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### Have stripe patterns influenced the social behaviour and cohesion of the plains zebra (Equus quagga)?

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# Have stripe patterns influenced the social behaviour and cohesion of the plains zebra (*Equus quagga*)?

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### Abstract

Uncovering the mystery of why zebras have a striped pelage has been widely theorised. There are many answers why, however, this study aimed to determine the role that stripes have on social behaviour and cohesion of zebras. The data used in this study was collected at Addo Elephant National Park (AENP) in the Eastern Cape of South Africa. The hypothesis has been supported by some studies that suggested stripes provide visual markers for social interactions such as grooming, thus enhancing the social bond between two individuals. This study aims to prove or disprove this hypothesis. AENP is home to plains zebras (Equus quagga) that have a large variety of stripe numbers as a result of a selective breeding programme that aimed to bring back the quagga (Equus quagga quagga) phenotype. I tested the role that striping plays in social interactions, nearest neighbour distances, group size and group leadership. The results cast doubt on the hypothesis that stripes provide visual markers or enhances social bonding as there is no relationship between striping, social behaviour and cohesion. The study also discovered that nearest neighbour distances were influenced by factors that were non-striped related such as age, sex and habitats. Results showed that males distanced themselves further away than females in their social groups. Also, juveniles remained closer to other group members than adults. In open grassland habitats individuals displayed greater nearest neighbour distances, whereas individuals remained very close together by waterholes. ANEP historically was home to the quagga and so selection may be favoured for plains zebra with the quagga phenotype in this area. With the wide variety of stripe numbers at ANEP, it still represents an ideal site to continue with this study on the mystery of stripes. Following this study, a greater emphasis should be placed on studying the non-social functions of stripes.

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### Introduction

Social behaviour and cohesion are often actively observed within many species of animals. Social animals generally unify together and form social groups which in turn can influence the fitness of an individual (Bronikowski & Altmann 1996; Whitehead & Rendell 2004; Lusseau *et al.*, 2006). Sociality can often determine the survival and reproduction of a species (Dunbar, 1988; Brent, 2015). The increase of social cohesion can provide fitness benefits for each individual (Krause & Ruxton, 2002). An increased number of relationships with different individuals can result in an increased rate of reproduction (Wey *et al.*, 2008). Grouping of individuals in prey species can be used as an effective anti-predator mechanism (Krause & Ruxton, 2002). The use of this mechanism can increase predator vigilance (Treherne & Foster, 1980), confusion (Fels *et al.*, 1995) and communal defence (Bertram, 1975). Social grouping can also benefit carnivorous hunting species. African wild dogs (*Lycaon pictus*) undertake group hunting which increases their chance of kill success (Creel & Creel, 1995).

Although social cohesion provides many fitness benefits, it can provide some fitness costs as well. Examples of these consequences can include the increased exposure of pathogens and parasites as highly socially active individuals encounter a greater number of different individuals (Wey *et al.*, 2008). Also, intraspecific competition for resources can occur within a social group (Krause & Ruxton, 2002). Even though there are costs of sociality, the positive outcomes seem to be highly beneficial to most socially active species.

Intraspecific pelages are evident in the natural world, which can provide a wide array of advantageous adaptations. Pelage is often defined in zoological terms as the fur, hair, or wool of a mammal. Examples of the variation found on pelages can be the darkness of a pelage; number of spots and stripes. Often variation in pelage colouration is a mechanism used in individual concealment (Stoner *et al.*, 2003; Caro, 2005). However, in some cases, the levels of social behaviour and cohesion can correlate with the variation of a species' pelage. Studies have found the dominance ranking, leadership and sexual selection of an individual can correlate with the darkness of a pelage. Examples of this can be found within the Dall sheep (*Ovis dalli*) where males with darker faces have a higher hierarchical rank (Loehr *et al.*, 2008). Colouration can also show indicators of sexual selection succession in African Lions (*Panthera leo*). This is observed via the darkness of the individual's mane (West & Packer, 2002). However, in both cases, the darkness of the pelages can often relate to the condition of the individual. In lions, older males with a high nutrient intake often will display a darker mane. So, darkness of a pigment is more likely an indication of condition rather than an adaptation to increase fitness. Stoner *et al.* (2003) had suggested spotted pelages in adult ungulates may be used as a mechanism to reduce intraspecific aggression. This is suggested as spotted pelages are often

represented by young and subordinate individuals which discouraged the agonistic interactions against them. However, the study concluded the main function for spotted pelages was a mechanism for concealment.

The evolutionary forces leading to the development of striping on animal pelage has perplexed many biologists including the founding fathers of evolutionary biology Charles Darwin (1871) and Alfred Russel Wallace (1891). One notable striped pelage is of the zebra. There are three extant species of zebra, with each species possessing striping along the entirety of their bodies. The zebra species include the plains zebra (Equus quagga); mountain zebra (Equus zebra); and Grevy's zebra (Equus *grevyi*). It is still unclear why the zebra evolved these striped pelages (Gosling, 2017). The three zebra species are part of the Equus genus in which there are currently seven extant wild species. The other four species of wild equids are African wild ass (*Equus africanus*); Asiatic wild ass (*Equus hemionus*); kiang (Equus kiang) and Przewalski's horse (Equus ferus przewalskii). Thin black stripes are present on the legs of the African wild ass and occasionally on the Przewalski's horse. However, stripes are completely absent on the pelages of the Asiatic wild ass; kiang and often on the Przewalski's horse. Prominent striping is found on other non-equid species however the numbers of species are very few (especially in ungulates, similar to the zebra). Examples of striped ungulates include the bongo (Tragelaphus eurycerus); okapi (Okapia johnstoni) and zebra duiker (Cephalophus zebra). Although the striping patterns found on these ungulates differ to the zebra. Furthermore, hypotheses on the functionality of the stripe patterns on the ungulate also differ to the zebra (Kingdon, 1979; 2015). The origins of stripe patterns have been subject to much research and debate, and many questions surrounding the function of stripes remain unanswered.

Recent discoveries identified that the extinct quagga species (*Equus quagga quagga*) is in fact a subspecies of the plains zebra (Higuchi *et al.*, 1984, 1987; Lowenstein & Ryder, 1984). The quagga only possessed stripes on the front half of its body whereas the plains zebra possesses stripes throughout the entirety of its body. This raises questions as to why the plains zebra has evolved more stripes than its subspecies counterpart (Ruxton, 2002). Leonard *et al.* (2005) suggested that the reduction in striping of the extinct quagga was as a result of their habitat, which was more open and drier. This may be linked with the hypothesis that stripes help ectoparasite prevention (Waage, 1981; Caro *et al.*, 2014). It is suggested that fewer ectoparasites can survive drier climates compared with more mesic and temperate environments (Kimura, 2000; Malenke *et al.*, 2010). This potentially could explain why the quagga had an absence of stripes, since the species had fewer conflicting interactions with ectoparasites. However, there have been multiple hypotheses as to why these stripes have evolved on the plains zebra. These hypotheses include anti-predator avoidance & confusion (Kingdon, 1984; McLeod, 1987; Ruxton, 2002), ectoparasite prevention (Waage, 1981; Caro *et al.*, 2014), thermoregulation (Morris, 1990) and social behaviour & cohesion (Kingdon, 1979, 1984; Morris, 1990; Ruxton, 2002). The hypotheses identified in the literature completed by Kingdon (1979, 1984), Morris (1990), Ruxton (2002) and Caro (2016) were of particular interest as there has been very little testing on how social behaviour and cohesion relates to striping on zebras (Ruxton, 2002). I hypothesised that striping has an influence over the social behaviour and cohesion of the plains zebra.

The plains zebra are a gregarious equid that heavily rely on group cohesion during their lifetimes (Klingel, 1974). The social organisation of the plains zebra is classified as a Type I, in which a polygynous mating system occurs (Klingel, 1975). Polygynous mating system meaning multiple females to one sexually active stallion in a harem type group (Rubenstein, 1994). Group stability is considered an important aspect of social cohesion. A study by Overdorff et al. (2005) defined group stability as the consistency of leadership for group movement. As a result of the suggestion made by Overdorff et al. (2005), harems are considered to be a stable unit owing to the tight knit interactions between each individual and the despotism, which is evident in some groups (Neuhaus & Ruckstuhl, 2002; Fischhoff et al., 2007a). A harem is usually expected to have around one to eight adult females (Fischhoff et al., 2007a). The females create strong social bonds with each other and will usually remain in the same harem for the rest of their reproductive life, even with the turnover of different stallions (Rubenstein, 1986; Rubenstein & Hack, 2004). The offspring will eventually break away from their natal families and join other groups once they have reached their sexual maturity. The age at which young individuals disperse from their natal families is usually from 2 to 4 years old (Berger, 1987). The young females (fillies) will move into other harems, whereas the young males (colts) will tend to join and form bachelor groups. Plains zebras do have a multi-level society system. The multi-level societies consist of a two-tiered system in which the first tier is the harem (core breeding group) and the second tier is the herd (Rubenstein & Hack, 2004). Herds will usually contain multiple harems. Plains zebra are not considered to be territorial and, so it is not uncommon to see multiple harems together in one location (Klingel, 1977). Rubenstein & Hack (2004) suggest that harems form together to counter the effects of bachelor harassment. However, herds tend to be fluid and unstable as a result a lack of consistent leadership within.

As there is a high ratio of females in a harem, there can often be a surplus of males. This surplus of males will consolidate to form bachelor groups which are exclusive to males (Penzhorn, 1984). The males will remain in these bachelor groups until they improve their condition and are able to outcompete other stallions and gain a harem (Rubenstein, 1994; Fischhoff *et al.*, 2007a, 2007b). Most of the members of the bachelor groups are colts however stallions that have been displaced from harems also join bachelor groups (Penzhorn, 1984). In addition, males can be seen alone; however,

these are usually stallions that have been recently displaced from their harem due to driving factors such as old age and illness (Klingel, 1975; Rubenstein, 1986; Boyd & Keiper, 2005; Boyd *et al.*, 2016)

As social cohesion and behaviour is important in the life of the plains zebra, the hypotheses that stripe patterns influence these social factors should be investigated. Kingdon (1979, 1984) suggested that social interactions, such as grooming, favours animals that display stripes. This hypothesis assumed that stripes are used as visual markers to direct companions to certain parts of the body (neck and withers) for grooming, thus, promoting mutual grooming and social bonding. Cloudsley-Thompson (1984) also supported the hypothesis of visual markers. However, there are some flaws to this hypothesis as stripes are visible on parts of the zebra which wouldn't ordinarily be an area where grooming would occur (Ruxton, 2002). In addition, mutual grooming is an intraspecific interaction that is evident between individuals of non-striped species (Mooring *et al.*, 2004). A study made by Melin *et al.* (2016) could not support the suggestion that striping enhances social grooming and bonding, as evidence indicated a zebras' vision is less capable of seeing stripes than humans.

Morris (1990) suggested that "the stripes operate as a form of visual bonding between members of each herd. They are thought to make each zebra feel it belongs more strongly to its group than it would do if its colours were nondescript or dull". As a result of this suggestion, it is assumed that the striped equids would have the tighter-knit groups. The strength of a species sociality can be displayed via the group size and nearest neighbour distances within the social group. Kingdon (1979) noted that Grevy's zebra have a shorter nearest neighbour distances than domestic horses (*Equus ferus caballus*), in which he suggested that the stripes could be the driver.

Identification of individuals is also a hypothesis suggested by Morris (1990) in which he states that zebras can identify individuals via their unique stripe patterns. Plain zebras have been observed searching for lost members and so individual identification is evident (Klingel, 1972). An example of recognition, which is found in equids, is the relationship with a mother and her foal. Wallace (1877) also speculated stripes could be used as a mechanism for identification. He stated, "stripes therefore may be of use by enabling stragglers to distinguish their fellows at a distance". However, the study by Morris (1990) goes on to say that wild horses have the same identification mechanisms without the stripe coating. Individual recognition can also be found in domestic horses where Proops *et al.* (2009) discovered that domestic horses use vocal recognition as well as visual recognition to identify individuals within their social group. This information relating to other equid species rejects the hypothesis of personal recognition due to stripe patterns. Kingdon (2015) suggested that stripes may also be served as a visual bonding device that causes individuals with stripes to be very attractive. As

a result of numerous recent suggestions that individual identification is not a function caused by striping, no further testing was required in this study.

The overall aim of this study was to discover whether stripe patterns on the plains zebra are related to aspects of their social behaviour or cohesion.

- The first hypothesis of this study examined the social interactions between individuals within a social group. The relationship between social interactions and stripe numbers was hypothesised as individuals with more stripes exhibit more social interactions between other members with their social group. This hypothesis is promoted by Kingdon (1984) and Cloudsley-Thompson (1984) hypothesis of stripes are used as visual markers aiding interactions such as grooming.
- 2. The second hypothesis of this study considered nearest neighbour distances to see whether the number of stripes influenced the distance between individuals in a social group. This was promoted by Morris (1990) as he suggested that striping helps form strong bonds between individuals in social groups. Kingdon (1979) also suggested that Grevy's zebra have short nearest neighbour distances than domestic horses as a result of their stripes. This hypothesized that individuals with less stripes exhibit greater distances to their nearest neighbour.
- 3. The third hypothesis of this study examined group size to see whether zebras with less stripes will be part of social groups containing less individuals. This hypothesised that individuals with more stripes will be members of larger social subgroups. This also coincides with the assumption that stripes increase the social bonding of individuals (Morris, 1990).
- 4. The final hypothesis of this study identified the leaders within each group to establish if leadership has a relationship with striping. It is hypothesised that individuals with more stripes show greater leadership within their harem. The studies put forward by West & Packer (2002) and Loehr *et al.* (2008) supported that pelage colouration correlates with the hierarchical rank of an individual. However, these studies were not investigated on equids or striped pelages.

### Methods

### Study site and species

### Study Site

The study site for this research was Addo Elephant National Park (AENP) (33°30'S, 25°45'R). AENP is located near the southern coast of South Africa and is north-east of Port Elizabeth. AENP is the third largest national park in South Africa and has an area of 1,640km<sup>2</sup>. The data collection took place in the Main Camp and inland Colchester section of the park. The altitude ranges between 60 to 350 metres above sea level within the study site (Gray *et al.*, 2017). The park is mainly made of up of semi-arid grasslands and woodlands mainly dominated by the shrub *Portulacaria afra* (Archibald, 1955). The annual rainfall of AENP is around 400 mm, however most of this rainfall occurs during spring and autumn (Hoffman, 1989). The mean temperature is around 18°C; however, temperature can reach up to 45°C in the summer and very rarely temperatures drop below 0°C in winter (Lombard *et al.*, 2001). The field data was collected during a period of nine weeks between the months of January to March 2018. The research was conducted within the summer season and there were no extreme differences in climate during the time of data collection.

### Study Species

The target species in this research is the plains zebra (*Equus quagga*). Plains zebras are found throughout East and Southern Africa in semi-arid grassland and open woodland habitats (Fischhoff *et al.*, 2007b; King & Moehlman, 2016). They are a mid-sized equid with a shoulder height between 1.27-1.40 metres and weigh between 175-322 kg (Kingdon, 2015). Males are usually around 10% larger than the females. This is the only visible dimorphism between the two sexes other than the sexual organs (Estes, 1991).

Currently AENP has a large population of plains zebra within the park boundaries with a variety of stripe patterns which makes it an ideal study site to test and complete research. The variety of striping was as a result of the Quagga Project that undertook selectively breeding plains zebras to reduce their stripes, that would be similar to the quagga (*Equus quagga quagga*) phenotype. These zebras have been released into the National Park.

During this study age was categorised into two categories being adults and juveniles. The adults were fully grown and over the age of four years, whereas the juveniles were not fully grown and were dependant on an adult female. Whether an individual was fully grown or not, was based on the height of the individual. The social organisation of each group was also identified and recorded as part of the study. All known social groups of plain zebras were identified (bachelor, harm and mixed group). An unknown group was also categorised and included individuals that could not be identified or sexed. This was generally as a result of poor visibility of the group. A unique group was defined as a group consisting of over 50% of the same individuals from a previously observed group.

My research identified 614 unique individuals at AENP: 50% were found in harems, 29% found in mixed groups, 27% in bachelor groups and <5% of the unique population were found on their own (the percentage identified in the mixed group includes some individuals from both harems and bachelor groups). Two-hundred and thirty (230) individuals were female (37%), 322 were male (52%) and 62 were unknown. The total number of social groups observed were 211 and 153 of them were unique. One-hundred and thirty-two (132) individuals were found in two or more unique groups.

The mean harem size at AENP number was within the average group sizes suggested by Fischhoff *et al.* (2007a), which was two to nine adults (including the stallion; Fig. 1). Bachelor and harem mean adult group size were also very similar (Fig. 1). The results from mean group sizes show that bachelor and harems have similar group sizes (4.8 & 5.8 [overall], 4.8 & 4.6 [adults only] respectively) within the park (Fig. 1). Also, because mixed groups are a collection of harems and bachelor groups, it was of no surprise that the mean group size of mixed groups was more than double that of bachelor and harem groups (Fig. 1).





All individuals within the bachelor subgroup were male (Fig. 2). This evidence shows that colts will leave harems (forcefully and voluntarily) and join up with other males until they are strong enough to

lead a harem of their own (Penzhorn, 1984). Fig. 2 also shows that more females were found within harems than males (3 & 2 respectively). This evidence is also supported by other studies as plains zebra form polygynous mating systems (Rubenstein, 1994). Also, females were found more in mixed groups than males (6 & 4 respectively; Fig. 2). It was established that mixed groups are mostly a collection of harems (Klingel, 1977; Rubenstein & Hack, 2004). However, the difference between females and males was smaller in mixed groups than harems as bachelor groups were also found with the mixed groups. Lone individuals were also more likely to be male (Fig. 2). It is likely this is as a result of a stallion being displaced by another male or a colt that has reached sexual maturity and has left his natal group. Overall, there were more males at AENP than females (3 and 2 respectively; Fig. 2).



**Fig. 2:** The mean number of each sex within the population at AENP. The mean has been split between each subgroup and shows the overall mean. This data included adults and juveniles.

The majority of individuals in the bachelor groups were adults (Fig. 3). This is as a result of colts reaching sexual maturity and displaced stallions forming groups My results noted that there were no juveniles found on their own – juveniles were only found in harems and mixed groups (1 & 2 respectively; Fig. 3). Juveniles stay in their natal groups and depend on their mother's care.

Harems were the most common sub-group within AENP populating 42% of the 162 unique groups. Harems are the main breeding core within a plains zebra's population. Thirty Percent (30%) of the groups were bachelor groups. 13% of the observed groups were found mixed groups, 9% were noted to be lone individuals and 6% were unknown groups.



**Fig. 3:** The mean number of each age group within the population at AENP. The means have been split between each subgroup and show the overall mean.

### Field Methods

### Stripe Collection

Zebras were detected while driving along the tracks of AENP. Usually two sectors could be covered in a day and I made sure each sector was covered equally. Data collection started around 7am and finished around 4pm, in between these times the light available was sufficient enough to analyse the stripe patterns. Each individual zebra observed during the period of research was scored via a zebra striping scoring system, which I and other associates designed. This scoring system considered the number of stripes on six sections of the zebra's body, including the head; neck; torso; underbelly where the strips are connected to the groin line; rump; foreleg; and hindleg (Fig. 4). The scoring system allowed me to see the number of stripes on each section on the body, overall stripe number, and the mean overall stripe number of individuals in a social group. Photographs on both the right and left flank of the individual were taken and used to support the scoring system. The scoring system was similar to the measures which Caro *et al.* (2014) and Larison *et al.* (2015) used. However, the thickness of the stripes (Larison *et al.*, 2015) was not considered in my study. The saturation of the stripes was also not quantified to the extent that Caro *et al.* (2014) and Larison *et al.* (2015) made. Although in my study, the dark pigment was distinguished between stripes and shadow stripes based on the saturation. Plains zebra are the only extant zebra species to possess shadow stripes (Bard, 1977; Caro



**Fig. 4:** A diagram of the different regions for stripe scoring. 1. = Head, 2. = Neck, 3. = Torso, 4. = Underbelly, 5. = Foreleg, 6. = Hindleg.

et al., 2014). Shadow stripes are a faded grey coloration and are usually found in between the dark striping predominantly on the rump, legs and torso of a plains zebra. Although, shadow striping is also evident on the neck of plain zebra. As part of the stripe count, shadow stripes were included and counted separately to the dark black stripes on the individual. Photographs taken of individuals helped contribute to а stripe code algorithm 'StripeSpotter' (sourced from code.google.com/archive/p/stripespotter/ a program developed by the University of Illinois and Princeton University) that allowed me to identify each individual zebra. To ensure a consistent approach was made to counting stripes in the different sections on the body of the zebra, myself and two other participants counted the stripes on the same twenty images of zebras and compared each other's stripe count. The aim of this approach sought to ensure stripes were being counted consistently and each region of the body was being differentiated. The images were then categorised into levels of quality. Quality was split into four different levels:

- Level one identified that the image displayed all regions of the body with no distortion.
- Level two identified that the image displayed all the regions however there was slight distortion present.
- Level three identified that the image was distorted.
- Level four identified that the image did not display all regions of the body.

After quality scoring each image, level three and four quality scores were disregarded in the stripe scoring database however, these images did have regions in which stripes could be compared with other individuals to see whether they had previously been sampled. The images used in the stripe code algorithm helped identify resamples of individuals allowing me to maximise the chance of a unique stripe score for each individual.

### Hypothesis 1 – Social Interactions

As part of the social cohesion aspect of my research, I utilised multiple working hypotheses to test the influence striping may have on social interaction. Social interactions were identified as part of mutual grooming; threats and agonistic behaviour (such as biting and kicking); body rubbing; head resting; play; suckling and threats and recorded for each individual. This research was achieved by recording a 5-minute focal sample of each social group observed. All visible members of the group present in the 5-minute video clip were observed to see the number of social interactions they gave and received. The data taken from this focal sample allowed me to see whether stripes had an influence on the number of social interactions. The rate and the duration of each interaction was recorded. This allowed me to discover whether striping influenced how many times an individual interacted and how long each interaction lasted. In contrast to Caro's (2016) testing on mutual grooming, I considered

grooming as an overall interaction and did not specify which regions of body were groomed. Testing also considered the habitat type, group size and group type during the period of observation to determine if this had an influence on the rate and duration of interactions. Habitats were considered in this testing because there are higher risks of predation in different habitats (Hayward & Kerley, 2005; Fischhoff et al., 2007b). Predators such as the African lion are present at AENP and so predation can occur. Lions will hunt during the day; however, it is less frequent than they would at night (Schaller, 1972). During the day, lions are more likely to hunt at more closed bushier areas of the park (Elliot et al., 1977). This can cause zebra to become more vigilant in these habitats (Périquet et al., 2012), thus discouraging social interactions between group members. The analysis will determine whether social interactions are influenced by stripe number in the different habitats at ANEP. Studies show that smaller groups of prey species tend to show higher levels of vigilance (Creel et al., 2014). This vigilance may also have an influence of the levels of social interactions. Social interactions were also compared between the different social groups. Females within a harem tend to have strong bonds between each other (Rubenstein, 1986; Rubenstein & Hack, 2004), thus potentially initiating more interactions in harems compared with bachelor and mixed groups. A total of 19.17 and 16.17 hours of footage was recorded for the total interaction and mutual grooming analysis respectively.

### *Hypothesis 2 – Nearest Neighbour Distances*

Nearest neighbour distances were measured as part of this study by using a range finder that gave an approximation of the distances between each individual and the observer. In addition, the angle between each individual and the observer was measured using a compass. The distance between the two zebras was calculated by using trigonometry calculations. Only the smallest distance for each individual was regarded as the nearest neighbour distance. The distances between the individuals were calculated in metres. Resamples were recorded during this testing, and as a result resampled individual's distances were averaged into a mean nearest neighbour distance. The striping score of an individual was analysed to consider whether there were any relationships with the nearest neighbour distances. Similar to the social interaction testing, variables such as habitat type, group size and group type were considered. As a result of the different vigilance levels for the variation of habitat types and group sizes (Périquet *et al.*, 2012; Creel *et al.*, 2014), this may result in a difference in nearest neighbour distances. The analysis investigated to see whether striping influenced the nearest neighbour distances within the different habitats and group sizes. On the grounds that each group type is structured differently, I investigated to see whether striping influenced nearest neighbour distances between the three social groups.

### *Hypothesis 3 – Group Size*

The research considered if there was a relationship between group sizes and the number of stripes in a group. This was achieved by calculating the mean striping score of an observed group and comparing it with the number of members within that social group. Group type was considered in this testing. My study also investigated whether striping had an influence on group size between the three social groups. This is because all three social groups have a different group composition where some groups are expected to contain females whereas others are exclusively male. Solitary individuals were not included for this hypothesis.

### Hypothesis 4 – Group Leadership

Finally, my research considered whether the number of stripes had an influence on the leadership of a social group. Dunmont et al. (2005) provides a definition of a leader within a social group as an "individual that is consistently the one who initiates long-distance spontaneous group movements toward a new feeding site". Usually social groups such as harems show signs of despotism, which means the group is consistently being led by one individual. A method of identifying leadership is analysing the movement of a group (Fischhoff et al., 2007a). The individual that edges to the front of the group when movement occurred was considered as the leader (Dunmont et al., 2005). Then the individuals behind the leader were positioned based on their ranked order of dominance (Klingel, 1972). Because the highest ranked female usually leads the group's movement and the stallion positions himself parallel or at the rear of the group, males were not included when analysing harems (Klingel, 1972). Bachelor groups were not included in the analysis. This is because Klingel (1972) suggested that within bachelor groups dominance ranking only occurs between the sub-adult members whereas all adult members are equal. Mixed groups were also not included. This is because leadership in herd movement is generally down to individuals with the strongest motivations to shift to another area to seek resources based on their needs (Rands et al., 2003). An example of this is that Fischhoff et al. (2007a) discovered that lactating females were usually at the leading edge of the herd and had strong motivations to seek resources. Signs of despotism are usually minimal due to the turnover of harems within the herd. Juveniles were not included in the analysis as they are usually found following directly behind their mothers during movement (Klingel, 1972). I also investigated whether leadership ranking influenced striping in different habitats of AENP. Movements of groups can last up to an hour (Fischhoff et al., 2007a), however as part of my study only one recording of each movement observed was measured. This data was recorded by taking images from a camera of the group whilst they were travelling to a different location. The observed individuals were identified and allocated a ranked order in relation to the position whilst travelling (e.g. rank 1 went to the individual at the front). A comparison was then made of the stripe scoring system relative to the individual's rank.

### Analysis

As part of the analysis for each hypothesis RStudio (v.1.1.453) was used. There were two types of linear models were used in the study. One being Mixed Effect Models (MEM). This was used when variables such as group ID and individual ID were regarded as random effects. In order to carry out the MEM, the Imer () function was used with "nIme", "Ime4" and AICcmodavg" R packages installed. Stargazer () function was also used in the analysis to create a visual table including all the necessary information, the stargazer R package was installed for this. The other linear model used in the study was a Generalized Linear Model (GLM). This was used when group ID and individual ID were not regarded as random effects. I used the Poisson GLM when the mean and variance of data were equal. In order to carry out the Poisson GLM, the glm () function was used with the "sandwich", "msm" and "ggplot2" R packages installed. Akaike's Information Criterion (AICc) was used for the model selection which assess the most supported models (Burnham & Anderson, 2004).

### Hypothesis 1 – Social Interactions

As group ID and individual ID were regarded as random effects for this hypothesis, the MEM was used. The models looked at relationships between rate and durations of interactions received and given with the predictor variables: total number of stripes and shadow stripes on an individual and total stripe number without shadow stripes. Habitat and group type variables were not included in a model as a single treatment as they are regarded as categorical data. As Cloudsley-Thompson (1984) and Kingdon (1984) suggest that stripes aid with mutual grooming, I ran GLMs that just focussed on mutual grooming. Mutual grooming was only observed between 9am and 2pm, this meant I only included footage between these times for the mutual grooming analysis. When group type was tested, bachelor groups were classed as the reference group. This is because the bachelor group were exclusively male and so have a different social organisation compared with harems and mixed groups which could cause a difference in social interactions. When habitats were tested, watering holes were classed as the reference group. This because the risk of predation at watering holes is high and so it is expected for individuals to be more vigilant when drinking or being in the vicinity of the watering hole (Crosmary *et al.*, 2012).

Candidate Models for Social Interaction Mixed Effect Models	n (overall Interactions)	n (mutual grooming)
Null	226	194
Group Size	226	194
Total Stripe and Shadow Stripe Number	160	136
Total Stripe and Shadow Stripe Number + Group Size	160	136
Total Stripe and Shadow Stripe Number + Group Type	160	136
Total Stripe and Shadow Stripe Number + Habitat	160	136
Total Stripe Number	160	136
Total Stripe Number + Group Size	160	136
Total Stripe Number + Group Type	160	136
Total Stripe Number + Habitat	160	136

**Table 1:** Structured candidate models assessed for the rate and duration of the total overall social interactions and mutual grooming interaction predictor variables.

*Hypothesis 2 – Nearest Neighbour Distances* 

Similar to the social interaction analysis, a MEM was used. However, because nearest neighbour distances were averaged for each individual, individual ID was not regarded as a random effect. Group ID was still regarded as a random effect for this analysis The models looked at relationships between nearest neighbour distance with the predictor variables: total number of stripes and shadow stripes on an individual; total stripe number without shadow stripes; total upper body stripe number and group size. I also investigated more complex MEMs and used variables such as habitat, group type and group size. When group type was tested, bachelor groups were classed as the reference group. This is because the bachelor group were exclusively male and so have a different social organisation compared with harems and mixed groups which could cause a difference in nearest neighbour distances. When habitats were tested, watering holes were classed as the reference group. This is because the area of the watering holes are the smallest compared with the other habitats at AENP. Also, the risk of predation at watering holes is high and so it is expected for individuals to be more vigilant when drinking or being in the vicinity of the watering hole (Crosmary *et al.*, 2012).

I also tested nearest neighbour distance with categorical variables that did not take stripe number into account. These variables were sex, age, habitat and group type. As these variables are not count data, GLM testing was not suitable. As a result, less complexed parametric tests such as t-tests and ANOVA's were used to analyse each different categorical variable. 
 Table 2: Structured candidate models assessed for the nearest neighbour predictor variable.

Candidate Models for Nearest Neighbour Mixed Effect Models	n
Null	346
Group Size	346
Total Stripe and Shadow Stripe Number	210
Total Stripe and Shadow Stripe Number + Group Size	210
Total Stripe and Shadow Stripe Number + Group Type	210
Total Stripe and Shadow Stripe Number + Habitat	205
Total Stripe Number	210
Total Stripe Number + Group Size	210
Total Stripe Number + Group Type	210
Total Stripe Number + Habitat	205
Total Upper Body Stripe Number	210
Total Upper Body Stripe Number + Group Size	210
Total Upper Body Stripe Number + Group Type	210
Total Upper Body Stripe Number + Habitat	205

Hypothesis 3 – Group Size

This data did not have group ID or individual ID as a random effect and so a GLM was used for this analysis. The variance and the mean of the data were similar and so the Poisson GLM was used. The model looked simple GLM's to investigate relationships between average group size with the predictor variables: total number of stripes and shadow stripes on an individual; total stripe number without shadow stripes. I also investigated more complex GLM's which included the variable group type because the use of categorical data as a single treatment was not suitable for a GLM. When group type was tested, bachelor groups were classed as the reference group as they were exclusively male and had a significantly different social organisation compared with harems and mixed groups.

 Table 3: Structured candidate models assessed for the group size predictor variable.

Candidate Models for Average Group Size GLM	n
Null	80
Average Stripe and Shadow Stripe Number	80
Average Stripe and Shadow Stripe Number + Group Type	77
Average Stripe Number	80
Average Stripe Number + Group Type	77

### *Hypothesis* 4 – *Group Leadership*

An index of leadership was established using the relationship between group leadership and stripe numbers via the formula developed by Fischhoff *et al.* (2007a) as Leadership =  $(2 \times \text{position} - 1)/(2 \times \text{Group size})$ . The index is scored from zero to one, and so individuals with smaller values represent greater leadership within a group. Similar to the Flschhoff *et al.* (2007a) study, I have not included harems with less than two females. Also, I did not include males, juveniles and members of bachelor & mixed group in the index. The Poisson GLM was used for this hypothesis. The model looked at simple GLM's with relationships between the group leadership rank index and with the predictor variables: total number of stripes and shadow stripes on an individual; total stripe number without shadow stripes; total upper body stripe number; total rump tripe number and group size. I also investigated more complex GLM's which included habitat type in the model. When habitats were tested, watering holes were classed as the reference group as the risk of predation is high and so it is expected that individuals are more vigilant when approaching and leaving the vicinity of the watering hole (Crosmary *et al.*, 2012). To support statistical significance in the GLMs a further test was used. Because the leadership rank data could not be transformed into normally distributed data, a nonparametric test was used. In this case the Kendall rank correlation coefficient test was used (Kendall, 1948).

Candidate Models for Group Leadership GLM	n
Null	29
Total Stripe and Shadow Stripe Number	29
Total Stripe and Shadow Stripe Number + Habitat	26
Total Stripe Number	29
Total Stripe Number + Habitat	26
Total Upper Body Stripe Number	29
Total Upper Body Stripe Number + Habitat	26
Total Rump Stripe Number	29
Total Rump Stripe Number + Habitat	26

**Table 4:** Structured candidate models assessed for the group leadership predictor variable.

### Results

### Hypothesis 1 – Social Interactions

Out of the 226 individuals that were observed, 76 individuals displayed social interactions between other members of their group. However, as a result of some individuals not having a full stripe score (or one at all), the value of 226 was not the actual sample size when analysing the relationship between social interactions and striping. The average rate for any social interaction to occur was 0.116 times per minute (Fig. 5). Mutual grooming which is an important interaction for the stripe marking hypothesis (Kingdon, 1984) was the most frequent social interaction in my study with an average of 0.032 times observed per minute (Fig. 5). This differs from the results produced by Caro (2016) that recorded mutual grooming to have a rate of 0.0003 times observed per minute being a much lower the rate than recorded in my study.). The agonistic interactions biting, and kicking were the least observed interactions both with an average of 0.004 and 0.003 (respectively) times observed per minute (Fig. 5). Play interaction was not observed at all during the focal samples.





There were twenty Poisson models used to test whether striping was a factor that influenced the rate or duration of the social interactions. The twenty models were split between received and given interactions. The models which are within 95% of the total AICc weight were taken into account (Table 5). There were no AICc weight differences when the received and given social interactions were compared.

The results from the social interactions GLMs (Table 6, 7) indicated that stripes and shadow stripe numbers do not have an influence over the number of interactions given or received. For the social interaction rate analysis, no factors showed to be significant as each p-value was over 0.05. Yet, for the social interaction duration analysis, results showed that individuals would interact for longer

periods at grassland habitats compared with watering holes. However, striping was not a driver for

these results.

**Table 5:** Top models accounting for 0.95 of the AICc weight for received and given interaction predictor variables.

Overall Interactions predictor variables	Delta AICc	AICc Weight
Total Received Interactions (Rate)		
Total Stripe and Shadow Stripe Number	0.00	0.43
Total Stripe Number	0.65	0.31
Total Stripe and Shadow Stripe Number + Group Type	3.64	0.07
Total Stripe Number + Group Type	4.02	0.06
Total Stripe and Shadow Stripe Number + Group Size	4.22	0.05
Total Stripe Number + Group Size	4.86	0.04
Total Given Interactions (Rate)		
Total Stripe and Shadow Stripe Number	0.00	0.43
Total Stripe Number	0.31	0.37
Total Stripe and Shadow Stripe Number + Group Type	4.38	0.05
Total Stripe Number + Group Type	4.65	0.04
Total Stripe and Shadow Stripe Number + Group Size	4.94	0.04
Total Stripe Number + Group Size	5.13	0.03
Total Received Interactions (Duration)		
Total Stripe and Shadow Stripe Number + Habitat	0.00	0.47
Total Stripe and Shadow Stripe Number + Group Type	1.53	0.22
Total Stripe Number + Habitat	3.15	0.10
Total Stripe and Shadow Stripe Number	3.45	0.08
Total Stripe Number + Group Type	4.29	0.06
Total Stripe and Shadow Stripe Number + Group Size	4.42	0.05
Total Given Interactions (Duration)		
Total Stripe and Shadow Number + Habitat	0.00	0.42
Total Stripe Number + Habitat	1.62	0.19
Total Stripe and Shadow Number + Group Type	2.01	0.15
Total Stripe and Shadow Number	3.25	0.08
Total Stripe and Shadow Number + Group Size	4.02	0.06
Total Stripe Number + Group Type	4.02	0.06

Table 6: The observed results from the MEM for received and given interactions which measured the rate of the
overall social interactions.

Predictor Variables	Estimate	Std. Error
Total Received Interactions		
Total Stripe and Shadow Stripe Number	-0.002	0.003
Total Stripe Number	-0.001	0.002
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.001	0.003
-Harems	-0.30	0.200
-Mixed Groups	-0.06	0.300
Total Stripe Number + Group Type		
-Total Stripe Number	-0.001	0.002
-Harems	-0.30	0.200
-Mixed Groups	-0.06	0.300
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.002	0.003
-Group Size	0.04	0.130
Total Stripe Number + Group Size		
-Total Stripe Number	-0.001	0.002
-Group Size	0.04	0.100
Total Given Interactions		
Total Stripe and Shadow Stripe Number	-0.001	0.003
Total Stripe Number	0.0004	0.002
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	0.001	0.003
-Harems	-0.20	0.200
-Mixed Groups	-0.08	0.300
Total Stripe Number + Group Type		
-Total Stripe Number	0.001	0.002
-Harems	-0.20	0.200
-Mixed Groups	-0.09	0.300
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.001	0.003
-Group Size	-0.04	0.100
Total Stripe Number + Group Size		
-Total Stripe Number	0.0005	0.002
-Group Size	-0.04	0.100

Predictor Variables	Estimate	Std. Error
Total Received Interactions		
Total Stripe and Shadow Stripe Number + Habitat		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Grassland	2.00*	1.000
-Scrub Edge	1.50	1.100
-Scrub	0.60	1.600
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Harems	-1.40	0.900
-Mixed Groups	1.00	1.200
Total Stripe Number + Habitat		
-Total Stripe Number	-0.005	0.010
-Grassland	2.00*	1.000
-Scrub Edge	1.50	1.100
-Scrub	0.50	1.700
Total Stripe and Shadow Stripe Number	-0.02	0.010
Total Stripe Number + Group Type		
-Total Stripe Number	-0.001	0.010
-Harems	-1.70	0.900
-Mixed Groups	-1.10	1.200
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Group Size	-0.40	0.600
Total Given Interactions		
Total Stripe and Shadow Number + Habitat		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Grassland	1.80	1.000
-Scrub Edge	1.50	1.100
-Scrub	0.40	1.700
Total Stripe Number + Habitat		
-Total Stripe Number	-0.01	0.010
-Grassland	2.1*	1.000
-Scrub Edge	1.60	1.100
-Scrub	0.60	1.700
Total Stripe and Shadow Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Harems	-1.20	0.900
-Mixed Groups	-1.00	1.300
Total Stripe and Shadow Number	-0.02	0.010
Total Stripe and Shadow Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Group Size	-0.04	0.600
Total Stripe Number + Group Type		
-Total Stripe Number	-0.01	0.010
-Harems	-1.40	0.900
-Mixed Groups	-1.00	1.300

**Table 7:** The observed results from the MEM for received and given interactions which measured the duration of the overall social interactions.

\* p-value <0.05

The same MEMs were used to analyse mutual grooming. After the AICc weight was calculated (Table 8), around the same number of models were supported compared with the rate and duration of the overall social interactions analysis (Table 5).

The results from the MEMs showed that total stripe and shadow stripe number had no influence over the rate or duration of mutual grooming bouts (Table 9, 10). Similar to the overall social interaction duration analysis, results showed that individuals would groom for longer periods at grassland habitats compared with watering holes. This also showed that striping was not a driver for these results.

Mutual Grooming Predictor Variables	Delta AICc	AICc Weight
Total Received Interactions (Rate)		
Total Stripe and Shadow Number	0.00	0.47
Total Stripe Number	0.88	0.30
Total Stripe and Shadow Number + Group Size	3.82	0.07
Total Stripe and Shadow Number + Group Type	4.67	0.05
Total Stripe Number + Group Size	4.72	0.04
Total Stripe Number + Group Type	5.26	0.03
Total Given Interactions (Rate)		
Total Stripe and Shadow Number	0.00	0.46
Total Stripe Number	0.59	0.34
Total Stripe and Shadow Number + Group Size	4.30	0.05
Total Stripe Number + Group Size	4.87	0.04
Total Stripe and Shadow Number + Group Type	5.03	0.04
Total Stripe Number + Group Type	5.42	0.03
Total Received Interactions (Duration)		
Total Stripe and Shadow Number + Habitat	0.00	0.56
Total Stripe and Shadow Number + Group Type	2.82	0.14
Total Stripe Number + Habitat	2.95	0.13
Total Stripe and Shadow Number	4.10	0.07
Total Stripe and Shadow Number + Group Size	5.24	0.04
Total Stripe Number + Group Type	5.41	0.04
Total Given Interactions (Duration)		
Total Stripe and Shadow Number + Habitat	0.00	0.47
Total Stripe Number + Habitat	1.47	0.23
Total Stripe and Shadow Number + Group Type	2.89	0.11
Total Stripe and Shadow Number	3.93	0.07
Total Stripe Number + Group Type	4.73	0.05
Total Stripe and Shadow Number + Group Size	4.90	0.04

 Table 8: Top models accounting for 0.95 of the AICc weight for received and given mutual grooming bouts.

Mutual Grooming Predictor Variables	Estimate	Std. Error
Total Received Interactions		
Total Stripe and Shadow Stripe Number	-0.003	0.003
Total Stripe Number	-0.001	0.002
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.003	0.003
-Group Size	0.10	0.100
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.002	0.003
-Harems	-0.20	0.200
-Mixed Groups	0.10	0.300
Total Stripe Number + Group Size		
-Total Stripe Number	-0.001	0.002
-Group Size	0.10	0.100
Total Stripe Number + Group Type		
-Total Stripe Number	-0.001	0.002
-Harems	-0.20	0.200
-Mixed Groups	0.05	0.300
Total Given Interactions		
Total Stripe and Shadow Stripe Number	-0.002	0.003
Total Stripe Number	-0.0003	0.003
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.002	0.003
-Group Size	-0.006	0.100
Total Stripe Number + Group Size		
-Total Stripe Number	-0.0003	0.003
-Group Size	-0.01	0.100
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.001	0.003
-Harems	-0.20	0.200
-Mixed Groups	-0.03	0.300
Total Stripe Number + Group Type		
-Total Stripe Number	0.00001	0.003
-Harems	-0.20	0.200
-Mixed Groups	-0.05	0.300

**Table 9:** The observed results from the MEM for received and given interactions which measured the rate of the mutual grooming bouts.

**Table 10:** The observed results from the MEM for received and given interactions which measured the duration of the mutual grooming bouts.

Mutual Grooming Predictor Variables	Estimate	Std. Error
Total Received Interactions		
Total Stripe and Shadow Stripe Number + Habitat		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Grassland	2.30*	1.100
-Scrub Edge	1.90	1.300
-Scrub	0.90	1.800
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.02	0.010
-Harems	-1.20	1.000
-Mixed Groups	-0.80	1.400
Total Stripe Number + Habitat		
-Total Stripe Number	-0.005	0.010
-Grassland	2.30*	1.100
-Scrub Edge	1.80	1.300
-Scrub	0.70	1.900
Total Stripe and Shadow Stripe Number	-0.03	0.010
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.03	0.010
-Group Size	-0.20	0.600
Total Stripe Number + Group Type		
-Total Stripe Number	-0.001	0.010
-Harems	-1.50	1.000
-Mixed Groups	-1.00	1.400
Total Given Interactions		
Total Stripe and Shadow Stripe Number + Habitat		
-Total Stripe and Shadow Stripe Number	-0.03	0.020
-Grassland	2.20	1.100
-Scrub Edge	1.80	1.300
-Scrub	0.70	1.900
Total Stripe Number + Habitat		
-Total Stripe Number	-0.02	0.010
-Grassland	2.50*	1.200
-Scrub Edge	2.00	1.400
-Scrub	0.90	2.000
Total Stripe and Shadow Stripe Number + Group Type		
-Total Stripe and Shadow Stripe Number	-0.03	0.020
-Harems	-1.10	1.000
-Mixed Groups	-0.90	1.400
Total Stripe and Shadow Stripe Number	-0.03	0.020
Total Stripe Number + Group Type		
-Total Stripe Number	-0.01	0.010
-Harems	-1.30	1.000
-Mixed Groups	-1.00	1.400
Total Stripe and Shadow Stripe Number + Group Size		
-Total Stripe and Shadow Stripe Number	-0.03	0.020
-Group Size	-0.20	0.600

\* p-value <0.05

### Hypothesis 2 – Nearest Neighbour Distances

During the data collection period, 525 different nearest neighbour distances were recorded. These recordings were averaged from 346 unique individuals. For the mixed effect models, the highest sample size was 346. However, as some individuals did not have a total stripe score, the highest sample size included a stripe number as a predictor variable was 210. Within the population of AENP, the mean nearest neighbour distances between individuals was 13 metres.

**Table 11:** The observed results from the negative binomial nearest neighbour distances model which accounted for95% of the AICc weight.

Nearest Neighbour Distances Predictor Variables	Delta AICc	AICc Weight
Total Upper Body Stripe Number + Habitat	0.00	0.497
Total Stripe Number + Habitat	1.08	0.290
Total Stripe and Shadow Stripe Number + Habitat	1.70	0.213



**Figure. 6:** (a) the mean nearest neighbour distances between the different ages within the population, (b) the mean nearest neighbour distances between the different sexes within the population, (c) the mean nearest neighbour distances between the habitats at AENP and (d) the mean nearest neighbour distances between the different group types.

There were fourteen mixed effect models used for this hypothesis. The AICc weight greatly supported the models which included habitat (Table 11). These models, however, did not show any support that the number of stripes or shadow stripes on an individual influenced the distance between neighbours when habitats were accounted for (Table 12). However, results showed that the reference group (watering holes) were significantly different compared with grasslands (Table 12). Results suggest that individuals are further apart in grassland habitats compared with watering holes.

**Table 12:** The observed results from the Poisson GLM for received and given interactions which measured the rate and duration of the interactions.

Nearest Neighbour Distance Predictor Variables	Estimate	Std. Error
Total Upper Body Stripe Number + Habitat		
-Total Upper Body Stripe Number	-0.002	0.007
-Grassland	1.10*	0.300
-Scrub Edge	0.10	0.400
-Scrub	0.80	0.500
Total Stripe Number		
-Total Stripe Number	0.003	0.003
-Grassland	1.10*	0.300
-Scrub Edge	0.10	0.400
-Scrub	0.90	0.500
Total Stripe and Shadow Stripe Number + Habitat		
-Total Stripe and Shadow Stripe Number	-0.0001	0.003
-Grassland	1.10*	0.300
-Scrub Edge	0.10	0.400
-Scrub	0.80	0.500

\*p value <0.001

Whilst striping does not appear to have any influence on nearest neighbour distances, other factors do in fact appear to have an influence (Fig. 6). T tests and ANOVA's were used to provide additional evidence to support these graphs (Table 13, 14). Adults were significantly more widely spaced than juveniles (Table 13). Males also had significantly larger mean nearest neighbour distances compared with females (Table 13). This test was repeated when juveniles were removed from the dataset and still showed that male distance was significantly greater (Table 13). Zebras had a significantly smaller mean nearest neighbour distance at watering holes than the other habitats tested (Table 14). Individuals in open grassland habitats displayed greater distances than those reviewed in scrub edge habitats (Table 14). However, the tests showed that there was no statistical significant difference between scrub habitats and open grasslands (Table 14). Bachelor groups also displayed larger nearest neighbour distances than harems, however, there was no significant difference between mixed groups (Table 14). Tests also identified that harems and mixed groups showed no significant difference (Table 14).

 Table 13: Nearest neighbour t-test results from age and sex explanatory variables.

	t-value	degrees of freedom	p-value
Age (Adult - Juvenile)	4.91	103	0.000003
Sex (Male - Female)	-4.34	432	0.00002

Table 14: Nearest neighbour ANOVA results from group and habitat type explanatory variable.

	F-value	p-value
Group Types		
Harem - Bachelor	F(4,520) = 4.89	0.020
Mixed - Bachelor	F(4,520) = 4.89	0.758
Mixed - Harem	F(4,520) = 4.89	0.756
Habitats		
Scrub - Grassland	F(5,513) = 14.09	0.663
Scrub Edge - Grassland	F(5,513) = 14.09	0.002
Scrub Edge - Scrub	F(5,513) = 14.09	0.463
Watering Hole - Grassland	F(5,513) = 14.09	0.000
Watering Hole - Scrub	F(5,513) = 14.09	0.001
Watering Hole - Scrub Edge	F(5,513) = 14.09	0.037

The nearest neighbour distances were also tested between the different sexes in each group type. This was provided by testing multiple ANOVA models in turn. Males in bachelor groups and harems showed significant differences in nearest neighbour distances to females in harems (Table 15). However, no other results show any statistical significance.

	F-value	p-value
Harem Male - Harem Female	F(5,432) = 4.00	0.011
Bachelor Male - Harem Female	F(5,432) = 4.00	0.027
Mixed Male - Harem Female	F(5,432) = 4.00	0.349
Harem Male - Mixed Female	F(5,432) = 4.00	0.871
Bachelor Male - Mixed Female	F(5,432) = 4.00	0.927
Mixed Male - Mixed Female	F(5,432) = 4.00	0.939
Mixed Female - Harem Female	F(5,432) = 4.00	0.998
Harem Male - Bachelor Male	F(5,432) = 4.00	1.000
Mixed Male - Bachelor Male	F(5,432) = 4.00	1.000
Mixed Male - Harem Male	F(5,432) = 4.00	1.000

**Table 15:** Nearest neighbour ANOVA results showing whether there aredifferences between sexes in different group types.



Figure. 7: The mean nearest neighbour distances of each sex within the different group types at AENP.

### Hypothesis 3 – Group Size

For the Poisson GLM's, which were used to test the factors effecting group size, a maximum sample size of 80 groups were used. The models that included the 80-sample size were the simple GLM's (average stripe and shadow number and average stripe number). The sample size was reduced to 77 when group type was introduced into the GLM.

There were five Poisson models used for this hypothesis. AICc was used for the modelling selection (Burnham & Anderson, 2004). The models that were within 95% of the total AICc weight were considered. Only the models that had group type as an interaction were within the 95% threshold (Table 16).

 Table 16: Top models accounting for 0.95 of the AICc weight for total number of group size.

Group Size Predictor Variables	Delta AICc	AICc Weight
Average Stripe Number + Group Type	0.00	0.58
Average Stripe and Shadow Stripe Number + Group Type	0.68	0.42

With all the models within the 95% threshold accounted for, the results from the GLMs showed that striping had no statistical significance as no p value was <0.05 (Table 17). As a result, this rejects the hypothesis that stripes have an influence over the size of groups within the plains zebra population. Whilst the results showed that striping did not have an influence over group size, I investigated to see whether the different habitats within AENP had any influence. After plotting the results of each of the habitats onto a graph, it was apparent that different habitats did not identify any significant results (Fig. 8). To support the graph, I used a parametric ANOVA that found no significant difference in group size between habitats (p-value >0.05).





 Table 17: The observed results from the Poisson GLM for group size.

Group Size Predictor Variables	Estimate	Std. Error
Average Stripe Number + Group Type		
-Average Stripe Number	0.002	0.003
-Harems	0.30*	0.100
-Mixed Groups	1.30**	0.200
Average Stripe and Shadow Stripe Number + Group Type		
-Average Stripe and Shadow Stripe Number	-0.0001	0.003
-Harems	0.30*	0.100
-Mixed Groups	1.30**	0.500

\* p-value <0.05; \*\* p-value <0.001

### *Hypothesis* 4 – *Group Leadership*

The dataset for the hypothesis that tested whether striping influenced group leadership had the smallest sample size (Table 4). Six models were selected using the AICc (Burnham & Anderson, 2004), with the total stripe and shadow stripe number variable giving the highest supported score with 48% of the AICc weight (Table 18). The null model was the third highest supported model with 10% of the AICc weight, which suggested that the models with fewer percentage of AICc weight are poor. This could be as a result of the small sample size. Total stripe and shadow stripe number variable holds 48% of the AICc weight and was considered my top model.

**Table 18:** Top models accounting for 0.95 of the AICc weight for the group leadership rank.

Group Leadership Predictor Variables	Delta AICc	AICc Weight
Total Stripe and Shadow Stripe Number	0.00	0.52
Total Stripe Number	1.93	0.20
Null	3.04	0.11
Total Upperbody Stripe Number	3.06	0.11
Total Rump Stripe and Shadow Stripe Number	5.00	0.04

From the models that were supported by the AICc, most did not have a p-value that showed any significance (Table 19). However total stripe and shadow stripe number and the null model had a relationship with leadership rank within harems as the p-value <0.05 (Table 19). A further analysis was taken as a result of this statistical result. Since the relative leadership rank data cannot be transformed to a normal distribution, a nonparametric test (Kendall rank correlation coefficient test) was used. After completing the correlation test, no statistical significance was found between total stripe and shadow stripe with leadership rank (N = 29, p-value = 0.3). This may be as a result of the small sample size acquired in the field.

**Table 19:** The observed results from the Poisson GLM for group leadership rank.

Estimate	Std. Error
0.006*	0.003
0.004	0.002
0.5**	0.050
0.009	0.006
0.001	0.007
	Estimate 0.006* 0.004 0.5** 0.009 0.001

\* p-value <0.05; \*\* p-value <0.001

### Discussion

Striping in zebra is still under debate and many hypotheses have arisen stating the function of the famed stripes. The hypotheses include anti-predator avoidance & confusion (Kingdon, 1984; McLeod, 1987; Ruxton, 2002), ectoparasite prevention (Waage, 1981; Caro *et al.*, 2014), thermoregulation (Morris, 1990) and social behaviour & cohesion (Kingdon, 1984; Ruxton, 2002). The overall aim of this study was to discover whether striping on the pelage of zebras had any influence over their social behaviour and cohesion. Four different hypotheses were tested to achieve the overall aim which focussed on their social interactions, nearest neighbour distances, group size and leadership. Considering that the plains zebras are known to be sociable animals (Klingel, 1974), very little social interactions were observed during the five-minute focal recordings. On average there were 0.12 interactions per minute during these samples. As a result of the small number of interactions, it was difficult to establish whether stripe number had a relationship with the rate or duration of interactions. The results from the MEMs (Table 6, 7) confirmed that there were no relationships between stripe numbers and social interactions. Whilst observing the population at AENP, most individuals grazed in the open grasslands or remained idle in one location.

Individuals are unable to groom parts of their own bodies and rely on being groomed by other individuals. The grooming allows individuals to shed their hair and to remove ectoparasites from the body (Tyler, 1972; Barton, 1985; Mooring et al., 2004). Literature also suggested the grooming helps with the maintenance of social cohesion within a group as social bonds between the interacting individuals strengthen (Penzhorn, 1984; Crowell-Davies et al., 1986; Kimura, 2000). As a result, the hypothesis that stripes provide visual markers for mutual grooming (Cloudsley-Thompson, 1984; Kingdon, 1984) was also tested in this study. The hypothesis assumed that individuals that possess more stripes on their body, have a higher rate in mutual grooming bouts than less striped individuals. The assumption also suggested that plains, mountain and Grevy's zebra are more sociable than the other non-striped equids. The improved social behaviour and cohesion could result in greater social interaction between larger and more tight-knit groups. The group size and social organisation of equids has been frequently featured in literature allowing a comparison between the striped and nonstriped equids. However, there is insufficient evidence in literature to compare rates and duration of social interactions between the plains zebra and other wild equids. It is noted that mutual grooming very rarely occurs amongst Grevy's zebra; African wild ass and kiang individuals (Caro, 2016). However, studies suggest mutual grooming bouts are more frequent between non-striped domestic horses (Clutton-Brock et al., 1976; Sigurjonsdottir et al, 2003). If this is the case, this would contradict Kingdon's (1979, 1984) hypothesis that interactions such as mutual grooming favour striped species.

I discovered from my results that there was no relationship between striping and the rate or duration of mutual grooming bouts (Table 9, 10). This rejects the hypothesis that stripes are used as visual markers for grooming (Kingdon, 1984). Caro (2016), discovered that the rump and neck were the regions that mutual grooming occurred the most (rump being the highest groomed region). These areas are not distinguishable compared with other regions of the body in terms of thickness and abundance of stripes. Caro (2016), also questions if the purpose of striping is to aid the mutual grooming of regions that cannot be self-groomed. The tail of the plains zebra is able to reach the rump region on its own body and is therefore capable of removing ectoparasites in this region (Siegfried, 1990). This would then contradict Kingdon's hypothesis as stripes are readily visible on the rump. Although the results showed there was no relationship between striping and mutual grooming bouts, the results showed that individuals partaked in longer grooming bouts in grassland habitats compared with being in a vicinity of a watering hole (Table 10). This may be as result of a higher risk of predation near watering holes, and so greater time is spent being vigilant rather than being social (Hayward & Slotow, 2009; Crosmary et al., 2012). A further review of literature rejects the mutual grooming hypothesis as the social and ectoparasite removal mechanism is present within a wide variety of nonstriped Mammalia (Mooring et al., 2004). Mutual grooming had the highest rate compared with the other interactions observed (Fig. 4). However, the rate was very low compared with other studies observing mutual grooming bouts of plains zebra (Kingdon, 1979; Kimura, 2000; Klingel, 2013). It is unclear why individuals at AENP groomed less, however, it is suggested that mutual grooming rates is influenced by the intensity of ectoparasites (Tyler, 1972). Studies show that zebra in more moist areas have higher mutual grooming rates than zebra in drier places (Klingel, 1967; Kimura, 2000). This was also evident in studies researching asses that concluded the rate of grooming bouts were five times greater in mesic areas than arid areas (Moehlman, 1998). It was suggested that fewer ectoparasites can survive drier climates (Kimura, 2000; Malenke et al., 2010). Grasslands at AENP are semi-arid and potentially could be the reason for the low rates of mutual grooming. This review and analysis suggested that striping is not a driver for mutual grooming.

The results from the nearest neighbour analysis noted some significant results. However, in line with the social interaction analysis, no relationships with stripe numbers and the response variable were established (Table 12). A significant result identified that adult zebras have a greater nearest neighbour distance compared to juveniles (Fig. 6). This finding was expected as juveniles are reliant on their mothers and often stay in close proximity to their mothers (Penzhorn, 1984). An additional finding identified that males had a greater nearest neighbour distance than females (Fig. 6). This maybe as a result of females within harems forming stronger bonds with each other (Rubenstein, 1986; Rubenstein & Hack, 2004). It is likely that these bonds are stronger than bonds between males

in bachelor groups. The analysis between the different habitats within AENP identified that individuals were closer to other members of their group when situated by watering holes compared with other habitats (Fig. 6; Table 12). Zebra are a common prey for predators such as African lions (Hayward & Kerley, 2005). Usually prey avoid places where predators are abundant (Moll et al., 2016) or times when they are most at risk (Hayward & Slotow, 2009). However, all mammals need to drink despite watering holes presenting a high risk of predation (Crosmary et al., 2012). Members of a group remaining in close proximity to one another in risky areas provide a defensive mechanism to reduce their vulnerability. Individuals had the furthest nearest neighbour distances when situated in grassland habitats. In grassland habitats, the risk of predation is low despite the chance of getting attacked being high as a result of the greater predator detection distances (Thaker et al., 2010). The nearest neighbour survey was conducted during the day, as grasslands often provide clearer visibility allowing the easier the detection of predators (Elliot et al., 1977). As a result, this might give individuals more confidence to increase distances between individuals in their social groups. Individuals within bachelor groups usually displayed further nearest neighbour distances compared with harems as most males in bachelor groups are not related, and so bonds are not as strong as individuals within a harem. Harems are family groups hence the reason why bonds between individuals are usually stronger.

In line with the other hypotheses results, the group size analysis identified that stripe numbers had no relationship with the number of members in each group. This can be supported by a study on other equids (Asiatic wild ass) in which the main driver for group size was the presence of predators (Feh et al., 2001). The average size of these two subgroups were similar within the population at AENP (Fig. 10). Both harems and bachelor groups had an average size of five members (when adults were only included in the count). Harems had an extra member on average when juveniles were also included. Mixed groups had over double the number of members than the two subgroups with an average of 12 (adults only), as mixed groups are made up of a cluster of subgroups (Klingel, 1977). ANEP presented various types of open and closed habitats that I used to form a comparison of group sizes. After completing an ANOVA test to establish whether group sizes changed in different habitats, the results showed that were no differences between habitats. This contradicts Creel et al. (2014) suggestion that the size of the group for prey species is larger in more open habitats. It is considered that groups such as harems are usually permanent, and the size of the group does not change dramatically (Klingel, 1972). Literature focussing on the plains zebra and other equids suggested that group size is not influenced by the presence of stripes. The mean group sizes between the heavily striped equids (plains, mountain and Grevy's zebra) ranged from two to nine (Klingel, 1968; Penzhorn, 1984; Llyod & Rasa, 1989; Rubenstein, 1994; Fischhoff et al, 2007a, 2007b; Sundaresan et al., 2007; Kingdon, 2015); the slightly striped African wild ass ranged from two to seven (Klingel, 1977;

Moehlman, 1998) and the non-striped equids (Asiatic wild ass, Przewalski's horse and Kiang) ranged from three to thirty-five (Schaller, 1998; Reading *et al.*, 2001; Feh, 2005; King & Gurnell, 2005; Kaczensky *et al.*, 2008; Hoseli *et al.*, 2009; Ransom *et al.*, 2012). Since there are no obvious differences between the group sizes of striped and non-striped equids, this rejects the hypotheses that striping enhances social behaviour and cohesion.

The group leadership hypothesis was the most challenging to analyse. Observations identified that it was rare to witness a group moving to different locations, as they generally remain in the same location for most of the day. It was also difficult to view and note both stripe scores on individuals when groups were on the move. As a result, the sample size for this hypothesis was significantly smaller than the others. Klingel (1972) suggested that hierarchical order in group movement is consistently observed in harems therefore if there was any evidence that striping influenced group leadership, harems were the most ideal group to analyse. However, most of the models from the Poisson GLM identified that that stripe numbers had no relationship with group leadership (Table 19). One model identified that the number of stripes and shadow stripes influenced the ranking of the individual (Table 19). The more stripes and shadow stripes on an individual often presented dominance during group movement and supported my hypothesis for group leadership. However, a Kendall rank correlation coefficient test was used to further investigate the relationship between the total stripe and shadow stripe number with group leadership. The result showed no statistical significance and rejected the hypothesis that striping influences group leadership.

There are seven wild extant species of equid distributed on the African and Asiatic Continent. The African species being the plains zebra; mountain zebra; Grevy's zebra and African wild ass. The Asiatic species being the Asiatic wild ass; Przewalski's horse and Kiang. Three of the extant equids possess prominent stripes that run through the entirety of the body (plains, mountain & Grevy's zebra). The African wild ass also features stripes on their pelage; however, these thin black stripes are only found on the legs of the species. In some Przewalski's horse individuals, thin black stripes are found on the legs (Caro, 2016). Literature suggested that stripes do not influence the social organisation of the *Equus* genus, which in turn rejects the social behaviour and cohesion hypothesis. The hypothesis assumed that the striped equids have more permanent and closer social bonds. In fact, plains and mountain zebra do form permanent social groups where each individual usually has strong bonds with each other (Joubert, 1972; Klingel, 1972; Rubenstein, 1986; Rubenstein & Hack, 2004; Kingdon, 2015). However, the Grevy's zebra form temporary social groups where the interindividual bonds are not as strong (Klingel, 1972; Ginsberg & Rubenstein, 1990; Feh, 2005). Similar to the Grevy's zebra, the African wild ass does not form permanent social groups nor strong bonds between adults (Klingel, 1972; Moehlman, 1998). There is also variation between the social organisation of the non-striped

equids. The Asiatic wild ass and kiang do not form permanent social groups (Klingel, 1977; Groves & Willoughby, 1981; Schaller, 1998; Saltz *et al.*, 2000). Whereas, Przewalski's horse form permanent social groups (Ruxton, 2002; Feh, 2005), and you would expect Przewalski's horse to be fully striped. However, Przewalski's horses do not possess a fully striped pelage but only have thin black stripes on the legs amongst some individuals (Caro, 2016). The social organisation evidence from the literature rejected the social behaviour and cohesion hypothesis but suggested that the climate in which the different equids inhabit was the main driver. The equids that formed permanent social groups tend to inhabit temperate areas, whereas the temporary social grouped equids inhabit more arid areas. Rubenstein (1989, 1994) suggested that the scarcity of food and resources can cause difficulty for individuals to maintain a strong social structure. In conclusion the comparison between the *Equus* genus identifies there is no definitive evidence that the striped pelage has any influence over their social behaviour and cohesion.

Striping does not just occur amongst the equid species. It can be found on many other species in the animal kingdom, for instance it can be found on other ungulate species. Ungulates such as the zebra duiker, okapi and bongo possess the striping coloration however, their stripe patterns differ compared with the famed zebra stripes. Ungulates are similar in terms of possessing the striped coloration patterns however, they display differences in relation to social organisation and composition. The okapi and bongo are usually found in small non-territorial groups or solitary (Lydekker, 1908; Lang, 1918; Hillman, 1986; Hart & Hart, 1988, 1989; Bodmer & Rabb, 1992; Klaus-Hügi et al., 2000; Kingdon, 2015). Zebra duiker are usually found in monogamous pairs (Kingdon, 2015). Female defence polygyny does not occur between these species, unlike the plains zebra. These ungulates all inhabit the rainforests of Africa. Observations of their social behaviour are difficult and have resulted in a lack of literature on this topic. There is also minimal literature in relation to the relationship between striping and their social behaviour and cohesion. However, Kingdon (2015) suggested that the striping on the dorsum of the zebra duiker is for social attraction. He also goes onto to say, that potentially the stripes are used as a target for other rival aggressors. This means that the damage of an attack by a rival aggressor will be diverted away from more vulnerable areas of the body (soft abdomen) thus reducing the overall damage to the defender. Kingdon (1979) also suggested that striping may be used in the intraspecies communication of okapis. The suggestion goes onto say the communication may be between mother and calf (when the calf is following or suckling) and between male and female (during the courtship process). However, there is little evidence that can support the suggestion by Kingdon in relation to the function of striping in zebra duiker and okapi.

As previously mentioned in the introduction of this study, colouration of some species can have an influence over an individual's social behaviour and cohesion. For example, species like the Dall sheep

and African lion have social hierarchies and sexual selection advantages which are evident based on their pelage colouration (West & Packer, 2002; Loehr *et al.*, 2008). However, in these cases the colouration change is the darkness of the pelage and not the quantity of stripes. The analysis from my study confirmed that the quantity of stripes did not influence or display social rankings of an individual. In some ungulates, adults possess spotted colourations on their pelages. Studies suggested the function of the spots can act as a form of crypsis in dense habitats which in turn is a mechanism of anti-predator avoidance (Stoner *et al.*, 2003). My study did not analyse anti-predator avoidance in plains zebra and so I cannot compare whether stripes and spots have different functions. Although stripes have been hypothesised as being a driver for anti-predator avoidance and confusion in past studies (Kingdon, 1984; McLeod, 1987; Ruxton, 2002). Coloration can have other influences which are non-social specific (Stoner *et al.*, 2003; Caro, 2005). Multiple hypotheses regarding the role that zebra stripes play also include non-social specific. These hypotheses include ectoparasite prevention (Waage, 1981; Caro *et al.*, 2014) and thermoregulation (Morris, 1990). Although this study cannot support any of the non-social influences, it can certainly remove social behaviour and cohesion from the list of many hypotheses.

### Conclusion

The research and analysis to establish why zebras have a striped pelage have led to many different hypotheses including social behaviour, thermoregulation, predator confusion and avoidance and ectoparasite prevention. In this study, I focussed on the social behaviour and cohesion aspect and came to the following conclusion.

Results from the social interactions and nearest neighbour distance analysis identified some statistical significance. Although these had no relation to the presence of stripes. The results showed individuals interacted with each other for a longer duration in grassland habitats compared with being in the proximity of watering holes. The results also showed the age, sex and habitats have an influence over the distance between individuals, with young and female individuals having smaller nearest neighbour distances. I also established that individuals present at watering holes had the smallest nearest neighbour distance compared to individuals at open grasslands who had the greatest.

I found that that stripes on a plains zebra's pelage had no influence over their unique and fascinating social behaviour and cohesion. Tests which focussed on social interactions, nearest neighbour distances, group size and group leadership showed no relationship with stripe and shadow stripe number.

A comparison between the *Equus* genus identified that stripes did not have an influence over social behaviour and cohesion. The evidence from the literature show no links between group size and striping. Further review also identified that striping was not the driver for the social organisation within the genus. Rates and durations of interactions were not reviewed as a result of the lack of evidence within the literature to compare between the plains zebra and the other equids. A literature review also discovered that other striped ungulates did not have similar social traits with the plains zebra. The hypotheses for the function of their stripes were also different to the zebra's.

The overall outcome and results of my study rejected the hypothesis that stripe numbers influence the social behaviour and cohesion of the plains zebra. Thus, reducing the list of hypotheses as to why zebras have their stripes.

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