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Sexual Dimorphism Affects Herd Composition in African Antelopes

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ABSTRACT

Herd behaviour is a crucial aspect of antelope development and survival. Understanding determinants of differences in herd composition is necessary to predict patterns of habitation, social interaction, and life history; thus, the possibility of sexual dimorphism acting as a dictator of herd size and composition in African antelope was explored. Sexual dimorphism is a key factor in determining intersexual and intrasexual interactions, which can create selection pressures driving divergence in behavioural and social traits. Consequently, it was predicted that sexually dimorphic species would exhibit increased social behaviour and be found in larger groups when compared to sexually monomorphic species. Two closely related species, sexually dimorphic impalas and non-sexually dimorphic hartebeests were compared using 60 camera trap photos obtained through the WildCam Gorongosa project to determine if there was a difference in herd size and the number of young observed. It was discovered that impalas were found in larger groups than hartebeests and that there was no difference in the proportion of offspring. This discrepancy can be attributed to sexually dimorphic females needing to group together for protection against predation as they lack horns for self-protection. Group size differences can imply tendencies to inhabit different habitats and exhibit unique social interactions within the herd while foraging. These findings are key in understanding herd behaviour in African antelopes and can be applied to accurately track and monitor antelope species' success in relation to conservation.

Introduction

Sexual dimorphism, describing the morphological differences between sexes in adults of the same species, is observed in most animals; differences commonly include variations in body sizes, weight, colouration, structures, facial compositions, behaviours, presence of ornaments, disease prevalence, and aggression levels (Nikitovic, 2018). Across most species, one sex faces more pressure to be competitive, while the other sex faces more pressure to choose mates of high quality (Miller & Somjee, 2014). Although there are exceptions, males across most animal species face larger pressures to be competitive as they only contribute sperm to reproductive processes rather than parental care or reproductive efforts through pregnancy (Brennan, 2010). Thus, males with larger numbers of mates will be evolutionarily favoured and have a greater chance of passing on their genes, increasing their fitness (Brennan, 2010). These pressures may drive male development of increased body size and weapons like horns to defend their mates against other males, attract females, and defend against predators. Females drive intersexual selection between males as they choose attractive male phenotypes, and males also face intrasexual selection as they compete with other males (Harris & Uller, 2009). This explains how males, on average, have more exaggerated features, larger sizes, increased aggression levels, and more pronounced ornaments to create observed sexual dimorphism.

Differences between sexes may also be seen in herding behaviour and roles within communities. Group sizes, travel distance, presence of young, and geographical distribution can differ with the sex ratio in groups (Zheng et al., 2021). Herding behaviour describes the sociality of individuals as they live and travel in groups to receive benefits such as increased resource acquisition, camouflage, and protection from predators as there are more individuals to fight and forage (Elischer, 2015). As animals travel in groups, they may take turns caring for young and forging for food to increase their likelihood of succeeding at both tasks (Elischer, 2015). Animal social groups can also foster social learning acquired by observing other members in the group; for example, species can learn various behavioural cues, migratory paths, and locations of mating sites and food sources from their social group (Reader, 2016). There may also be disadvantages to travelling in groups such as the increased risk of inbreeding, infection, disease, and competition, so, individuals must evaluate the risks as they can vary significantly between species (Kebede, 2019).

Sexual dimorphism manifests itself in many species of African antelopes. Typically, males have larger body sizes and weaponized horns used for intrasexual fighting to attract mates or defend against predators while females have smaller or non-existent horns (Packer, 1983). Observable differences between the sexes are an adaptation to increase survival and reproductive success; females exert less energy to grow horns as there is a trade-off between protection from predation and resource allocation (Packer, 1983). Like impalas (*Aepyceros melampus*), most antelope species exhibit sexual dimorphism, but some, like hartebeests (*Alcelaphus buselaphus*), do not (East, 1999).

Impalas and hartebeests are phylogenetically closely related species of antelope and have evolved into unique subfamilies (Brashares et al., 2000). Although genetically similar, the antelopes have many distinguishing traits which make them easy to visually identify; impalas have long, S-shaped horns that are only found on males, while hartebeests have shorter, wide-spread horns found on both males and females (NHPBS, n.d.). This difference in sexual dimorphism may be a contributing factor towards other behavioural differences in antelopes, namely herd structure and size. Additionally, the presence of sexual dimorphism can create differing selection pressures on the species, driving increased genetic variation and variability in niche partitioning (Marcaigh et al., 2020). It is not well understood why different antelope species exhibit unique social behaviours, and little research has been done using sexual dimorphism to categorize test species. Analyzing the differences in behaviour between impalas and hartebeests may lead to a deeper understanding of how sexual dimorphism impacts a species and could explain why related species can have very different, complex social systems (Kappeler et al., 2019).

Nearly all animals socialize with members of their own species to develop characteristic patterns of habitation, behaviour, and life history (Petak, 2018). Antelopes are highly social animals and tend to live in groups known as herds, which vary in size and composition depending on the species. Impalas gather in groups of 15 to 100 animals and exhibit many different herding behaviours (Smith & Cain, 2009). Large herds tend to contain only females and their newborn young while males congregate in smaller bachelor herds. However, during the breeding season, sexually mature males will gather and monopolize a herd of females to mate with them. The male is tasked with defending the herd from predators and external males trying to mate with the females in the herd (African Wildlife Foundation, n.d.). This is likely because only males possess the horns needed to deter enemies (NHPBS, n.d.). In comparison with impalas, hartebeests tend to form herds of up to 300, and offspring tend to remain with their mother for the first 3 years after birth (African Wildlife Foundation, n.d.). Males occasionally form bachelor groups containing less structure compared to those of the impalas. Both male and female hartebeests have horns and can adequately survive on their own (NHPBS, n.d.). Mothers will protect their young from other males trying to separate the family and will periodically move in and out of male groups to mate (African Wildlife Foundation, n.d.).

Consequently, a plausible explanation for this discrepancy is sexual dimorphism, the target of this study. Through camera trap photo analysis, it will be determined how sexual dimorphism affects herd composition in impalas and hartebeests. It is hypothesized that sexually dimorphic species, such as impalas, tend to live in larger groups with animals of the same age, while non-sexually dimorphic species, such as hartebeests, tend to live in smaller groups with their young. It is also predicted that impalas will have larger average herd sizes with fewer offspring present, while hartebeests will have smaller average herd sizes with more offspring in the group. This is predicted because sexually dimorphic species are prone to more male aggression and females have no method of defending themselves from predators as they lack horns (Pandolfi et al., 2021). This may push females to live together in large groups for increased protection. Comparatively, non-sexually dimorphic animals all have horns so females can be self-sufficient in defending themselves and their young. Newborn offspring whose horns have not fully developed will have to remain by their mother's side until they can fend for themselves. Additionally, animal independence can be a favourable trait as it allows animals to spread out more and disperse, decreasing intraspecific competition for food (Packer, 1983).

Methods

To form our data set, 60 images from camera trap photos acquired from the "WildCam Gorongosa" project on the WildCam Gorongosa online website were collected. Photos were collected from their existing data set and were taken at random through the "classify" function which displays the images one at a time for viewing. The study site, Gorongosa National Park, is located in the Great Rift Valley in Mozambique and contains many habitats including savannah, woodlands, and grasslands where sexually dimorphic and non-sexually dimorphic species are found. Cameras are positioned adjacent to landmarks, important ecological structures, and food sources throughout the park to gather data in areas with high species richness and animal density. The cameras run continuously, including at night, and utilize software that automatically takes a picture when it detects movement. The first 30 photos that included hartebeests and the first 30 photos that included impalas were collected, regardless of the number of animals or species present. For a photo to be valid, all animals in it must be identifiable without any confusion or approximation of how many animals can be seen. Impalas and hartebeests are easily distinguishable as they have distinctive horns and fur colouration. There were no other requirements for the photos, and they were obtained by manually refreshing the WildCam Gorongosa website on the "classify" tab to generate a new image until the data set was complete.

The behaviours and categories that were measured were herd size and the number of offspring present. To determine the effects of sexual dimorphism on herd size, the total number of impalas or hartebeests in each photo for the target species was counted. To measure the proportion of offspring present, the number of young seen in all photos was counted where young was defined as an animal that was not fully mature in size and physiological features. In addition, the proportion of the herd that was offspring was calculated, by dividing the number of identified offspring by the total number of animals seen in the photo.

The species-specific data sets are independent of each other as they feature different species with no overlap. Additionally, both data sets did not follow a standard normal distribution, so a non-parametric test was required. Thus, the Mann-Whitney U statistical test was used to determine the significance between the data sets. The p-value between the subject groups for each of the suspect behaviours, herd size and offspring count, was counted. Our p-value and data were visualized using box plots. A p-value threshold of 0.05 was applied and Microsoft Excel 2016 was used to record and compile data, perform calculations, and generate figures.

Results

Table 1: Table containing the sample size, sum, mean, and standard deviation for the number of animals seen in photos taken from the WildCam Gorongosa website for both impalas and hartebeests.

	Impalas	Hartebeests
Number of Pictures Analyzed	30	30
Total Number of Individuals Seen	115	64
Mean Number of Individuals Seen Per Photo	3.833	2.133
Standard Deviation	3.60	1.55

Table 2: Table containing the sample size, sum, mean, proportion, and standard deviation for the number of young seen in photos taken from the WildCam Gorongosa website for both impalas and hartebeests where young is defined as an animal that is not fully mature in size and physiological features.

	Impalas	Hartebeests
Number of Pictures Analyzed	30	30
Total Number of Young Seen	12	21
Mean Number of Young Seen Per Photo	0.4	0.7
Mean Proportion of Young Seen Per Photo	0.104	0.208
Standard Deviation	0.813	1.24

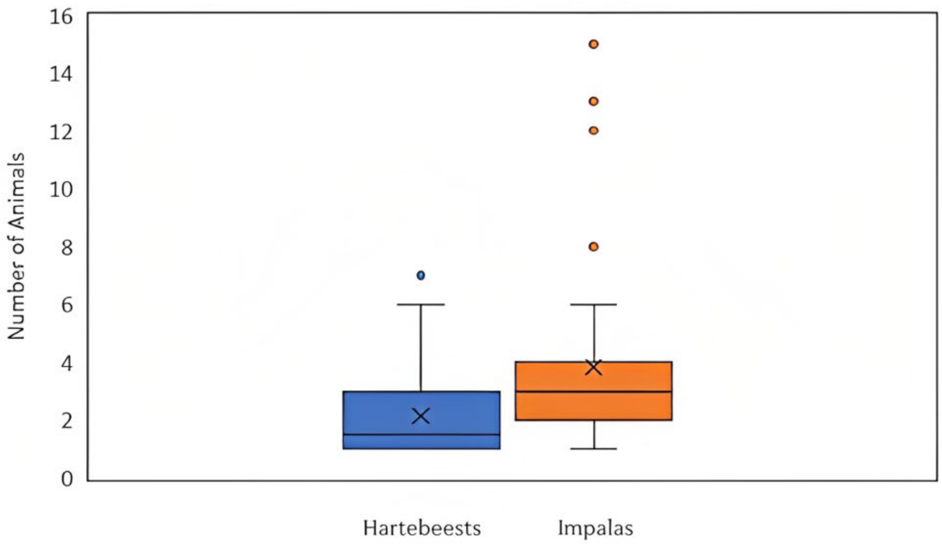

Figure 1: Numbers of hartebeests and impalas across 30 photos of each species gathered from the WildCam Gorongosa project. On average per photo, 2.13 +/- 1.55 hartebeests and 3.83 +/- 3.60 impalas could be seen (Mann-Whitney U test p-value = 0.0191).

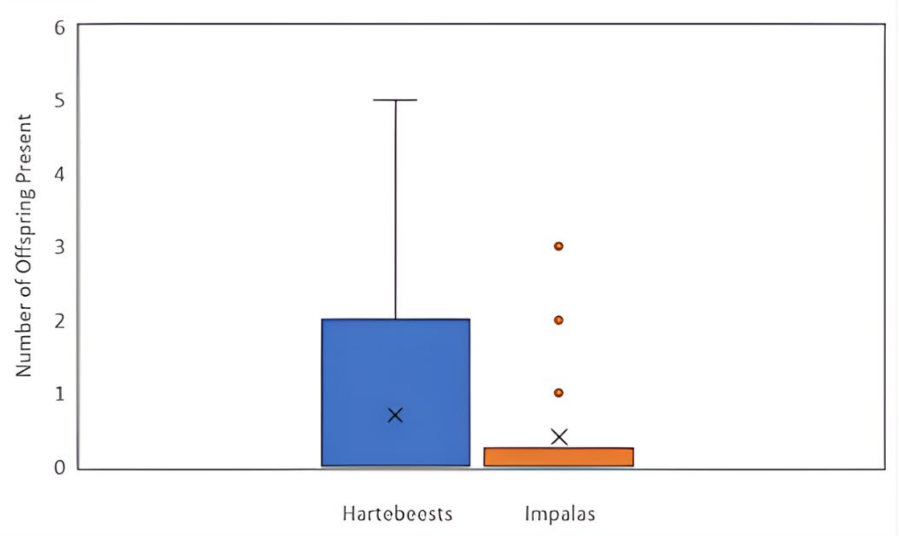

Figure 2: Numbers of hartebeest and impala offspring seen across 30 photos of each species gathered from the WildCam Gorongosa project. On average per photo, 0.7 +/- 1.24 hartebeest young and 0.4 +/- 0.813 impala young could be seen (Mann-Whitney U test p-value = 0.554).

Comparing impalas to hartebeests, the mean number of impalas seen per photo (3.833 +/- 3.60) was higher than the mean number of hartebeests seen per photo (2.133 +/- 1.55), and the result was statistically significant with a significance level of 0.05 ($p = 0.0191 < 0.05$) (**Figure 1**). Additionally, across all 30 photos, there were more impalas sighted (115) than hartebeests (64) (**Table 1**). Impalas are found living in larger groups than hartebeests.

Comparing the number of young impalas to young hartebeests, the mean number of impala young per photo (0.4 +/- 0.814) was lower than the mean number of hartebeest young seen per photo (0.7 +/- 1.24); however, this result was not statistically significant with a significance level of 0.05 ($p = 0.554 > 0.05$) (**Figure 2**). Across all 30 photos, there were more hartebeest young sighted (21) than impala young (12), and the proportion of offspring present was higher in hartebeests (0.208 > 0.104) (**Table 2**), but the difference was also not significant. Impala and hartebeest herds had similar composition and number of offspring present.

Discussion

It was determined that there were more impalas than hartebeests seen in photos and the result was statistically significant ($p = 0.0191 < 0.05$), meaning impalas tend to live in larger groups than hartebeests. Thus, this supports the prediction that sexually dimorphic species, like impalas, tend to live in larger groups than non-sexually dimorphic species, like hartebeests, and the null hypothesis with relation to herd size can be rejected. A plausible explanation for this is that sexually dimorphic males typically compete with each other for females which might encourage females to group up into large herds. Females also do not have any weapon to defend themselves with so they may cluster together for increased protection in numbers (Smith & Cain, 2009). Contrarily, non-sexually dimorphic species may roam around freely or in smaller groups as each animal is equipped with a defence mechanism, horns, and females do not need help protecting themselves from other females or males. In a study on *Ourebia ourebi* (oribi), a smaller sexually dimorphic species of antelope, it was determined that female oribi tend to gather in large groups and recruit other animals to join their group for protection against predation (Goldspink et al., 2002). It was also found that males were at a significantly higher risk of predation as they were found to be protecting the females when predators approached (Goldspink et al., 2002). This agrees with the findings from this study and similar behaviour patterns can be seen in impalas and oribi.

It was also discovered that there was no statistically significant difference between the number of young found in impala and hartebeest herds. This means the null hypothesis with regard to herd composition can not be rejected, and there is likely no difference between the age composition of sexually dimorphic species' herds and non-sexually dimorphic species' herds. The number of juveniles in a herd is not significantly affected by any factors and follows a very linear pattern across species of antelope (O'Kane, 2016). Predation and environmental factors have a larger effect on the adult species which are forced to adapt to changing conditions rather than on the reproductive and parental processes (O'Kane, 2016). It is probable that life history traits have a strong genetic basis and are predetermined at birth, decreasing the impact of environmental effects (Pettay et al., 2005).

The results of this study also agree with Jarman's hypotheses, a theory that sexual dimorphism is a result of variation in habitats and feeding methods (Szemán et al., 2021). Jarman postulated that these factors would influence the geographical distribution of females which would in turn affect a male's ability to find a mate. Because females tend to group together, it is easy for one male to monopolize a group of females leading to polygamous mating. It is ultimately an interspecific conflict between males defending their females from other males that evolutionarily gave rise to sexual dimorphism as males with horns would easily outcompete those without horns (Jarman, 1974). This is highly applicable as it illustrates that large imbalances in population distribution are the cause of sexual dimorphism. Consequently, it is logical that sexually dimorphic species would be seen in species that exist in larger groups of females. The offspring ratio remains unaffected as antelope breeding patterns remain fairly consistent.

Additionally, herd composition may also apply to conservation and animal monitoring efforts (East, 1999). It has been shown that high levels of anthropogenic disturbance in the Serengeti National Park led to a behavioural change in impalas where the animals demonstrated social conformity and a strong, female-biased sex ratio (Setsaas et al., 2018). This bias is a consequence of sexually dimorphic traits being favourable and targeted during hunting, implying that certain species may be at a higher risk of population decline (Setsaas et al., 2018). A skewed sex ratio also disrupts the social balance within the species' herds, and the lack of males may make defending against predators more difficult, further pushing the population decline. Consequently, the large group sizes typical of impalas are predicted to begin to break down as males are not around and the reproductive rate will plummet (Setsaas et al., 2018). Sexually monomorphic species likely do not experience these pressures to the same degree because of the physical similarities between the sexes.

The limitations of this study include a lack of phylogenetic analysis and limited sample size. Impalas and hartebeests are phylogenetically related species; however, the resources were not available to conduct a complete analysis of the phylogenetics for other antelope species. These results are limited in relation to which animal species it applies to because other sample species could generate different results (Brashares et al., 2000). Additionally, our data set was limited to the photos from the WildCam Gorongosa project in the Gorongosa National Park. The habitat types and number of camera traps are limited, so the photos may not be a fully accurate representation of the entire ecosystem. The data could have been skewed as only the most common habitats in the Gorongosa grasslands are represented. A Mann-Whitney U test was also used which is a non-parametric test as our data did not fit into a normal distribution which makes the statistical analysis less rigorous.

Future studies could expand the study zone and incorporate multiple different species of antelope to investigate if the findings can be generalized to a broader range of species or populations in different areas. This may ultimately provide insight into environmental or phylogenetic influences on behaviour-based decision-making. Additionally, sex distribution and herd composition should be analyzed to provide further support for Jarman's hypothesis and to verify the proposed mechanism behind the variation in herd size that was discovered. Moreover, genetic analyses can be done to identify potential genetic factors or genes that may influence herding behaviour. Their potential varying presence between sexually and non-sexually dimorphic species may provide insight into the evolutionary stresses on specific social behaviours and decisions such as the increased likelihood of group travel in sexually dimorphic females.

Conclusion

By analyzing camera trap photos from the WildCam Gorongosa project, it was discovered that impalas tend to live in larger groups than hartebeest and that there was no difference in the age distribution of the populations. Sexual dimorphism in impalas does impact their herding behaviour in relation to size, and our findings agree with previous studies in the literature (Goldspink et al., 2002). Sexually dimorphic species are seen in larger groups because females need to cluster together for protection as they do not have horns to defend themselves. These findings are important as they provide a mechanism to explain common herding behaviour and provide a better understanding of why these antelope species behave the way they do. With these findings, conservation efforts can be more effectively applied, and tracking the population size and composition of both impalas and hartebeests in the Gorongosa grasslands will become easier as a result of knowing what herd behaviour is expected. Anthropogenic impact on natural habitats is exponentially increasing so it is necessary to monitor any changes that are occurring. Measuring anthropogenic effects on the populations may also become easier to do and illustrate as a result of this deeper understanding (Jah & Isvaran, 2022). If this study is repeated and deviations from the results are seen, it could indicate a change in antelope behaviour and further investigation should be done to assure that the population is not threatened, and antelope habitats have not been negatively altered.

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