	2.36 (±0.21)		
Species in Mixed Habitats	102	1.32 (±0.03)	43	1.81 (±0.19)		
Browsers	87	1.18 (±0.02)	28	1.84 (±0.22)		
Frugivores	14	1.10 (±0.03)	9	2.16 (±0.23)		
Omnivores	20	1.19 (±0.07)	12	1.70 (±0.18)		
Grazers	103	1.33 (±0.03)	60	1.88 (±0.18)		
Mixed Feeding Species	108	1.33 (±0.03)	51	2.30 (±0.25)		

**Table 6**. The mean SDI and standard error for ungulate species, when body mass is taken as the dimorphic trait and when weaponry length is taken as the dimorphic trait.

When comparing the average SDI of each habitat type it can be seen that ungulates in open habitats are more dimorphic and species in closed habitats are the least dimorphic, both in body size SDI and weaponry SDI (Table 6, Figure 4 & 5). The models focused on habitat type showed that mixed habitats and open habitats have a significant positive effect on body mass SDI, demonstrating that ungulate species in more open habitats will have a greater difference in body mass between the sexes (Table 7). Closed and mixed habitats both have a significant negative effect on weaponry SDI, indicating that the weaponry of species in open habitats will be more dimorphic (Table 7).



**Figure 4.** The average body mass SDI value and corresponding standard error for different groups of ungulate species, the number of species within each group is included in parentheses.



**Figure 5.** The average weaponry length SDI value and corresponding standard error for different groups of ungulate species, the number of species within each group is included in parentheses.

Mixed feeding species have the highest SDI for both body mass and weaponry lengths with frugivores and omnivores showing the least dimorphism for body mass and weaponry respectively (Table 6, Figure 4 & 5). GLM models showed that mixed feeders have a significant positive effect on body mass SDI but browsers and frugivores have a significant negative effect, while omnivores do not significantly influence SDI (Table 7). This means that mixed feeding species of ungulate will exhibit more SSD than those that graze, while browsers and frugivores will have express a reduced SSD. Lastly although omnivorous ungulates appear to show less SSD than grazing species the difference isn't statistically significant. The foraging groups do not have a significant effect on weaponry SDI, so while there are differences in the average SDI exhibited in ungulate weaponry between foraging groups these differences are nonsignificant (Table 7).

Solitary species are the least dimorphic in body mass and the sexually segregated species are the most dimorphic (Table 6, Figure 4). Sexually segregated species are also the most dimorphic social group for weaponry with the largest weaponry SDI, with species that form harems having the lowest weaponry SDI (Table 6, Figure 5). The models focused on social structure show that gregarious and sexually segregated species have a significant positive effect on body mass SDI, but species that form harems have a nonsignificant effect (Table 7). Illustrating that more gregarious species will have a greater magnitude of SSD in comparison to more solitary species. Sexual segregation has a significant positive effect on the weaponry SDI, but species that form harems and solitary species don't have a significant relationship with weaponry SDI (Table 7). Thus, sexually segregated species have more dimorphic weaponry than those that are gregarious but being solitary or living in harems doesn't influence the difference in SSC compared to gregarious species significantly.

**Table 7**. The statistical outputs of GLMs testing the influence of different variables on SDI. The models focused on body mass used body mass SDI as the dependent variable and the models focussed on weaponry used weaponry SDI as the dependent variable. The baseline of the independent variable for each model is indicated in bold.

		Body Mass		Weaponry				
Independent Variable	Driver	Number of Species	Significance of Influence on SDI	Driver	Number of Species	Significance of Influence on SDI		
	Solitary Species	124	-	Gregarious Species	44	-		
Social Organisation	Gregarious Species	76	F=0.119, p=0.002	Species that Form Harems	Species that Form 14 Harems			
	Species that Form Harems	31	F=0.067, p=0.208	Sexually Segregated Species	56	F=0.615, p=0.032		
	Sexually Segregated Species	98	F=0.366, p<0.001	Solitary Species	46	F=-0.188, p=0.528		
	Grazers	103	-	Browsers	28	-		
	Browsers	87	F=-0.152, p<0.001	Frugivores	9	F=0.324, p=0.563		
Foraging Strategy	Frugivores	14	F=-0.227, p=0.007	Grazers	60	F=0.039, p=0.907		
	Mixed Feeders	108	F=0.003, p=0.941	Mixed Feeders	51	F=0.463, p=0.179		
	Omnivores	20	F=-0.138, p=0.055	Omnivores	12	F=-0.138, p=0.785		
	Species From Closed Habitats	97	-	Species From Open Habitats	74	-		
Habitat Type	Species From Mixed Habitats	102	F=0.171, p<0.001	Species From Closed Habitats	44	F=-0.746, p=0.007		
	Species From Open Habitats	133	F=0.17, p<0.001	Species From Mixed Habitats	43	F=-0.543, p=0.048		

## Discussion

#### **Rensch's Rule**

This study provides evidence that ungulate species show statistically significant allometry consistent with Rensch's rule when considering body mass as a measure of sexual dimorphism. Though they do not show significant allometry to Rensch's rule when weaponry is taken as a measure of sexual dimorphism. In summary, species with male-biased sexual size dimorphism (SSD) will be more dimorphic when a species is larger and species with female-biased SSD will be more dimorphic when species are smaller. The fact that this study found ungulates to follow Rensch's for body size but not for weaponry indicates that there is a benefit to more pronounced male-biased SSD in larger species, but that this benefit is reduced in the smaller species making it less viable. Whereas the benefit of female-biased SSD is reduced and selected against in larger species of ungulates but becomes advantageous in the smaller species. The sexual dimorphism of weaponry, however, is not seen to follow this pattern. This indicates that there is a cost to increased weaponry in larger species that prevents the scaling of secondary sexual characteristics (SSC) with species mass (Tidière, *et al*, 2017).

The findings of this study contrast with those of an earlier study into Rensch's rule, which found that ungulates showed a non-significant relationship with the rule (Abouheif & Fairbairn, 1997). The discrepancy in findings was likely caused by the differences in sample size, with the earlier study using data from 82 species compared with 334 in this study. Similarly, other studies have found Artiodactyls to break from Rensch's rule (Lindenfors, *et al*, 2007), but their sample size was only 115. However, it should also be noted that this study did not account for phylogenetic discrepancies as past studies with smaller sample sizes were able to do.

However, with many biological rules there are exceptions, as although ungulates when tested as one group follow Rensch's rule for body mass, not all ecological variables show allometry when tested separately. The habitat type of ungulates had a significant effect on sexual dimorphism, but it did not influence whether ungulates follow Rensch's rule. Species from all three habitats showed significant allometry with Rensch's rule, whereas the social structure and foraging strategies of ungulates caused certain groups of species to break from Rensch's rule. Gregarious, sexually segregated, grazing and omnivorous species do not follow Rensch's rule. Grazing species of ungulate are predominantly gregarious and sexually segregated species, so it is logical that all three of these groups have similar allometric relationships and break form Rensch's rule. These species break from Rensch's rule as the magnitude of sexual dimorphism exhibited does not change with species mass in a way consistent with this rule. There are hierarchies within gregarious species and male bachelor herds established through aggressive displays and fighting, which leads to sexually dimorphic species (Forsyth, *et al*, 2005; Pelletier, *et al*, 2006; McPherson & Chenoweth, 2012). So, these groups of ungulates do not break from Rensch's rule for a lack of SSD but because there isn't a large range of species mass within these groups. This is reinforced by the fact that species from open habitats follow Rensch's rule, this group includes large numbers of the grazing, gregarious and sexually segregated species but covers a wider range of species masses. Omnivorous ungulates contain more species that exhibit female-biased SSD and are monomorphic than exhibit male-biased SSD. It has been shown in the past that the way in which omnivores forage means that mating systems where males guard females isn't as viable as their food sources are more sporadically dispersed, causing other groups of omnivorous mammals to break Rensch's rule (Noonan, *et al*, 2016).

Ungulate weaponry does not follow Rensch's rule when all ungulates are analysed together and when different categories are tested independently. Unlike body mass, the sexual dimorphism of weaponry reduces as species mass increases. This closely ties to the functional versatility of ungulate weapons, as although weaponry can provide an increase in reproductive success overcoming selection pressures, they are also used as a means of predator defence (Bro-Jørgensen, 2007; Emlen, 2008). Weaponry is common in solitary species and they are predominantly male-biased. The weapons present are also as large in relation to species mass as the weapons of the more gregarious species of ungulates. In these solitary species, there is a reduction in drive for SSD, but there is still a drive for dimorphic weaponry within these smaller species. When defending a territory either on their own or in a breeding pair the males of these species invest in secondary sexual characteristics (SSC) as these, unlike having a larger mass, provide an advantage when fighting members of their own species but does not hinder them when moving quickly in a more closed environment for instance when running from a predator (Bro-Jørgensen, 2008; Emlen, 2008; Tidière, et al, 2017). This trend is reflected in the SDI values of frugivores, omnivores and browsers. These species have much higher SDI for weaponry than they do body mass. Larger species within closed habitats include those that shed any weaponry after their breeding season, as these elaborate weapons reduce the speed at which they can escape predators in closed environments (Metz, et al, 2018). For instance, in some cervid species, males will develop weaponry that will be lost after the breeding season (Caro, et al,

2003; Kruuk, *et al*, 2003; McPherson & Chenoweth, 2012). These weapons are primarily used during the breeding season and are intrasexually selected weapons (Rico-Guevara & Hurme, 2018). They provide an advantage when competing with other males for access to females but provide no great advantage to make them energetically cost-effective when they return to being solitary or part of bachelor herds, so are shed (McPherson & Chenoweth, 2012; Kiltie, 1985). In larger species that are more social, inhabiting more open environments the females also use weapons for defence against predators and establishing female hierarchies (Stankowich & Caro, 2009). When it comes to predator responses females of large species in more open habitats are unable to take refuge in deep vegetation and so invest in larger weaponry (Stankowich & Caro, 2009; Kiltie, 1985). Additionally, it has been demonstrated that the weaponry of male bovids has a decreasing allometric slope with body mass due to the physical constrains of developing increasingly large horns (Tidière, *et al*, 2017). Thus, the reduction in weaponry SDI of larger ungulates is derived from an increased drive for female weaponry and an increased cost to larger weaponry in males.

#### **Drivers of Sexual Dimorphism**

The drivers of sexual dimorphism must be taken into consideration when investigating Rensch's rule, as species mass and the sexual bias of the dimorphic trait alone do not drive the evolution of sexual dimorphism in ungulates. The social structure of mammals is closely tied to reproductive behaviour and strategies, such as sexual dimorphism. This is reflected in the models of this study that show the more gregarious social systems have a significant positive effect on SSD. Habitat, predator avoidance and foraging strategy also drive the evolution of sexual dimorphism in ungulates (Blanckenhorn, 2005; Bowyer, et al, 2020; Plavcan, 2001; Rico-Guevara & Hurme, 2018). The results of this study show that open habitats have a significant positive effect on body mass SDI when closed habitats are used as a baseline. Furthermore, that closed habitats have a significant negative effect on weaponry SDI when open habitats are used as a baseline. Habitat type not only informs foraging behaviour but social dynamics as it provides physical limitations to group size and available feeding resources (Bowyer, et al, 2020). It has been hypothesised that the evolution of sexual size dimorphism (SSD) in African ungulates was driven by the species radiating from closed environments to more open grassland (Bowyer, et al, 2020; Perez-Barberia, *et al*, 2002).

The drivers of sexual dimorphism in ungulates, mean that species of different sizes will respond to selection pressures in a way that supports the relationship described by Rensch's rule. The larger species tend to form larger polygynous groups in more open habitats, where the males of the species invest heavily in body mass as it provides an advantage for sexual selection through intrasexual competition. Whereas the smaller species are more likely to be solitary and form monogamous breeding pairs in closed habitats. In these social structures there is a reduced benefit to males investing in costly sexual dimorphism and an increased pressure for females to develop a larger body mass and weapons to defend their own territory. This trend is reflected in the significant positive effect more open habitats and gregarious social structures have on the body mass SDI of ungulates.

The smaller ungulates are mostly comprised of solitary species that inhabit closed habitats. Ungulates as a whole follow Rensch's rule as the smaller species are less sexually dimorphic, with an increased drive for species with female-biased SSD. These smaller more solitary species and those that form monogamous breeding pairs are not under the same selection pressures as those in polygynous species, this is represented in their reduced SDI values for both body mass and weaponry length. There is far less intrasexual competition for mates and if there is, it is for a much shorter period of time (Bowyer, et al, 2020; Clutton-Brock, 1989; Weckerly, 1998). Additionally, in many monogamous species, the mate selection is based on female choice rather than male-male combat (Clutton-Brock, 1989). This means that there is reduced pressure for males to have larger mass or weaponry length, as the benefits do not match the energy expended developing and maintaining these traits (McPherson & Chenoweth, 2012). This is reflected in the low SDI values for solitary ungulate species, additionally gregarious and sexually segregated social structures have a significant positive effect on the body mass SDI of solitary species. In closed habitats, there is an advantage to being small when it comes to anti-predator strategies. These species are more likely to run and hide than fight, especially as they are more likely to be on their own or in a small group. This is referred to as the Manoeuvrability hypothesis (Bro-Jørgensen, 2008; Janis, 1982; Sridhara, et al, 2013; Stankowich & Caro, 2009). This increases the cost of a sexually dimorphic trait that may hinder predator avoidance.

The species of smaller ungulates are more likely to exhibit female-biased SSD, this paired with a reduction in pressure for males to be larger leads to these species following Rensch's rule. The females of these smaller, solitary species are more likely to take an active role in territory defence and any aggressive behaviour (Roberts & Dunbar, 2000). The reduced group size places more pressure on the mothers to protect their offspring on their own, providing a selection pressure for larger more aggressive females (Brotherton & Rhodes, 1996; Geist, 1977). Additionally, it has been shown that female fecundity is greater in larger females, causing a simultaneous drive for increased female mass (Lindenfors, *et al*, 2007). It

has been found that in roe deer and bighorn sheep the larger the females the longer their average lifespan. These larger females have increased fitness and a lower metabolic rate meaning they have a higher survival rate during resource scarcities. These females are able to live through more breeding seasons thus increasing their reproductive success (Gaillard, *et al*, 2000). This leads to an increase in female-biased SSD in solitary species.

Whereas, larger species of ungulate are commonly found in more open habitats. The ungulates in mixed habitats are commonly sexually segregated species that come together during a specific breeding season (Hanley, 1982; Ruckstuhl & Neuhaus, 2002). Species in open habitats have the greatest mass range and contain higher numbers of gregarious and sexually segregated species. These species have the highest weaponry sexual dimorphism and the lowest count of female-biased SSD. Species in both mixed and open environments have the largest body mass SDI, these environments allow the development of larger sizes without restricting their movements around their habitat. Territories in more open habitats are larger with more widely dispersed resources. This means that they can more easily support larger species and larger group sizes (Lagory, 1986; Marino & Baldi, 2014; Perez-Barberia, et al, 2002). The species in open habitats are commonly comprised of large territorial males that are either segregated until a breeding season or remain with the females and juveniles year-round. Females benefit from joining a resource rich area defended by a male, as it increases the nutrition available to their offspring (Geist, 1977). This strategy of resource defence to attract females causes a shift in the sex's territoriality to male only, driving these males to become larger and more aggressive (Bowyer, et al, 2020; Geist, 1977; McPherson & Chenoweth, 2012; Perez-Barberia, et al, 2002).

The polygynous reproductive strategies that are used by the majority of larger ungulate species commonly relies on intrasexual competition between the males of species (Pelletier, *et al*, 2006; Pérez-Barbería, *et al*, 2002). A species that is gregarious and lives in a mixed-sex group year-round will have a hierarchy within it, with the most dominant males gaining more mating rights than the subordinates (Bowyer, *et al*, 2020; Jarman, 1983; McPherson & Chenoweth, 2012). This is similar to those species that form harems but with the competition for dominance coming from solitary males or bachelor herds rather than subordinate males within a social group (Berger, 1987; Ruckstuhl & Neuhaus, 2002). This study found that ungulate species that live in these harems and gregarious herds have high SDI's for both body mass and weaponry. Grazers and mixed feeders are the most dimorphic among the different foraging strategies for both body mass and weaponry length, with the other foraging strategies common in closed habitats exhibiting significantly lower SDI.

Species that graze out in the open are at greater risk of predation and so being in a larger social group becomes advantageous as it increases group vigilance (Childress & Lung, 2003; Hunter & Skinner, 1998). Additionally, the dilution effect occurs, where the chances of an individual's survival increase in a larger group (Gochfeld & Burger, 1994; Hebblewhite & Pletscher, 2002; King, *et al*, 2012). In larger groups, there is less pressure for a mother to actively defend their young from predators in the same way a solitary parent would, as they can rely on the dilution effect within a larger herd and on the dominant males to take an active role in anti-predation behaviour (O'Donoghue & Boutin, 1995).

Those species that spend the majority of the year in sexually segregated groups are very common in more open habitats. In these social systems, the males are ejected from the herds of females and juveniles when they mature, these males remain solitary or form bachelor herds (Ruckstuhl & Kokko, 2002; Ruckstuhl & Neuhaus, 2000; Ruckstuhl & Neuhaus, 2002). These groups will come together during a breeding season, during which the males will compete for access to the females. This competition can take the form of harems, leks and pairs with mate bonding (Clutton-Brock, *et al*, 1993; Isvaran, 2005). Sexually segregated species of ungulates have the highest SDI for both body mass and weaponry for all social systems tested. There is a short window of time for the males to access the females, so the male combat and dominance displays are often more aggressive and intense due to the increased selection pressure (Bro-Jørgensen, 2003; Clutton-Brock, *et al*, 1993; Vanpé, 2005). This results in these larger species of ungulate exhibiting greater SSD, this reinforces the allometry of ungulates to Rensch's rule.

# Conclusion

From the analysis of 334 species of ungulate, this study provides new insights into the drivers of sexual dimorphism in ungulates and their allometry to Rensch's rule. Ungulates were shown to follow Rensch's rule for both body mass but not for weaponry length. The body mass of gregarious, sexually segregated, omnivorous and grazing species all break from Rensch's rule, as although they are sexually dimorphic there isn't a wide enough mass range for Rensch's rule to be exhibited. When testing the weaponry of ungulates based on ecological variables, they still did not show allometry to Rensch's rule. Despite ungulates possessing highly dimorphic weaponry, the weaponry SDI does not increase with species mass at a rate consistent with this biological rule. The habitat type, foraging strategy and social organisation, along with species size, provide evolutionary pressures to the development of sexual dimorphism in ungulate species. It is the finding of this study that the type of habitat and social dynamics of a species has a significant effect on both SSD and SSC's. However, the foraging strategy has a significant effect on SSD but not SSC's of ungulates. Ungulates in larger polygynous groups inhabit more open habitats exhibiting a greater degree of sexual dimorphism both on body size and weaponry as these provide a direct benefit to their reproductive success, whereas the more solitary species are more likely to inhabit more closed off environments, reducing the benefits of more exaggerated sexual dimorphism. The smaller species are more commonly solitary in closed environments where larger females are selected for territory defence and protecting juveniles outside a herd. Contrasting with the larger species where male-biased sexual dimorphism is selected for, and increasingly so in more open habitats and in polygynous groups. It is this general trend, driven by evolutionary pressures, within ungulate species that leads to this group of mammals' sexual size dimorphism showing allometry to Rensch's rule. Future studies should investigate further into the sexual dimorphism of wild suids, as this is heavily understudied. There should also be more research done into the smaller and more reclusive species of ungulate as the current knowledge shows a large bias toward the larger more conspicuous species especially those of Bovidae.

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# Appendix

**Table i.** The compiled dataset of ungulate species and the morphological and ecological data used in this study along with its corresponding source reference. A dashed entry indicates that the information was not found. An entry of 0.00 as a weaponry length distinguishes the lack of weaponry in one sex as opposed to a lack of information in the source material. Previous species and genus names included if the species' taxonomy has been redefined and referred to as different names between sources.

Family	Genus	Species	Mean Species Mass (kg)	Mean Male Mass (kg)	Mean Female Mass (kg)	Weaponry Presence / Absence	Mean Male Weaponry Length (cm)	Mean Female Weaponry Length (cm)	Social Composition	Habitat Type	Feeding Type	Sources
Equidae	Equus	africanus	248.88	-	-	Absent	-	-	Sexually Segregated	Open	Grazer	11; 15; 25; 29; 41
Equidae	Equus	burchellii	259.00	267.50	242.50	Absent	-	-	Harem	Mixed	Grazer	7; 12; 15; 24; 25; 26; 29; 30; 33
Equidae	Equus	grevyi	407.09	415.00	388.67	Absent	-	-	Gregarious	Open	Grazer	8; 11; 15; 24; 25; 26; 29; 30; 33; 41
Equidae	Equus	hemionus	230.53	200.00	145.00	Absent	-	-	Sexually Segregated	Open	Grazer	12; 15; 24; 25; 26; 27; 29; 30; 41
Equidae	Equus	khur		-	-	Absent	-	-		-	-	-
Equidae	Equus	kiang	317.86	387.50	275.00	Absent	-	-	Sexually Segregated	Open	Grazer	11; 15; 26; 29; 39; 41
Equidae	Equus	przewalskii	344.86	-	325.00	Absent	-	-	Harem	Open	Grazer	8; 15; 24; 25; 26
Equidae	Equus	quagga	315.00			Absent	-	-	Gregarious	-	Grazer	15; 41
Equidae	Equus	zebra	288.75	299.00	265.75	Absent	-	-	Harem	Open	Grazer	11; 12; 15; 24; 25; 26; 29; 30; 33; 41
Rhinocerotidae	Certotherium	simum	2067.36	2349.94	1825.17	Present	/1.83	/6.4/	Solitary	Mixed	Grazer	/; 8; 12; 15; 25; 29; 30; 33; 41
Rhinocerotidae	Certotherium	cottoni	-	-	-	Present	-	-	-	-	-	-
Rhinocerotidae	Dicerorninus	sumatrensis	822.07	800.00	800.00	Present	-	-	Solitary	Closed	Browser	11; 15; 24; 26; 30; 41
Rhinocerotidae	Diceros	DICOMIS	1255.96	1513.17	1253.00	Present	63.53	/0.53	Sexually Segregated	Mixed	Browser	7; 8; 12; 15; 24; 25; 29; 30; 33; 41
Rhinocerotidae	Rhinoceros	SONUAICUS	1455.73	1250.00	1400.00	Present	20.50	0.00	Solitary	Closed	Browser	10; 15; 25; 26; 29; 30; 41
Tapiridao	Acrocodia / Tapirus	indica ( indicus	1815.27	2150.00	227 50	Abcont	47.90	47.90	Solitan	Closed	Browcor	8; 11; 15; 24; 25; 26; 29; 30; 41 9: 0: 11: 15: 25: 26: 20: 41
Tapinuae	Actocould / Taplitus	liiuica / liiuicus	290.94	-	327.30	Absent	-	-	Solitany	Closed	Browser	0, 9, 11, 13, 23, 20, 30, 41
Tapiridae	Tapireila / Tapirus Tapirus	kabomani	- 270.71	-	- 230.00	Absent	-	-	SUILAI y	-	-	-
Tapiridae	Tapirus	pinchaque	201.49	180.00	180.00	Absent	-	-	Solitary	Closed	Mixed Feeder	8; 9; 11; 15; 25; 26; 31; 41
Tapiridae	Tapirus	terrestris	206.67	160.00	135.00	Absent	-	-	Solitary	Mixed	Browser	9; 15; 25; 26; 30; 41
Antilocapridae	Antilocapra	americana	50.09	53.71	46.36	Present	33.10	6.80	Sexually Segregated	Open	Browser	4; 8; 11; 12; 14; 15; 23; 24; 25; 26; 29; 32; 41; 42
Bovidae	Addax	nasomaculatus	97.17	115.90	79.13	Present	85.74	75.54	Harem	Open	Mixed Feeder	3; 7; 8; 11; 13; 24; 25; 26; 27; 29; 32; 38; 41
Bovidae	Aepyceros	melampus	53.88	62.12	44.65	Present	62.76	0.00	Gregarious	Mixed	Mixed Feeder	3; 5; 7; 8; 11; 12; 13; 23; 24; 25; 26; 28; 29; 30; 32; 33; 38; 41
Bovidae	Aepyceros	petersi	57.00	63.00	51.00	Present	92.00	0.00	Gregarious	Closed	Mixed Feeder	5
Bovidae	Alcelaphus	buselaphus	155.68	160.92	153.83	Present	57.40	57.40	Gregarious	Open	Grazer	8; 11; 12; 13; 24; 25; 26; 29; 32; 33; 38; 41; 42
Bovidae	Alcelaphus	caama	139.50	149.33	119.33	Present	56.00	56.00	Harem	Mixed	Grazer	5; 13; 30
Bovidae	Alcelaphus	cokii	141.00	150.00	132.00	Present	70.00	70.00	Harem	Mixed	Grazer	5
Bovidae	Alcelaphus	lelwel	182.00	196.50	167.50	Present	70.00	70.00	Sexually Segregated	Open	Grazer	5
Bovidae	Alcelaphus	lichtensteini	172.28	182.77	166.33	Present	51.36	50.66	Harem	Open	Grazer	3; 5; 13; 24; 25; 29; 30; 32; 38
Bovidae	Alcelaphus	major	160.00	160.00	160.00	Present	57.50	57.50	Sexually Segregated	Mixed	Grazer	5
Bovidae	Alcelaphus	swaynei	158.75	167.50	150.00	Present	57.50	57.50	Sexually Segregated	Open	Grazer	5
Bovidae	Alcelaphus	tora	160.00	160.00	160.00	Present	48.00	48.00	Sexually Segregated	Open	Grazer	5
Bovidae	Ammodorcas	clarkei	28.04	28.74	27.26	Present	23.53	0.00	Solitary	Open	Browser	3; 5; 11; 13; 24; 25; 26; 29; 32; 38; 41
Bovidae	Ammotragus	lervia	86.16	113.48	61.16	Present	82.68	39.47	Solitary	Open	Mixed Feeder	3; 5; 8; 11; 14; 23; 24; 25; 26; 27; 29; 32; 38; 41; 42
Bovidae	Antidorcas	angolensis	29.25	33.50	25.00	Present	38.00	22.00	Gregarious	Mixed	Browser	5
Bovidae	Antidorcas	hotmeyri	30.00	35.00	25.00	Present	38.00	22.00	Gregarious	Mixed	Mixed Feeder	5
Bovidae	Antidorcas	marsupialis	33.24	35.65	29.40	Present	36.48	25.83	Gregarious	Open	Mixed Feeder	3; 5; 8; 12; 13; 24; 25; 26; 28; 29; 30; 32; 33; 38; 41; 42
Bovidae	Antilope	cervicapra	35.16	38.77	31.60	Present	56.03	0.00	Gregarious	Open	Grazer	3; 8; 11; 12; 14; 23; 24; 25; 26; 29; 30; 32; 38; 41
Bovidae	Bison / Bos	hicon	90.20	99.00 719.0E	442 41	Present	55.90	47.40	Crogorious	Open	Grazer	5, 0, 11, 24, 25, 20, 34, 41 11, 12, 14, 22, 24, 25, 26, 20, 20, 20, 22, 29, 41, 42
Bovidae	BISOTI / BOS	DISOTI	605.60	/18.95	442.41	Present	-	-	Gregarious Sovuelly Cogregated	Open	Grazer Mixed Fooder	11; 12; 14; 23; 24; 25; 20; 28; 29; 30; 32; 38; 41; 42 5, 9, 11, 24, 25, 26, 27, 22, 29, 41
Bovidae	Boc	DUNASUS	772.90	072.99	627 52	Procont	e2 22	20.22	Harom	Mixed	Grazor	2, 0, 11, 24, 25, 20, 27, 32, 30, 41
Bovidae	Bos	iavanicus	670.08	775.00	525.00	Present	02.25	29.55	Harem	Closed	Mived Feeder	23, 24, 23, 20, 29, 30, 32, 30, 42
Bovidae	Bos	mutue	553 50	785 33	318 67	Present	87 50	51.00	Sevually Segregated	Open	Mixed Feeder	5. 11. 24
Bovidae	Bos	cauvali	700 05	800.00	800.00	Present	80.00	40.00	Sexually Segregated	Miyed	Mixed Feeder	5. 11. 12. 24. 25. 20. 41
Bovidae	Boselanhus	trancamelus	193.06	238.43	148 34	Present	10.37	0.00	Sexually Segregated	Mixed	Mixed Feeder	3, 11, 12, 27, 23, 23, 71 3, 5, 11, 14, 77, 73, 74, 75, 76, 70, 30, 37, 38, 41, 47
Bovidae	Bubalus	amee	937.60	1033 33	900.00	Present	110.00	110.00	Sexually Segregated	Mixed	Grazer	5, 9, 11, 11, 22, 25, 21, 25, 20, 25, 50, 52, 50, 11, 12
Bovidae	Bubalus	denressicornis	191.55	190.50	185.00	Present	29.25	25.11	Solitary	Closed	Mixed Feeder	3: 5: 9: 11: 24: 25: 26: 32: 41
Bovidae	Bubalus	mindorensis	250.60	255.50	248.50	Present	41.36	37.80	Solitary	Mixed	Grazer	3: 5: 11: 24: 25: 41
Bovidae	Bubalus	quarlesi	118.67	103.00	103.00	Present	17.77	17.84	Solitary	Closed	Mixed Feeder	5: 9: 11: 24: 25: 41
Bovidae	Budorcas	bedfordi	250.00	250.00	250.00	Present	51.50	-	Gregarious	Closed	Mixed Feeder	5
Bovidae	Budorcas	taxicolor	257.59	287.81	223.86	Present	48.55	50.50	Gregarious	Closed	Mixed Feeder	3: 4: 5: 11: 24: 25: 26: 29: 32: 41
Bovidae	Budorcas	tibetanus	250.00	250.00	250.00	Present	44.50		Gregarious	Closed	Mixed Feeder	5
Bovidae	Budorcas	whitei	250.00	250.00	250.00	Present	31.00	-	Gregarious	Closed	Browser	5
Bovidae	Capra	aegagrus	44.72	54.54	34.83	Present	108.23	26.97	Sexually Segregated	Mixed	Mixed Feeder	4; 5; 12; 23; 24; 25; 27; 29; 32; 42
Bovidae	Capra	caucasica	67.84	81.11	55.56	Present	74.25	26.25	Sexually Segregated	Open	Grazer	3; 4; 5; 8; 12; 27; 29; 32; 38; 41
Bovidae	Capra	cylindricornis	70.17	90.63	51.54	Present	86.62	23.18	Sexually Segregated	Open	Mixed Feeder	3; 5; 23; 24; 25; 27; 29; 32; 38; 41
Bovidae	Capra	falconeri	66.06	91.52	36.74	Present	129.97	26.78	Sexually Segregated	Open	Mixed Feeder	3; 4; 5; 11; 23; 24; 25; 29; 32; 38; 41

Bovidae	Capra	ibex	71.58	91.83	45.77	Present	97.93	29.18	Sexually Segregated	Open	Mixed Feeder	3; 5; 11; 23; 24; 25; 26; 27; 28; 29; 32; 38; 41
Bovidae	Capra	nubiana	57.81	69.00	51.00	Present	108.75	30.83	Sexually Segregated	Open	Mixed Feeder	3; 5; 11; 27; 38; 41
Bovidae	Capra	pyrenaica	55.54	71.54	39.05	Present	75.07	22.70	Sexually Segregated	Mixed	Mixed Feeder	3; 5; 23; 24; 25; 27; 28; 29; 32; 38; 41
Bovidae	Capra	SIDIFICA	/4.0/	92.00	48.40	Present	107.70	28.43	Sexually Segregated	Open	Mixed Feeder	3; 4; 5; 8; 11; 12; 38; 41
Bovidae	Capra	Walle	103.00	115.00	85.00	Present	105.25	17.75	Gregarious	Open	Mixed Feeder	3; 5; 11; 29; 38
Bovidae	Capricornis	Crispus maritimus	59.29 112 E0	52.25 112 E0	49.00	Present	14.33	14.33	Solitany	Closed	Browser	4; 5; 6; 11; 29; 41; 42
Bovidae	Capricornis	milneedwardcii	112.50	112.50	112.50	Present	26 70	26.70	Solitan	Closed	Browser	5
Bovidae	Capricornis	rubiduc	133.00	130.00	135.00	Present	18.00	20.70	Solitany	Closed	Browser	5.11
Bovidae	Capricornis	sumatraensis	99.83	110 58	92 10	Present	21 10	21 10	Solitary	Mixed	Mixed Feeder	5. 8. 23. 24. 25. 26. 29. 32. 41
Bovidae	Capricornis	swinhoei	33.00	24.00	22.33	Present	12.87	12.87	Solitary	Mixed	Browser	5: 8: 11: 29
Bovidae	Capricornis	thar	112.50	112.50	112.50	Present	25.00	25.00	Solitary	Closed	Browser	5
Bovidae	Cephalophus	adersi	9.48	9.40	9.65	Present	4.13	2.20	Solitary	Closed	Browser	3: 5: 11: 25: 38
Bovidae	Cephalophus	arrhenii	17.50	17.50	17.50	Present	4.50	2.35	Solitary	Closed	-	5
Bovidae	Cephalophus	brookei	17.00	17.00	17.00	Present	7.20	2.30	Solitary	Closed	Frugivore	5
Bovidae	Cephalophus	callipygus	18.68	19.05	18.95	Present	8.75	4.90	Solitary	Closed	Omnivore	3; 5; 11; 13; 24; 25; 32
Bovidae	Cephalophus	castaneus	21.00	21.00	21.00	Present	21.00	21.00	Solitary	Closed	Omnivore	5
Bovidae	Cephalophus	crusalbum	20.00	20.00	20.00	Present	9.85	5.00	Solitary	Closed	Frugivore	6
Bovidae	Cephalophus	curticeps	45.00	45.00	45.00	Present	-	-	Solitary	Closed	Frugivore	7
Bovidae	Cephalophus	doralis	19.81	20.42	19.67	Present	6.67	4.00	Solitary	Closed	Omnivore	3; 5; 8; 11; 13; 24; 25; 26; 32; 38; 41
Bovidae	Cephalophus	harveyi	12.21	12.33	12.33	Present	7.50	0.00	Solitary	Closed	Browser	5; 11; 42
Bovidae	Cephalophus	jentinki	71.78	72.77	76.17	Present	17.50	17.50	Solitary	Closed	Mixed Feeder	5; 11; 13; 24; 25; 32; 41
Bovidae	Cephalophus	johnstoni	17.00	17.00	17.00	Present	9.75	3.60	Solitary	Closed	Omnivore	5
Bovidae	Cepnalophus	lestradei	17.00	17.00	17.00	Present	10.00	4.25	Solitary	Closed	Omnivore	5
Bovidae	Cephalophus	leucogaster	16.31	17.15	16.38	Present	4.87	2.53	Solitary	Closed	Browser	5; 11; 13; 24; 25; 32; 38
Bovidae	Cephalophus	natalensis	12.31	13.14	12.74	Present	6.44	3.29	Solitary	Closed	Browser	3; 5; 11; 13; 23; 24; 25; 30; 32; 38; 41
Dovidae	Cephalophus	niger	19.12	20.30	19.56	Present	0.15	2.43	Solitary	Closed	Frugivore	3; 5; 11; 13; 24; 25; 32; 36; 41
Bovidae	Cephalophus	ngrinons	14.91	14.72	14.96	Present	0.50	3.94	Solitany	Closed	Frugivore	2; 5; 11; 12; 24; 25; 32; 36; 41 2; 5; 11; 12; 24; 25; 22; 28
Bovidae	Cephalophus	rubiduc	10.70	10.50	19.60	Fresent	10.00	4.75	Solically	Closed	Flugivore	5, 5, 11, 15, 24, 25, 52, 58
Bovidae	Cephalophus	rufilatus	11.23	11 64	11.43	Precent	- 7 73	3 50	Solitany	- Closed	Browser	- 3· 5· 8· 11· 13· 24· 25· 32· 38· 41
Bovidae	Cenhalophus	silvicultor / svlviculto.	62.81	62.50	63.63	Present	15.50	12.88	Solitary	Closed	Frugivore	5: 8: 11: 13: 24: 25: 26: 29: 38: 41
Bovidae	Cenhalophus	snadix	56.75	55.20	57.07	Present	10.00	0.00	Solitary	Closed	Frugivore	5: 11: 13: 24: 25: 26: 32
Bovidae	Cephalophus	wevnsi	17.18	17.00	17.00	Present	9.97	4.30	Solitary	Closed	Omnivore	5; 11
Bovidae	Cephalophus	zebra	16.01	16.66	16.98	Present	4.48	2.23	Solitary	Closed	Frugivore	3; 5; 11; 13; 24; 25; 32; 38; 41
Bovidae	Connochaetes	albojuatus	220.00	246.50	193.50	Present	83.00	83.00	Sexually Segregated	Mixed	Grazer	5
Bovidae	Connochaetes	gnou	157.45	167.74	132.67	Present	65.00	60.10	Sexually Segregated	Open	Grazer	3; 5; 8; 11; 12; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41
Bovidae	Connochaetes	johnstoni	170.00	170.00	170.00	Present	83.00	83.00	Sexually Segregated	Open	Grazer	5
Bovidae	Connochaetes	mearnsi	185.50	208.00	163.00	Present	83.00	83.00	Sexually Segregated	Open	Grazer	5
Bovidae	Connochaetes	taurinus	205.85	236.19	179.00	Present	60.80	49.04	Sexually Segregated	Mixed	Grazer	3; 5; 7; 8; 11; 12; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41; 42
Bovidae	Damaliscus	eurus	140.75	152.00	129.50	Present	72.00	72.00	Sexually Segregated	Open	Grazer	5
Bovidae	Damaliscus	jimela	119.50	129.00	110.00	Present	72.00	72.00	Sexually Segregated	Open	Grazer	5
Bovidae	Damaliscus	korngum	128.07	132.67	128.33	Present	84.00	84.00	Gregarious	Mixed	Grazer	5; 13; 30
Bovidae	Damaliscus	lunatus	127.56	137.55	117.46	Present	50.37	49.03	Harem	Mixed	Grazer	3; 5; 7; 9; 11; 12; 13; 23; 24; 25; 26; 29; 30; 33; 38; 41; 42
Bovidae	Damaliscus	phillipsi (dorcas)	69.59	/1.6/	63.25	Present	43.07	39.60	Gregarious	Open	Grazer	5; 8; 9; 13; 25; 26; 30
Dovidae	Damaliacus	pygargus (uorcas)	120 50	120 50	30./5	Present	37.42	33.03	Gregarious	Anen	Grazer	5; 6; 9; 11; 15; 24; 25; 20; 50; 53; 41
Bovidae	Damaliscus	tiana	128.50	128.50	128.50	Present	37.53	34.63	- Gregarious	Open	- Grazer	5,10
Bovidae	Damaliscus	toni	122.00	122.00	122.00	Present	72.00	72.00	Sexually Segregated	Open	Grazer	5
Bovidae	Damaliscus	ugandae	141 00	152.00	130.00	Present	72.00	72.00	Sexually Segregated	Open	Grazer	5
Bovidae	Dorcatragus	menalotis	12.57	10.10	10.68	Present	9.23	0.00	Solitary	Open	Mixed Feeder	3: 5: 11: 13: 24: 25: 26: 29: 32: 42
Bovidae	Eudorcas	albonotata	23.75	27.50	20.00	Present	26.00	10.00	Gregarious	Open	Grazer	5
Bovidae	Eudorcas	nasalis	16.00	16.00	16.00	Present	34.00	11.00	Gregarious	Open	Grazer	5
Bovidae	Eudorcas / Gazella	rufifrons	25.05	27.50	25.67	Present	31.83	29.20	Solitary	Open	Grazer	5; 8; 11; 13; 25; 41
Bovidae	Eudorcas / Gazella	thomsoni	20.76	22.42	18.11	Present	34.08	16.95	Gregarious	Open	Mixed Feeder	5; 8; 12; 13; 25; 26; 30; 33; 41; 42
Bovidae	Eudorcas	tilonura	23.75	27.50	20.00	Present	28.50	20.00	Solitary	Open	Grazer	5
Bovidae	Gazella	acaciae	19.50	19.50	-	Present	26.00	8.50	Sexually Segregated	Closed	Mixed Feeder	5
Bovidae	Gazella	arabica	17.50	17.50	17.50	Present	23.07	8.65	Sexually Segregated	Open	Grazer	5; 10
Bovidae	Gazella	bennetti	18.73	23.00	16.50	Present	26.00	12.50	Solitary	Mixed	Browser	5; 41
Bovidae	Gazella	christyi	18.67	23.00	16.50	Present	28.50	12.00	Sexually Segregated	Mixed	Browser	5
Bovidae	Gazella	cuvieri	22.84	28.04	18.33	Present	31.66	27.86	Harem	Mixed	Mixed Feeder	3; 5; 11; 25; 27; 32; 38; 41
Bovidae	Gazella	aaresnurii	18.50	18.50	18.50	Present	21.00	8.65	Sexually Segregated	Open	Mixed Feeder	5
Bovidae	Gazella	aorcas	17.38	16.70	14.65	Present	32.43	24.//	Gregarious	Open	Mixed Feeder	3; 8; 11; 13; 25; 26; 27; 32; 38; 41
Bovidae	Gazella Gazella	fuscifrons	25.00	25.00	25.00	Present	20.15	-	Gregarious	Open	Mixed Feeder	5, 10
Bovidae	Gazella	nazella	27.00	24.00 23.42	24.00	Present	24.50	15 59	Gregarious	Open	Grazer	J 3· 5· 8· 25· 27· 32· 38· 41
Bovidae	Gazella	gazena aracilicornis	22.00	23.42	20.35	Present	29.33	13.20	Gregarious	Open	Grazer	5, 5, 6, 23, 27, 32, 30, 41 5
Bovidae	Gazella	lentoceros	27.33	29.38	22.36	Present	35.36	28.66	Gregarious	Open	Browser	3: 5: 8: 11: 13: 25: 27: 32: 41
Bovidae	Gazella	marica	20.00	22.00	18.00	Present	27.00	15.00	Gregarious	Open	Mixed Feeder	5
Bovidae	Gazella	muscatensis	18.50	18.50	18.50	Present	21.00	8.65	Sexually Segregated	Open	Grazer	5

Bovidae	Gazella	pelzelni	20.80	21.50	21.50	Present	31.50	20.00	Harem	Open	Browser	5; 13
Bovidae	Gazella	salinarum	18.67	23.00	16.50	Present	27.50	14.50	Sexually Segregated	Mixed	Browser	5
Bovidae	Gazella	shikarii	25.00	25.00	25.00	Present	27.50	18.50	Gregarious	Open	Mixed Feeder	5
Bovidae	Gazella	spekei	19.55	21.02	17.78	Present	29.16	22.86	Gregarious	Open	Mixed Feeder	3; 5; 8; 11; 13; 25; 32; 38; 41
Bovidae	Gazella	subgutturosa	28.44	27.74	23.57	Present	34.02	0.00	Gregarious	Open	Browser	3; 4; 5; 8; 11; 12; 24; 25; 27; 32; 41
Bovidae	Gazella	yarkandensis	25.00	25.00	25.00	Present	29.00	0.00	Gregarious	Open	Mixed Feeder	5
Bovidae	Hemitragus / Nilgiritragus	nylocrius	74.44	92.50	50.00	Present	44.50	30.00	Sexually Segregated	Open	Grazer	5; 11; 29; 32; 41
Bovidae	Hemitragus / Arabitragus	jayakari	32.69	36.50	18.00	Present	36.95	28.50	Sexually Segregated	Open	Mixed Feeder	5; 29; 32; 41
Bovidae	Hemitragus	jemianicus	74.09	99.07	50.00	Present	37.25	19.30	Gregarious	Mixed	Mixed Feeder	3; 4; 5; 11; 23; 24; 26; 29; 32; 37; 38; 41; 42
Dovidae	Hippotragus	equinus	201.05	2/9.13	250.90	Present	/6.50	74.07	Gregarious	Open	Grazer	3; 6; 11; 12; 13; 24; 25; 26; 29; 30; 32; 33; 36; 41; 42
Bovidae	Hippotragus	nger	227.74	243.80	214.09	Present	117.23	88.90	Gregarious	Mixed	Browcor	5; 6; 11; 15; 25; 24; 25; 20; 50; 52; 55; 56; 41; 42
Bovidae	Hippotragus	roosevelti	195.00	220.00	170.00	Present	137.50	81.50	Harem	Open	Grazer	5
Bovidae	Kobus	ancelli	55.00	60.00	50.00	Present	72 50	0.00	Gregorious	Mixed	Grazer	5
Bovidae	Kobus	defacea	206 55	231 75	184 60	Present	72.50	0.00	Gregarious	Onen	Grazer	5· 8· 13· 38· 47
Bovidae	Kobus	ellinsinn/mnus	200.55	244 73	180 40	Present	78.81	0.00	Gregarious	Mixed	Grazer	3. 5. 11. 13. 24. 25. 26. 28. 30. 32. 33. 38. 41. 42
Bovidae	Kobus	kafuensis	93 50	107 50	79 50	Present	72 50	0.00	Sexually Segregated	Onen	Grazer	5, 5, 11, 15, 21, 25, 20, 20, 50, 52, 55, 50, 11, 12
Bovidae	Kobus	koh	77.93	94 00	62.09	Present	55 18	0.00	Sexually Segregated	Open	Grazer	3. 2. 8. 11. 13. 23. 24. 25. 26. 30. 32. 33. 38. 41. 42
Bovidae	Kobus	leche / lechwe	92.38	108.87	77.10	Present	62.37	0.00	Sexually Segregated	Open	Grazer	3: 5: 8: 11: 13: 23: 24: 25: 26: 28: 30: 32: 33: 38: 41: 42
Bovidae	Kobus	leucotis	59.00	68.50	40.00	Present	55.00	0.00	Sexually Segregated	Mixed	Grazer	5
Bovidae	Kobus	loderi	52.50	60.00	45.00	Present	50.50	0.00	Sexually Segregated	Open	Grazer	5
Bovidae	Kobus	menaceros	89.19	105.10	75.00	Present	69.58	0.00	Gregarious	Open	Grazer	3: 5: 11: 13: 24: 25: 38: 41
Bovidae	Kobus	smithemani	55.00	60.00	50.00	Present	72.50	0.00	Gregarious	Open	Grazer	5
Bovidae	Kobus	thomasi	76.75	85.00	68.50	Present	59.50	0.00	Gregarious	Open	Grazer	5
Bovidae	Kobus	vardonii	72.45	76.79	64.42	Present	44.67	0.00	Harem	Open	Grazer	3: 7: 11: 13: 23: 24: 25: 26: 30: 32: 38: 42
Bovidae	Litocranius	sclateri	39.00	41.50	36.50	Present	34.50	0.00	Harem	Open	Browser	5
Bovidae	Litocranius	walleri	38.68	40.19	35.23	Present	36.29	0.00	Sexually Segregated	Mixed	Browser	3: 5: 8: 11: 13: 24: 25: 26: 29: 30: 32: 33: 38: 41: 42
Bovidae	Madoqua	cavendishi	4.60	4.60	4.60	Present	11.40	0.00	Solitary	Onen	Browser	5
Bovidae	Madoqua	damarensis	5.35	5.10	5.60	Present	8.00	0.00	Solitary	Closed	Mixed Feeder	5
Bovidae	Madoqua	aventheri	4 26	4 00	4 32	Present	7 90	0.00	Solitary	Mixed	Browser	3. 2. 13. 24. 22. 26. 29. 32. 38. 41
Bovidae	Madoqua	hararensis	2 30	2 10	2 40	Present	9.00	0.00	Solitary	Mixed	Browser	5, 5, 15, 21, 25, 26, 25, 52, 56, 11
Bovidae	Madoqua	hinderi	4.60	4.60	4.60	Present	11.40	0.00	Solitary	Mixed	Browser	5
Bovidae	Madoqua	kirkii	5.01	4 89	5 16	Present	9.00	0.00	Solitary	Closed	Browser	3. 5. 8. 11. 12. 13. 23. 24. 25. 26. 28. 29. 30. 32. 33. 38. 41. 42
Bovidae	Madoqua	lawrancei	2 53	2 10	2 75	Present	9.00	0.00	Solitary	Mixed	Browser	5
Bovidae	Madoqua	nhillinsi	3.03	2.50	3.30	Present	9.00	0.00	Solitary	Mixed	Browser	5: 9
Bovidae	Madoqua	niacentinii	3.00	2.50	2 50	Present	-	0.00	Solitary	Mixed	Mixed Feeder	5, 5
Bovidae	Madoqua	saltiana	3 49	3 20	3 51	Present	6.80	0.00	Solitary	Onen	Browser	3. 5. 13. 24. 25. 29. 32. 38
Bovidae	Madoqua	smithii	4 00	4 00	4 00	Present	9.80	0.00	Solitary	Open	Mixed Feeder	5
Bovidae	Madoqua	swavnei	2 30	2 10	2 40	Present	9.00	0.00	Solitary	Mixed	Browser	5
Bovidae	Madoqua	thomasi	4.60	4.60	4.60	Present	11.40	0.00	Solitary	Mixed	Mixed Feeder	5
Bovidae	Naemorhedus / Nemorhaedus	hailevi	26.05	25.00	25.00	Present	13.33	11.83	Solitary	Closed	Mixed Feeder	5: 11: 29: 41
Bovidae	Naemorhedus / Nemorhaedus	bedfordi	38.50	38.50	38.50	Present	18.00	18.00	Sexually Segregated	Closed	Grazer	5, 11, 25, 11
Bovidae	Naemorhedus / Nemorhaedus	caudatus	32.92	37.50	33.50	Present	16.67	15.00	Gregarious	Closed	Mixed Feeder	5: 29: 41
Bovidae	Naemorhedus / Nemorhaedus	evansi	25.00	25.00	25.00	Present	16 50	16 50	Gregarious	Mixed	Browser	5
Bovidae	Naemorhedus / Nemorhaedus	aoral	32.88	35.32	31.27	Present	17.08	16.30	Gregarious	Closed	Mixed Feeder	3: 4: 5: 8: 11: 23: 24: 25: 26: 29: 32: 38: 41
Bovidae	Naemorhedus / Nemorhaedus	ariseus	27.50	27.50	27.50	Present	23.00	18.00	Gregarious	Mixed	Mixed Feeder	5
Bovidae	Nanger / Gazella	dama	65.68	-	-	Present	36.80	36.80	Gregarious	Open	Mixed Feeder	11. 13. 24. 25. 27. 41
Bovidae	Nanger / Gazella	aranti	54 58	63 67	45 50	Present	64 25	50.00	Gregarious	Open	Mixed Feeder	7. 8. 12. 13. 24. 25. 26. 30. 33. 41. 42
Bovidae	Nanger / Gazella	notata	53.75	67.50	40.00	Present	65.00	36.50	Gregarious	Mixed	Mixed Feeder	5
Bovidae	Nanger / Gazella	netersi	53 75	67 50	40.00	Present	65.00	36 50	Sexually Segregated	Open	Mixed Feeder	5
Bovidae	Nanger / Gazella	soemmerrinaii	41.99	-	40.00	Present	45.15	48.30	Gregarious	Open	Grazer	8: 11: 13: 24: 25: 41
Bovidae	Neotragus	hatesi	2.63	2 34	2 67	Present	3 40	0.00	Solitary	Closed	Mixed Feeder	3. 5. 9. 11. 13. 23. 24. 25. 29. 32. 42
Bovidae	Neotragus	kirchennaueri	4 50	4 50	4 50	Present	9 90	0.00	Harem	Closed	Browser	5
Bovidae	Neotragus	livinastonianus	5.65	5.65	5.65	Present	9.90	0.00	Solitary	Closed	Browser	5
Bovidae	Neotragus	moschatus	5.05	5.05	5.05	Present	9.23	0.00	Harem	Closed	Browser	3. 2. 11. 13. 23. 24. 22. 26. 29. 30. 32. 38. 41
Bovidae	Neotragus	nvamaeus	2.53	2.51	2.40	Present	2.95	0.00	Solitary	Closed	Browser	3: 5: 9: 11: 13: 24: 25: 26: 29: 32: 41
Bovidae	Oreamnos	americanus	78.92	88.36	60.02	Present	23.63	23.38	Sexually Segregated	Mixed	Mixed Feeder	3: 4: 5: 8: 11: 12: 14: 23: 24: 25: 26: 28: 29: 32: 38: 41: 42
Bovidae	Oreotragus	aceratos	13.00	13.00	13.00	Present	9.50	0.00	Gregarious	Open	Browser	5
Bovidae	Oreotragus	aureus	14.00	14.00	14.00	Present	9.35	0.00	Solitary	Open	Browser	5
Bovidae	Oreotragus	centralis	14 00	14 00	14 00	Present	10.00	0.00	Solitary	Open	Browser	5
Bovidae	Oreotragus	oreatraqus	12.96	11.78	13.81	Present	10.43	1.68	Solitary	Mixed	Browser	3: 11: 13: 23: 24: 25: 26: 29: 30: 32: 33: 38: 41: 42
Bovidae	Oreotragus	norteousi	13.00	13.00	13.00	Present	10.00	0.00	Solitary	Open	Browser	5
Bovidae	Oreotragus	saltatrixoides	13.00	13.00	13.00	Present	15.00	0.00	Solitary	Open	Browser	
Bovidae	Oreotragus	schillinasi	11.50	10.00	13.00	Present	8.35	8,10	Solitary	Open	Browser	5
Bovidae	Oreotragus	somalicus	14.00	14.00	14.00	Present	15.00	0.00	Solitary	Open	Browser	5
Bovidae	Oreotragus	stevensoni	10.40	10.30	10.50	Present	10.25	0.00	Solitary	Open	Browser	
Bovidae	Oreotragus	transvaalensis	12.50	10.50	14.50	Present	10.70	0.00	Solitary	Open	Browser	5
Bovidae	Oreotragus	tvleri	10.50	10.50	10.50	Present	9.25	0.00	Solitary	Open	Browser	5
Bovidae	Orvx	heisa	176.83	188.00	152.00	Present	82.00	82 00	Gregarious	Open	Mixed Feeder	- 5: 11: 13
Bovidae	Orvx	callotis	170.17	188.33	152.00	Present	-	78 50	Gregarious	Mixed	Mixed Feeder	5: 16
			1,0.1,	100.00	102.00				0.0901000		· mean couch	-,

Bovidae	Oryx	dammah	182.68	186.88	155.00	Present	112.83	112.83	Gregarious	Open	Mixed Feeder	5; 8; 11; 13; 24; 25; 27; 29; 38; 41
Bovidae	Oryx	gallarum	167.75	183.50	152.00	Present	75.50	-	Gregarious	Open	Mixed Feeder	5
Bovidae	Οιγχ	gazella	192.04	207.92	183.26	Present	99.94	99.44	Gregarious	Open	Mixed Feeder	3; 5; 7; 8; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41; 42
Bovidae	Οιγχ	leucoryx	84.04	82.26	72.58	Present	74.33	74.33	Gregarious	Open	Grazer	5; 8; 11; 23; 24; 29; 32; 38; 41
Bovidae	Ourebia	hastata	14.00	14.00	14.00	Present	13.00	0.00	Harem	Closed	Grazer	5
Bovidae	Ourebia	ourebi	16.02	15.15	16.17	Present	20.45	0.00	Harem	Mixed	Grazer	3: 5: 8: 13: 23: 24: 25: 26: 29: 32: 33: 38: 41: 42
Bovidae	Ourebia	montana	14.00	14.00	14.00	Present	13.00	0.00	Harem	Mixed	Mixed Feeder	5
Bovidae	Ourebia	quadriscopa	14.00	14.00	14.00	Present	10.00	0.00	Harem	Mixed	Mixed Feeder	5
Bovidae	Ovibos	moschatus	286.23	318.60	224.63	Present	-	-	Gregarious	Open	Mixed Feeder	4: 5: 11: 14: 23: 25: 26: 27: 28: 29: 32: 38: 41: 42
Bovidae	Ovis	ammon	97.96	116.19	70.54	Present	162.70	40.58	Sexually Segregated	Open	Grazer	3: 4: 5: 8: 11: 12: 24: 25: 28: 32: 38: 41
Bovidae	Ovis	arabica	-	-	-	Present	72 00	72.00	-	-	-	9
Bovidae	Ovis	hochariensis	57 50	76.00	39.00	Present	73.00	13.00	Gregarious	Onen	Grazer	5.10
Bovidae	Ovis	canadansis	91 22	116 75	73 52	Precent	126 50	13.00	Gregarious	Open	Mived Feeder	4. 5. 8. 11. 12. 14. 24. 25. 26. 32. 38. 40. 41. 42
Bovidao	Ovis	collium	02 50	122 50	53.52	Drocont	120.50	15.00	Sovually Sographic	Open	Mixed Feeder	r, 5, 6, 11, 12, 14, 24, 25, 26, 52, 56, 46, 41, 42
Bovidae	Ovis	cuclocarac	92.30	26.00	21 50	Present	124.00	12.00	Sexually Segregated	Open	Mixed Feeder	5
Dovidae	Ovis	dalli	33.00	30.00	31.30	Present	98.50	13.00	Sexually Segregated	Open	Mixed Feeder	5, 6, 10 2, 5, 8, 14, 24, 25, 26, 28, 20, 22, 28, 41, 42
Duvidae	Ovs	ualli domuini	71.34	124.00	49.00	Present	92.50	17.50	Sexually Segregated	Open	Mixeu reeuer	5, 5, 6, 14, 24, 25, 20, 26, 50, 52, 56, 41, 42
Bovidae	OVIS	darwini	95.50	134.00	57.00	Present	122.50	30.00	Sexually Segregated	Open	Grazer	5
Bovidae	OVIS	gmelini	46.13	55.88	36.38	Present	76.00	-	Sexually Segregated	Open	Grazer	5; 9; 27; 28
Bovidae	Ovis	noagsoni	90.33	101.50	68.00	Present	113.00	41.00	-	Open	Grazer	5
Bovidae	Ovis	isphaganica	48.75	55.00	42.50	Present	79.00	25.00	Sexually Segregated	Open	Grazer	5
Bovidae	Ovis	jubata	-	-	-	Present	32.00	-	-	-	-	9
Bovidae	Ovis	karelini	90.50	124.50	56.50	Present	147.00	30.00	Sexually Segregated	Open	Grazer	5
Bovidae	Ovis	laristanica	43.25	44.50	42.00	Present	79.00	25.00	Sexually Segregated	Open	Grazer	5
Bovidae	Ovis	nigrimontana	92.50	130.50	54.50	Present	79.00	-	Sexually Segregated	Mixed	Grazer	5
Bovidae	Ovis	nivicola	87.34	114.51	63.23	Present	81.00	25.50	Sexually Segregated	Open	Grazer	5; 8; 11; 23; 24; 25; 32; 38
Bovidae	Ovis	orientalis	61.50	-	-	Present	-	-	-	Open	-	24; 25
Bovidae	Ovis	polii	86.00	117.50	54.50	Present	190.00	41.25	Sexually Segregated	Open	Grazer	5
Bovidae	Ovis	punjabiensis	36.67	42.50	25.00	Present	80.00	12.00	Sexually Segregated	Open	Grazer	5
Bovidae	Ovis	severtzovi	92.50	130.50	54.50	Present	77.00	-	Sexually Segregated	Open	Grazer	5; 10
Bovidae	Ovis	vianei	57.50	76.00	39.00	Present	74.50	13.00	Sexually Segregated	Mixed	Grazer	5
Bovidae	Pantholops	hodasonii	35.35	40.48	26.60	Present	60.00	0.00	Gregarious	Open	Mixed Feeder	3: 5: 11: 20: 24: 25: 26: 28: 29: 32
Bovidae	Pelea	capreolus	24.78	24.39	24.99	Present	23.39	0.00	Harem	Open	Browser	3: 5: 11: 13: 23: 24: 25: 26: 29: 30: 32: 33: 38: 41: 42
Bovidae	Philantomha	aequatorialis	4.90	4.45	5.35	Present	3,30	3.30	Solitary	Closed	Omnivore	5
Bovidae	Philantomba	anchietae	5.00	5.00	5.00	Present	4 30	2 60	Solitary	Closed	Omnivore	5
Bovidae	Philantomba	hicolor	4 90	4 65	5.00	Present	3.80	2.00	Solitary	Closed	Browser	5
Bovidae	Philantomba	condicus	4 80	4 45	5.15	Precent	3.65	1 55	Solitary	Closed	Frugivore	5
Bovidae	Philantomba	defrieci	4.00	4.60	5.15	Present	4 30	2.80	Solitany	Closed	Browcer	5
Bovidae	Philantomba	becki	4.93	4.60	5.25	Present	4.30	2.00	Solitany	Closed	Browser	5
Dovidae	Philantomba	hanna	T.95	T.00	5.25	Dresent	4.30	2.00	Colitory	Closed	Ommisser	5
DOVIDAE	Philantomba	lugens	5.00	5.00	5.00	Present	4.30	3.20	Solitary	Closed	Omnivere	D F: 11: 24: 2F: 22: 41
Dovidae	Philantomba	IIIdXWellil	7.14	0.55	0.60	Present	5.00	0.00	Solitary	Closed	Unnivore	5; 11; 24; 25; 35; 41
Bovidae	Philantomba	monticola	5.37	4.30	5.13	Present	5.23	4.50	Solitary	Closed	Frugivore	5; 8; 11; 13; 24; 26; 29; 33; 41
Bovidae	Philantomba	walteri	7.50	7.50	7.50	Present	5.00	0.00	Solitary	Closed	Omnivore	5
Bovidae	Procapra	gutturosa	29.52	32.14	25.88	Present	28.60	0.00	Sexually Segregated	Open	Mixed Feeder	3; 4; 5; 8; 11; 12; 23; 24; 25; 26; 29; 32; 38; 41
Bovidae	Procapra	picticaudata	20.41	14.50	14.50	Present	28.95	0.00	Sexually Segregated	Open	Mixed Feeder	5; 24; 25; 28; 29
Bovidae	Procapra	przewalskii	25.60	24.50	24.50	Present	22.17	0.00	Sexually Segregated	Open	Mixed Feeder	5; 29
Bovidae	Pseudois	nayaur	51.67	60.99	40.71	Present	73.16	16.67	Gregarious	Open	Mixed Feeder	4; 5; 11; 23; 24; 25; 26; 29; 32; 38; 41; 42
Bovidae	Pseudois	schaeferi	39.00	42.67	26.75	Present	55.00	37.33	Sexually Segregated	Open	Grazer	5; 11; 29
Bovidae	Pseudoryx	nghetinhensis	90.00	85.00	85.00	Present	43.38	33.13	Solitary	Closed	Browser	5; 11; 24
Bovidae	Raphicerus	campestris	11.78	10.95	11.73	Present	13.36	0.00	Solitary	Open	Mixed Feeder	3; 8; 11; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41; 42
Bovidae	Raphicerus	colonicus	7.70	7.70	7.70	Present	5.00	0.00	Solitary	Open	Browser	5
Bovidae	Raphicerus	melanotis	10.62	10.62	10.50	Present	7.40	0.00	Solitary	Mixed	Mixed Feeder	3; 5; 13; 26; 29; 32; 38; 41
Bovidae	Raphicerus	sharpei	8.73	8.08	8.28	Present	5.92	0.00	Solitary	Mixed	Browser	3; 5; 13; 24; 25; 29; 32
Bovidae	Redunca	adamauae	47.50	47.50	47.50	Present	13.00	0.00	Harem	Mixed	Grazer	5
Bovidae	Redunca	arundinum	60.56	67.60	52.70	Present	35.70	0.00	Harem	Mixed	Grazer	3: 5: 11: 13: 23: 24: 25: 26: 28: 29: 30: 32: 33: 38: 41: 42
Bovidae	Redunca	bohor	44.50	49.00	40.00	Present	30.00	0.00	Sexually Segregated	Mixed	Grazer	5: 30
Bovidae	Redunca	chanleri	28.50	30.00	27.00	Present	24.50	0.00	Sexually Segregated	Mixed	Grazer	5
Bovidae	Redunca	cottoni	47.00	54.00	40.00	Present	36.50	0.00	Sexually Segregated	Mixed	Grazer	5
Bovidae	Redunca	fulvorufula	31 38	32.07	20.41	Precent	24 77	0.00	Sexually Segregated	Mixed	Grazer	5. 8. 11. 13. 25. 26. 29
Bovidae	Redunca	nineriensis	47.00	54 00	40.00	Precent	25.00	0.00	Sexually Segregated	Mixed	Grazer	5
Bovidao	Redunca	accidentalic	40.00	51.00	41.00	Drocont	20.00	0.00	Soliton	Open	Crazor	F
Dovidae	Redunca		46.25	55.50	41.00	Present	30.00	0.00	Solitary	Open	Grazer	J 2. E. 0. 11. 12. 22. 24. 25. 20. 22. 22. 20. 41. 42
DOVIDAE	Reduiled	redunca	40.22	50.69	41.70	Present	29.57	0.00	SUILdry	Mixed	GrdZer Mixed Feeder	5; 5; 8; 11; 15; 25; 24; 25; 29; 52; 55; 58; 41; 42
Dovide		dSidLiCd	31.00	40.00	22.00	Present	24.00	-	Sexually Segregated	Ciused	Mixed Feeder	5
волаве	kupicapra	carpatica	45./5	56.00	35.50	Present	26.50	-	Sexually Segregated	Mixed	Mixed Feeder	5
Bovidae	Kupicapra	ornata	28.50	34.00	23.00	Present	32.00	-	Sexually Segregated	Open	Mixed Feeder	5
Bovidae	Rupicapra	parva	26.00	27.00	24.00	Present	22.50	-	Gregarious	Open	Mixed Feeder	5
Bovidae	Rupicapra	pyrenaica	31.90	35.88	27.13	Present	20.92	17.75	Gregarious	Mixed	Mixed Feeder	5; 24; 27; 28; 29; 41
Bovidae	Rupicapra	rupicapra	36.75	39.73	32.53	Present	21.49	19.43	Sexually Segregated	Mixed	Mixed Feeder	3; 4; 5; 8; 11; 12; 23; 24; 25; 26; 28; 29; 32; 38; 41; 42
Bovidae	Saiga	mongolica	36.00	36.00	36.00	Present	22.00	0.00	-	Open	Mixed Feeder	5
Bovidae	Saiga	tatarica	37.30	40.71	32.87	Present	25.73	0.00	Harem	Open	Mixed Feeder	3; 4; 5; 8; 9; 11; 12; 23; 24; 25; 26; 27; 29; 32; 38; 41; 42
Bovidae	Sylvicapra	grimmia	17.23	17.67	19.09	Present	11.20	0.00	Solitary	Mixed	Browser	3; 8; 11; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41; 42

Bovidae	Syncerus	brachyceros	375.00	400.00	350.00	Present	74.00	74.00	Gregarious	Mixed	Grazer	5
Bovidae	Syncerus	caffer	593.30	673.22	506.98	Present	105.52	82.52	Gregarious	Mixed	Grazer	3; 4; 5; 8; 11; 12; 13; 23; 24; 25; 26; 29; 32; 33; 38; 41; 42
Bovidae	Syncerus	mathewsi	375.00	400.00	350.00	Present	62.50	62.50	Gregarious	Closed	Grazer	5
Bovidae	Syncerus	nanus	285.00	307.50	262.50	Present	37.50	20.00	Gregarious	Mixed	Grazer	5; 24
Bovidae	Taurotragus	derbianus	601.74	677.73	440.00	Present	118.15	106.65	Sexually Segregated	Mixed	Mixed Feeder	3: 11: 13: 23: 24: 25: 29: 41
Bovidae	Taurotragus	οινχ	536.43	617.67	427.43	Present	67.06	77.86	Sexually Segregated	Open	Mixed Feeder	3: 8: 11: 12: 13: 23: 24: 25: 26: 29: 30: 33: 41: 42
Bovidae	Tetracerus	quadricornis	19.23	19.33	19.25	Present	17.43	0.00	Solitary	Mixed	Mixed Feeder	5: 8: 11: 21: 24: 25: 26: 29: 32: 41
Bovidae	Tragelanhus / Nyala	angasii	92.90	110.81	69.95	Present	69.00	0.00	Sexually Segregated	Closed	Mixed Feeder	3. 5. 8. 11. 13. 22. 23. 24. 25. 26. 29. 30. 32. 33. 38. 41. 42
Bovidae	Tracelanhus	bor	51.00	60.00	42.00	Precent	24.00	0.00	Solitan	Mixed	Browcer	5
Bovidae	Tracelanhus	burtoni	204 69	237 33	172.00	Precent	94 30	0.00	Harem	Mixed	Browser	3. 5. 11. 13. 25. 26. 20. 32. 38
Bovidac	Tragolophus	docub	40.00	40.00	40.00	Drocont	25.00	0.00	Coliton	Mixed	Browcor	5, 5, 11, 15, 25, 20, 25, 52, 50
Bovidae	Tragolaphus		70.00	200.46	256 70	Present	23.00	62.75	Solically	Closed	Browcor	5
Dovide	Tragelaphus	faceiatura	2/4.04	509.46	250.79	Present	83.80	03.75		Closed	Browser	5; 11; 25; 24; 25; 20; 29; 55; 38; 41; 42
Bovidae	Tragelaphus	Tasciatus	51.00	60.00	42.00	Present	35.00	0.00	Solitary	Closed	Browser	5
Bovidae	l ragelaphus	gratus	80.00	80.00	80.00	Present	67.50	0.00	Solitary	Closed	Mixed Feeder	5
Bovidae	Tragelaphus / Ammelaphus	imberbis	79.86	94.95	66.01	Present	/2.86	0.00	Sexually Segregated	Closed	Mixed Feeder	3; 5; 8; 11; 13; 23; 24; 25; 26; 29; 30; 32; 33; 38; 41; 42
Bovidae	l ragelaphus	meneliki	51.00	60.00	42.00	Present	28.00	0.00	Solitary	Closed	Browser	5
Bovidae	Tragelaphus	ornatus	51.00	60.00	42.00	Present	30.00	0.00	Solitary	Closed	Browser	5
Bovidae	Tragelaphus	phaleratus	55.25	73.50	37.00	Present	23.00	0.00	Solitary	Mixed	Browser	5
Bovidae	Tragelaphus	scriptus	46.61	52.85	37.69	Present	40.43	0.00	Solitary	Closed	Mixed Feeder	3; 5; 8; 11; 13; 23; 24; 25; 26; 29; 30; 32; 38; 41; 42
Bovidae	Tragelaphus	selousi	77.50	100.00	55.00	Present	74.50	0.00	Sexually Segregated	Closed	Mixed Feeder	5
Bovidae	Tragelaphus	spekii	87.42	113.49	62.19	Present	63.76	0.00	Sexually Segregated	Closed	Mixed Feeder	3; 5; 8; 11; 13; 23; 24; 25; 26; 29; 32; 33; 38; 41; 42
Bovidae	Tragelaphus / Strepsiceros	strepsiceros	210.76	247.07	175.98	Present	133.96	0.00	Sexually Segregated	Mixed	Mixed Feeder	3: 5: 8: 11: 13: 23: 24: 25: 28: 29: 30: 32: 33: 38: 41: 42
Bovidae	Tragelaphus	svlvaticus	51.00	60.00	42.00	Present	40.00	0.00	Solitary	Closed	Browser	5
Camelidae	Camelus	ferus	710.36	-	600.00	Absent	-	-	Harem	Open	Mixed Feeder	8: 11: 25: 26: 29
Camelidae	l ama	quanicoa	114 46	99 75	109.67	Abcent			Gregarious	Open	Mixed Feeder	8: 12: 15: 24: 25: 26: 20: 30: 32: 41
Camelidae	Vicunana	vicuana	46 57	40.50	40.25	Absent	_	_	Gregarious	Open	Mixed Feeder	9, 11, 15, 24, 25, 26, 29, 50, 52, 41
Convidao	Alcoc	vicugna	427 20	405.50	271 71	Brocont	112.00	0.00	Colitan	Mixed	Browcor	0, 11, 13, 27, 23, 20, 23, 32, 71
Cervidee	Alles	alces	437.30	495.01	371.71	Present	112.00	0.00	Solitary	Classed	Biowsei	4, 0, 12, 13, 23, 24, 25, 20, 27, 20, 29, 50, 52, 50, 41, 42
Cervidae	Alces	americanus	407.50	480.00	335.00	Present	107.95	0.00	Solitary	Closed	Browser	
Cervidae	Axis	axis	64.48	//.48	48.36	Present	//.40	0.00	Harem	Mixed	Grazer	8; 11; 14; 15; 23; 24; 25; 27; 28; 29; 30; 38; 41; 42
Cervidae	Axis	calamianemsis	34.17	36.00	26.00	Present	25.00	0.00	Gregarious	Mixed	Grazer	11; 36; 41
Cervidae	Axis	kuhlii	55.00	-	-	Present	36.00	0.00	Solitary	Closed	Grazer	11; 41
Cervidae	Axis	porcinus	40.05	45.52	32.61	Present	34.22	0.00	Solitary	Mixed	Mixed Feeder	8; 9; 11; 15; 23; 24; 25; 26; 32; 38; 41; 42
Cervidae	Blastocerus	dichotomus	105.23	120.00	86.67	Present	57.77	0.00	Solitary	Open	Mixed Feeder	8; 11; 15; 24; 25; 26; 29; 32; 38; 41
Cervidae	Capreolus	capreolus	25.10	24.23	23.27	Present	30.50	0.00	Solitary	Closed	Browser	4; 6; 8; 12; 15; 23; 24; 25; 26; 27; 28; 29; 30; 32; 38; 41; 42
Cervidae	Capreolus	pygargus	40.73	43.15	40.67	Present	35.25	0.00	Solitary	Mixed	Browser	8; 15; 27; 29; 38; 41
Cervidae	Cervus / Przewalskium	albirostris	202.72	212.07	139.43	Present	69.65	0.00	Sexually Segregated	Mixed	Grazer	8; 11; 15; 18; 38; 41
Cervidae	Cervus	canadensis	306.11	340.55	250.22	Present	123.03	33.03	Sexually Segregated	Mixed	Mixed Feeder	4; 6; 8; 23; 24; 25; 26; 32; 38; 40
Cervidae	Cervus	elaphus	182.41	214.32	140.44	Present	175.00	0.00	Sexually Segregated	Mixed	Mixed Feeder	4; 6; 8; 12; 14; 15; 23; 26; 27; 28; 29; 30; 32; 38; 41; 42
Cervidae	Cervus	nippon	67.20	83.06	55.20	Present	52.90	0.00	Gregarious	Mixed	Mixed Feeder	4: 8: 11: 14: 15: 23: 24: 25: 26: 27: 28: 29: 32: 38: 41: 42
Cervidae	Dama	dama	61.46	78.07	44.55	Present	65.03	0.00	Sexually Segregated	Mixed	Mixed Feeder	4: 6: 8: 12: 14: 15: 23: 24: 25: 26: 27: 28: 29: 32: 38: 41: 42
Cervidae	Dama	mesonotamica	102.50	130.00	75.00	Present	-	-		Closed	Browser	ッ, , , , , , , , , , , , , , , , , , ,
Cervidae	Flanhodus	cenhalonhus	24 50	17 75	16.00	Present	2 50	0.00	Solitary	Closed	Mixed Feeder	4. 11. 15. 24. 25. 26. 29. 32. 41
Cervidae	Flanhurus	davidianus	178.83	214.05	150 27	Present	79 50	0.00	Sexually Segregated	Closed	Grazer	4. 8. 11. 15. 24. 25. 26. 29. 32. 41. 42
Cervidae	Hippocamelus	anticancic	52.67	60.00	46.00	Precent	27 40	0.00	Gregarious	Onen	Grazer	1. 11. 15. 20. 41
Cervidae	Hippocamelus	biculuc	62.10	65.00	55.00	Present	27.40	0.00	Gregarious	Open	Miyed Feeder	1, 11, 13, 23, 11 11, 15, 24, 25, 26, 20, 27, 41
Convidao	Hudropotoc	inormic	11 05	12.00	11 41	Present	27.95	0.00	Colitan	Open	Mixed Foodor	11, 13, 24, 23, 20, 23, 32, 41
Cervidee	Manage		11.95	12.00	11.41	Present	5.05	0.00	Solitary	Open	Finder Feeder	4, 0, 0, 11, 15, 25, 24, 25, 20, 27, 29, 52, 50, 41, 42
Cervidae	Mazama	americana	25.15	23.86	29.42	Present	11.45	0.00	Solitary	Mixed	Frugivore	8; 11; 15; 23; 24; 25; 26; 29; 32; 38; 41; 42
Cervidae	Mazama	bororo	25.00	-	-	Present	-	-	Solitary	-	Grazer	9; 15
Cervidae	Mazama	Dricenii	-	-	-	Present	5.25	0.00	Solitary	-	Browser	9; 15
Cervidae	Mazama	chunyi	13.75	16.50	-	Present	3.50	0.00	Solitary	Closed	Browser	9; 15; 29
Cervidae	Mazama	gouazoubira	17.48	17.02	18.40	Present	11.45	0.00	Solitary	Mixed	Grazer	8; 15; 23; 24; 25; 29; 32; 38; 41
Cervidae	Mazama	nana	15.20	-	-	Present	-	-	-	-	-	9
Cervidae	Mazama	nemorivaga	-	-	-	-	-	-	-	-	-	-
Cervidae	Mazama	pandora	-	-	-	Present	12.70	0.00	Solitary	-	Browser	9; 15
Cervidae	Mazama	rufina	16.50	16.50	-	Present	7.17	0.00	Solitary	Closed	Browser	9; 15; 24; 25; 29
Cervidae	Mazama	temama	-	-	-	Present	7.95	0.00	-	-	-	9
Cervidae	Muntiacus	atherodes	17.40	-	-	Present	5.25	0.00	Solitary	Closed	Browser	11; 15; 29
Cervidae	Muntiacus	aureus	-	-	-	Present	10.00	0.00	- '	-	-	9
Cervidae	Muntiacus	crinifrons	21.20	23.10	24.10	Present	6.75	0.00	Solitary	Closed	Mixed Feeder	9: 15: 24: 25: 29: 32: 41
Cervidae	Muntiacus	feae	20.75		-	Present	-	-	Solitary	-	Grazer	15.41
Cervidae	Muntiacus	aonachanensis	19.00		-	Precent	7 1 7	0.00	Solitany		-	Q: 15: 24
Cenvidae	Muntiacus	malabaricus	15.00	_	_	Precent	0.50	0.00	Solically	-	_	0
Cenvidae	Muntiacus	mandancus	-	_	-		9.30	0.00	-	-	-	-
Cervidae	Muntiacus	muntiak	-	-	-	- Droccat	- 11 50	-	- Colitera	- Cloced	- Mixed Feeds	-
Cervidae	Muntiague	IIIUIIEJAK	20.30	20.50	17.70	Present	11.58	0.00	Solitary	ciosea	mixea reeder	0; 9; 15; 25; 24; 25; 26; 32; 41
Cervidae	MUNTIACUS	ngripes	-	-	-	-	-	-	-	-	-	-
Cervidae	WULDEISCUC	punoatensis	12.00	-	-	Present	2.55	0.00	-	-	-	Э
Convidao	munuacus	·				-						
Cervidae	Muntiacus	putaoensis	11.00	-	-	Present	5.75	0.00	Solitary	-	Mixed Feeder	9; 15
Cervidae	Muntiacus Muntiacus	, putaoensis reevesi	11.00 12.23	- 12.37	- 11.38	Present Present	5.75 10.43	$0.00 \\ 0.00$	Solitary Solitary	- Closed	Mixed Feeder Mixed Feeder	9; 15 6; 8; 9; 11; 15; 23; 25; 26; 27; 32; 38; 41; 42
Cervidae Cervidae	Muntiacus Muntiacus Muntiacus	, putaoensis reevesi truongsonensis	11.00 12.23 15.00	- 12.37 -	- 11.38 -	Present Present Present	5.75 10.43 -	0.00 0.00 -	Solitary Solitary Solitary	- Closed -	Mixed Feeder Mixed Feeder Grazer	9; 15 6; 8; 9; 11; 15; 23; 25; 26; 27; 32; 38; 41; 42 15

Cervidae	Muntiacus	vuquangensis	38.75	-	-	Present	22.50	0.00	Solitary	-	-	15; 24
Cervidae	Odocoileus	hemionus	75.80	88.23	57.12	Present	69.90	0.00	Sexually Segregated	Mixed	Browser	4; 6; 8; 12; 14; 15; 23; 24; 25; 26; 28; 29; 30; 32; 38; 40; 41; 42
Cervidae	Odocoileus	virginianus	68.31	80.50	53.93	Present	55.88	0.00	Solitary	Mixed	Browser	4; 6; 8; 12; 14; 15; 23; 24; 25; 26; 27; 28; 30; 32; 38; 40; 41; 42
Cervidae	Ozotocerus	bezoarticus	36.15	40.00	34.50	Present	-	-	Gregarious	Open	Mixed Feeder	8: 15: 23: 26: 29: 38: 41
Cervidae	Pudu	pudu	10.46	10.32	12.26	Present	31.48	0.00	Solitary	Closed	Browser	4; 8; 11; 15; 23; 24; 25; 26; 29; 32; 38; 41
Cervidae	Pudu	mephistophiles	8.76	8.27	8.60	Present	100.00	-	Solitary	Closed	Browser	8; 15; 26; 29; 32; 38
Cervidae	Rangifer	tarandus	122.73	150.62	89.68	Present	130.06	37.00	Gregarious	Mixed	Browser	4; 6; 8; 11; 12; 14; 15; 23; 24; 25; 26; 27; 28; 29; 30; 32; 38; 41; 42
Cervidae	Rucervus	branderi	-	-	-	-	-	-	-	-	-	-
Cervidae	Rucervus / Cervus	duvaucelii	188.96	214.75	145.00	Present	94.50	0.00	Sexually Segregated	Mixed	Grazer	8; 11; 15; 23; 24; 25; 29; 30; 41
Cervidae	Rucervus / Cervus / Panolia	eldii	100.50	102.50	65.50	Present	99.37	0.00	Sexually Segregated	Open	Grazer	8; 15; 23; 24; 25; 29; 41
Cervidae	Rusa / Cervus	alfredi	47.16	59.00	36.00	Present	24.55	0.00	Sexually Segregated	Closed	Browser	2; 15; 29; 36; 41
Cervidae	Rusa / Cervus	mariannus / mariann	50.00	-	-	Present	28.00	0.00	-	Open	Browser	15; 29; 36; 41
Cervidae	Rusa / Cervus	timorensis	81.59	105.14	61.40	Present	99.95	0.00	Sexually Segregated	Mixed	Grazer	8; 11; 15; 24; 25; 29; 32; 38; 41; 42
Cervidae	Rusa / Cervus	unicolor	205.53	225.92	182.04	Present	86.67	0.00	Sexually Segregated	Closed	Mixed Feeder	8; 14; 15; 19; 24; 25; 26; 29; 30; 32; 38; 41; 42
Giraffidae	Giraffa	camelopardalis	902.98	1061.46	704.91	Present	13.50	13.50	Sexually Segregated	Mixed	Browser	7; 8; 12; 15; 24; 25; 26; 28; 29; 30; 32; 33; 41; 42
Giraffidae	Okapia	johnstoni	226.67	200.00	225.00	Present	-	-	Solitary	Closed	Browser	8; 11; 15; 25; 26; 29; 32; 41
Hippopotamidae	Choeropsis / Hexaprotodon	liberiensis	218.85	200.00	216.00	Present	-	-	Solitary	Closed	Browser	8; 11; 15; 24; 25; 26; 29; 30; 41
Hippopotamidae	Hippopotamus	amphibius	2228.93	2184.50	1493.70	Present	70.00	-	Gregarious	Open	Grazer	8: 11: 12: 15: 24: 25: 26: 29: 30: 33: 41
Moschidae	Moschus	anhuiensis	-	-	-	-	-	-	-	-	-	-
Moschidae	Moschus	berezovskii	11.03	-	9.10	Present	7.50	0.00	Solitary	Mixed	-	8: 29: 41
Moschidae	Moschus	chrvsogaster	11.44	10.20	11.45	Present	7.50	0.00	Solitary	Mixed	Browser	8: 11: 15: 29: 38: 41
Moschidae	Moschus	cupreus	-		-	-	-	-		-	-	-
Moschidae	Moschus	fuscus	12.00	-	-	Present	7.50	0.00	Solitary	-	-	29
Moschidae	Moschus	leucogaster	12.00	-	-	Present	7.50	0.00	Solitary	-	-	29
Moschidae	Moschus	moschiferus	12.26	12.06	12.62	Present	7.50	0.00	Solitary	Closed	Mixed Feeder	4: 8: 11: 15: 23: 25: 26: 29: 32: 38: 41: 42
Suidae	Bahvrousa	hahvrussa	86.20	-	-	Present	-	-	Solitary	Closed	Omnivore	11: 15: 24: 25: 26: 29: 41
Suidae	Babyrousa	celehensis	-	-	-	-	-	-	-	-	-	-
Suidae	Babyrousa	togeanensis	100.00	-	-	Present	-	-	Sexually Segregated	Closed	Omnivore	11
Suidae	Hylochoerus	meinertzhageni	203.07	230.00	180.00	Present	30.00	30.00	Harem	Closed	Omnivore	11. 15. 24. 25. 26. 29. 33. 41
Suidae	Phacochoerus	aethionicus	80.61	81.00	61.00	Present	52.25	20.35	Sexually Segregated	Mixed	Omnivore	8: 15: 25: 26: 29: 30: 33
Suidae	Phacochoerus	africanus	80.50	82.00	65.00	Present	36.50	36.50	Sexually Segregated	-	Grazer	15: 24: 41
Suidae	Potamochoerus	larvatus	80.67	-	-	Present	11 00	11 00	Harem	Closed	Omnivore	11: 15: 41
Suidae	Potamochoerus		79.60	67.00	67 25	Present	11.00	0.00	Harem	Mixed	Omnivore	8. 11. 15. 17. 24. 25. 26. 29. 41
Suidae	Sus	ahoenoharhus	-	-	-	-	-	-	-	-	-	-
Suidae	Sus	harhatuc	94 73			Precent			Gregarious	Closed	Omnivore	11. 15. 25. 41
Suidae	Sus	hlouchi	124 70	-	-	Present	-	-	-	-	-	25
Suidae	Sus	cehifmns	32 50	27 50	37 50	Present	-	-	Gregarious	Closed	Omnivore	11.15
Suidae	Sus	celehensis	55.00	27.50	57.50	Precent			Gregarious	Closed	Omnivore	11: 15: 25
Suidae	Sus	oliveri	-			-			Gregarious	-	-	-
Suidae	Sus	nhilinnensis	55.00			Precent			Gregarious	Closed	Omnivore	15
Suidae	Sus / Porcula	calvanius / calvania	8.04	0.50	6 50	Precent	_	_	Sexually Segregated	Open	Omnivore	11. 15. 25. 25. 41
Suidae	Sus	saivariius / saivariia	100 41	106.00	82.45	Present			Sexually Segregated	Mixed	Omnivore	11, 13, 23, 33, 71 A. 8. 11. 14. 15. 24. 25. 26. 27. 28. 41
Suidae	Sus	Sciula	115 22	100.00	115.00	Present	-	-	Sexually Segregated	Mixed	Omnivore	1, 0, 11, 17, 13, 27, 23, 20, 27, 20, 71
Tavaccuidae	Sus	woonori	26 14	47.50	115.00	Present	-	-	Sexually Seyregated	Mixed	Omnivore	11, 15, 24, 25, 41
Tayassuluae	Calayonus Pocari / Tavassu	toiscu	22.14	20.00	26.00	Present	-	-	Gregarious	Mixed	Omnivore	11, 15, 24, 25, 20, 29, 41
Tayassuluae	Tevener	lajacu	23.23	20.00	20.90	Present	-	-	Gregarious	Cleased	Omnivere	0, 11, 14, 15, 24, 25, 20, 29, 41 11, 15, 24, 25, 26, 41
Tragulidae	I dydssu	pecali	30.83		12.00	Present	-	-	Gregarious	Closed	Omnivore	11; 15; 24; 25; 26; 41
Tragulidae	Maaabiala	aquaticus	10.01	9.75	12.00	Present	-	-	Solicary	Closed	Frugivore	11; 15; 24; 25; 26; 29; 32; 41
Tragulidae	Masshiala	linuica	-	-	-	-	-	-	-	-	-	-
Tragulidae	Moschiele (Trequise	Kaliiygie	-	-	-	- Drocont	-	-	- Calitari	- Classed	-	-
Tragulidae	riusciilola / Tragulus	ineminna	3.09	-	-	Present	-	-	Solitary	Closed	Frugivore	15; 24; 25; 20; 41
Tragulidae	Traguius	Javanicus	2.03	1.30	1.82	Present	-	-	Solitary	Closed	Frugivore	0; 13; 23; 24; 23; 20; 32; 41
i ragulidae Tragulida -	i ragulus Tragulus	капспи	-	-	-	-	-	-	-	- Class -	-	-
i ragulidae	i ragulus Tragulus	ndpu	5.99	5.80	5.00	Present	-	-	Solitary	Closed	Omnivore	0; 11; 10; 23; 24; 25; 20; 32; 41
Tragulidae	Traguius	nigricans	-	-	-	Present	-	-	Solitary	Closed	Browser	11
i ragulidae	i raguius	versicolor	-	-	-	-	-	-	-	-	-	-
l ragulidae	l ragulus	williamsoni	-	-	-	-	-	-	-	-	-	-

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