

The effect of species associations on the diversity and coexistence of African ungulates.

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Abstract:

The effects of species associations on species diversity and coexistence were investigated in East Africa. The frequency and group sizes of African ungulates were observed and analyzed to determine for differences in species associations based on their density and distribution, as well as their associations with other species. Associations between species were determined to be nonrandom and seen to affect the demographics of associating herds. Such associations mirrored in other studies were shown to be the result of interspecific competition, habitat preferences and predation pressure which increases the potential for coexistence between species. This suggests a potentially important role in the regulation of species diversity by ecological dynamics in species rich communities. In the face of today's biodiversity crisis, such understanding of species associations and how they are regulated may have huge implications for conservation.

Introduction:

Sympatric coexistence of organisms within a community poses several questions for ecologists. High levels of species association occur with high species packing, as is seen within the Selous game reserve of Tanzania in east Africa. Sinclair (1985) notes that mixed herds are frequently seen in east Africa and Connor and Simberloff (1979) have observed competition to be responsible for the assemblages of species. The occurrence of more than 40 species of ungulates within the game reserve (Mammal Checklist, Game-Reserve.com) raises the issue as to whether such diverse species-rich communities are regulated by competition for resources (Sinclair, 1973; Wilmshurst et al., 1999), habitat selection (Rosenzweig, 1981), or predators (Roughgarden and Feldman, 1975; Sinclair et al., 2003).

Gause's principle states that coexisting species should possess different ecological niches (Roughgarden and Feldman, 1975), and resource partitioning has shown to promote the coexistence of species (MacArthur and Levins, 1967) as is

known with the famous Darwin's finches of the Galapagos Islands. However, there are many other guilds with what seems to be extensive overlapping in their resources, such as the grazing herds in Africa which eat common and widely dispersed foods. Sinclair (Sinclair, 1979 as cited in Sinclair, 1985) has found that this seemingly extensive overlap among these herds have also undergone niche separation. The partitioning of common resources such as habitat type, food species and even the consumption of various plant parts has resulted in interspecific competition, which has produced both the observed separation as well as the coexistence of these ungulates.

In addition to interspecific competition, Chesson and Rosenzweig (1991) attribute the idea of coexistence between species to be a result of the indirect interactions that occur between species that share common predators rather than similar resources. The behaviour of the predator has been shown to influence a wide variety of responses in the prey (Lima and Dill, 1990) and Holt (1984) has demonstrated that a predator's optimal foraging

behaviour can promote the coexistence of prey species.

The ungulate communities in Africa are one of the most diverse species-rich communities which constitute mostly of bovids, though equids are found coexisting with them virtually everywhere (Cumming, 1982 as cited in Grange et al., 2004). Since the Selous game reserve consists of a large ungulate community, with upwards of 15 species of large carnivores that prey on them, they are suitable as a model subject to study the dynamics of animal communities. The objective of this study is to determine whether there exists a spatial or temporal difference in the sharing of resources between guilds of mammals. More specifically, it is predicted within this study that the density and distribution of mammals will vary as a function of their association with different species and as a function of group size.

It was hypothesized that larger animals would form smaller groups due to the higher resource intake need per animal, thereby decreasing competition. Larger animals may also be more successful at fending off predators and therefore would not need the protection of a large group; unlike the smaller animals who may find safety in numbers (i.e. the "selfish herd"). It was also expected that some animals would be more likely to associate with certain species based on their physical size or their ability to spot certain predators, and may even occasionally adjust their group size accordingly. An increase in species packing due to the increase in associating species was also expected to decrease the size of the group; as species may stay closer together for mutual protection against predators, while avoiding each other in the face of competition for resources (Sinclair, 1985).

Materials and Methods:

The study site

This study took place within the grassland and savannahs of the Selous game reserve in Tanzania during the dry season for two weeks in July. The Selous is the largest protected area in Africa,

covering approximately 50,000 km², and consists of a wide range of different habitats from the mountain ranges of Kidi to the plains of the savannahs, including dense forested regions and sparse scrubland, as well as the receding river of Behobeho to the very large Lake Tagalala. We entered the park from the Kisaski train station and traveled 20 km east to the lodges of the park headquarters. From there, we hiked approximately 20 km into the park where we reached the river campsite of Behobeho. The following couple of days; we hiked the various grassland habitats within the vicinity of Behobeho and surveyed the landscape with binoculars for animals. After five nights, we hiked approximately 25 to 30 km further into the park to the campsite of Lake Tagalala. The ensuing days were also spent hiking the dry sands and surveying the sparsely treed habitats of the Tagalala savannah. Following five nights at the Tagalala campsite, we returned to Behobeho for one night before returning to the lodges. We exited the park via the train station at Matambwe. As a result of our movements between campsites, we were able to cover a larger portion of the park although we remained within the northwest corner of the park. Consequently, we were able to observe a variety of habitats as we moved from one area to another, however for the majority of observations, the animals were found mainly on the grassland or savannah.

The study species

A variety of species was observed within the habitats we frequented, although we were unable to observe their behavioural interactions as they would quickly become alerted to our presence and react by either fleeing or standing still and keeping a vigilant watch. As a result of the limited capacity for viewing these animals while remaining unnoticed, I was only able to obtain a rough estimate of the demographics for each species herd. With the aid of binoculars, information such as the number of animals in the herd, the sex of the animals if determinable, and type of species were recorded. Animals were

identified either on sight with the help of the guides or post hoc using Haltenorth and Diller (1988). Animal species were noted to be “alone” if observed with no other species within viewing distance. If a species was observed to be within the vicinity of another species in that I, or they, could obviously see each other or were at least aware of the other’s presence, then both species were recorded to be in association with each other. Some aquatic observations of species associations were also included from the pools at Behobeho as well as the shorelines of Lake Tagalala. Ungulates surveyed included the elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), waterbuck (*Kobus defassa*), impala (*Aepyceros melampus*), and warthog (*Phacochoerus aethiopicus*). Other animals seen were the baboon (*Papio cynocephalus anubis*) and vervet monkeys (*Cercopithecus aethiops*). The aquatic animals included the crocodiles (*Crocodylus niloticus*) and hippopotamuses (*Hippopotamus amphibius*). While carnivores were spotted at rare intervals in the evenings, their numbers were not sufficient to include in with the data analysis.

Statistical Analysis

The student’s t-test was administered to investigate for differences between the numbers of animals in each group; whether the group size of a particular species differed in relative to the group size of another species; and whether the frequency of animals in a group differed based on the group’s association with other species. The chi-square analysis was applied to test for a relationship between the number of animals observed in a group and the type of species it associated with, and to determine whether the association was specific or random. The chi-square analysis also tested for a difference between the frequencies of animals in a group relative to the number of associating species. Regression analyses were performed to determine whether a correlation existed between the number of animals in a group

based on the amount of its’ associating species. All statistical analyses were carried out using the Minitab software, Student’s Release 12.0 and adopted the standard appropriate level of significance ($\alpha=0.05$).

Results:

The most distinctive observation was a clear segregation between the carnivores and herbivores on a temporal scale. Therefore, this demonstrated the existence of a temporal difference between the guilds of mammals, although it was not conclusively proven by statistical analysis. Carnivores such as lions (*Panthera leo*), hyenas (*Crocuta crocuta*), and genets (*Genetta tigrina*) were seen frequently during dusk and dawn and on the road or around the campsite at night, but never during the daytime. A spatial difference between ungulates was also observed although not statistically tested. Elephants were seen commonly among areas of dense vegetation such as tall grasses and forested habitats. Giraffes, zebras, wildebeests, impalas and warthogs, as well as the baboons were frequently seen in the open savannah, or in open areas dotted with shrubs and acacia trees. Hippos and crocodiles, as well as waterbucks, were always seen in or near the water.

Figure 1 depicts a visual representation of the frequency of the type of animals (carnivores omitted) observed in the Selous. As is indicated by the various proportions in the figure, some animals were seen much more frequently than others and therefore this was taken into consideration when performing the analysis by correcting for the frequency of animals. The impala was by far the most common species observed with more than half the animals sighted. Although the impalas were seen in both bachelor and mixed herds, the t-test showed no differences between the group size of the two types of herds ($T = -0.28$; $df = 2$; $p\text{-value} = 0.80$). The wildebeest was the second most common species with half the frequency of the impala, while all the other animals seemed to occur in moderate frequency with respect to each other.

Tables 1 and 2 are a summary of the t-tests and chi-square analyses performed on the collection of observations on species association. Even within the limited data available, Table 1 demonstrates that the density of a species varies with respect to the group size of other species, although this was only seen twice out of all possible associations. The density of impalas, when associating with the wildebeest, were significantly greater than the density of wildebeests were when associated with impalas. On the other hand, the density of the wildebeest was significantly greater when associating with giraffes than when associated with impalas. Furthermore, the chi-square analyses resulted in a strong association between the types of species an animal was observed to associate with, and that such associations were not random (p -value < 0.0005). However, the analyses in Table 2 indicate that the number of species associated with did not significantly affect the size of the group, but that there was a significant association between certain types of species (p -value < 0.0005).

The idea that smaller animals form larger groups while larger animals form smaller groups is portrayed graphically although statistically insignificant (Figure 2). Impalas increased their group size when with other species than when alone, whereas wildebeest were seen in huge numbers when alone and decreased their group size when with other species. While the zebra was never seen alone, they increased their group size with increasing species. Giraffes and elephants were usually observed in small groups regardless of whether they were alone or associating with other species, although the giraffe did increase in number when observed with three other species. Even though the hippos were usually seen in large groups, they decreased their group size when associated with one other species whereas the group size of crocodiles increased slightly. It is difficult to comprehend the effects of the differences in the group sizes of the elephants, zebras, baboons, and warthogs as they were observed infrequently.

A further analysis of the information of the group sizes of animals influenced by species association as seen in Figure 2 is undertaken in Figure 3 where the group sizes of frequently observed species such as the impala, wildebeest and giraffe are compared. Impalas were observed to form larger herds when associated with other species such as wildebeests or giraffes than when observed alone. Wildebeests were observed in larger groups when associated with giraffes rather than impalas, and seen in very large numbers when alone. Giraffes showed barely any differences in their group size regardless of whether they were alone or in association with other species.

Figures 4 to 8 represents the differences in the frequency of association between an animal with various other species. Impalas and wildebeests were frequently seen in association with each other as indicated by Figures 4 and 5. The giraffe associated with the impalas, wildebeests and zebras with relatively equal frequencies (Figure 6) whereas the warthog associated mostly with impalas and wildebeests (Figure 7). Although the zebra was rarely observed and never alone, the zebra was seen in association with giraffes nearly half the time, as well as with wildebeests and impalas in descending order (Figure 8).

Table 3 is a summary of the regression analyses performed on the observed associations. While almost all of the animals did not demonstrate a significant correlation between the group size and the number of associating species, the hippopotamus exhibited a significant reduction in their group size with the increase in species association ($R^2 = 52.4\%$; p -value = 0.008).

Discussion:

Group size and species diversity played an influential role in the types of species association seen within the savannahs and grasslands of East Africa. This study has demonstrated that such associations were not random, and that there exists a relationship between the group size and density of a herd with respect to the type of species (and in

the case of the hippo, the number of species) it associated with. These findings coincide with a previous study in which various species distributions were found to be significantly different from random (Sinclair, 1985). Within this current study, smaller sized animals were seen to occur in greater numbers when associated with a larger sized species, unless they were alone in which case they formed very large groups such as the wildebeests (Figures 2 & 3). In fact, Figure 3 demonstrates that animals adjusted their group size in accordance with the type of species they were associating with. While the impala occurred in large groups when associating with the larger wildebeests and giraffes, the wildebeest were observed in greater numbers with the larger giraffe rather than the smaller impala. These trends may be explained by the findings set forth in Sinclair et al. (2003) which demonstrated that smaller ungulates were exposed to more predators than larger ungulates; and that they also suffered greater predation rates and experienced stronger predation pressure.

Study Species

Although the impalas were seen alone a quarter of the time (Figure 4), they were by far the most abundant animals in the Selous occurring with a frequency of over 50% (Figure 1). However, it is interesting to note that 65% of the observed associations of impalas were with animals larger than themselves (Figure 4). This is also true for the small sized warthogs that were observed to have associated with larger animals 90% of the time (Figure 7). While Figure 5 shows the wildebeest to be in association with the impalas nearly 60% of the time, this is probably best explained by the fact that it was to the benefit of the impalas to be with the wildebeest as there were several occasions in which a herd of impalas were seen in association with only one solitary wildebeest. In all observations of impala and wildebeest associations, the impalas were the first to flee and the wildebeest stood their ground for a longer time before fleeing. This observation

supports the idea that the smaller sized impalas (and warthogs) were using the larger animals for protection, similar to the zebra in their associations with the larger giraffes and wildebeests (Figure 8). Zebras are known to suffer higher predation than wildebeests (Cooper 1990) which generally move together as a large herd so the predation risk per individual is reduced (Grange et al., 2004). As a result, zebras associate with wildebeests significantly more often to obtain protection from predators (Sinclair, 1985).

The largest animals, the giraffes and elephants, were always seen in small groups (Figure 2) except in the case of the giraffe in association with three other species. However, the giraffe showed no differences in their numbers regardless of whether they were alone or with the smaller impala or wildebeest (Figure 3). Therefore this exception could be explained by the proportion of the giraffe's associations as seen in Figure 6. The giraffe associated with all three smaller species (impalas, wildebeests and zebras) with nearly equal frequencies which suggests that none of these associations are ultimately beneficial to the giraffe. Instead, the benefits of such an association may be attributed to the other three species more so than the giraffe as larger ungulates are preyed on by lions only, and very large herbivores such as elephants and hippos hardly ever suffer predation (Sinclair et al., 2003). Adding strength to the argument would be the results of the differences in the food preferences of these animals which would contribute to the kinds of area that they would be found in (Jarman, 1972). The giraffes are more restricted spatially as they eat only certain types of plants such as the leaves of the acacia trees; whereas the impala, wildebeest and zebra eat the same type of vegetation which is the more common grass found nearly all over the savannah (Sinclair, 1985).

The observations of the hippopotamuses and crocodiles seem to merit a special case as they generally associated with each other for the most part and very rarely with any other species (once hippos were seen with elephants, and once both hippos and crocodiles were seen with waterbucks).

While the hippos showed a significant reduction in their group size with the increase in species association (Figure 2; Table 3), this is most likely the result of sampling bias as the majority of species association with the crocodiles was within Lake Tagalala while the hippos were usually seen alone within the pools along the Behobeho River. The major difference between these two sites was the availability of the resource, which in this case was water. The small confined pools of the Behobeho were the only available source of water bodies from the receding river (which was completely dry to the sand in some parts), whereas Lake Tagalala was a very large lake covering a large surface area with an abundance of available water. The hippos were seen in very large numbers (45 at one pool) and clustered tightly together within the pools of the Behobeho, but were often seen spread out and in smaller numbers, sometimes even solitarily, in Lake Tagalala. Since hippos are one of the largest animals and suffer almost no natural predators (Sinclair et al., 2003), it is doubtful that they would cluster together for mutual protection but more likely due to competition because of the declining water resource. In fact, the hippos of the Behobeho were observed to be more behaviourally aggressive and had more frequent altercations than was observed in Lake Tagalala. While the crocodiles share the water resource with the hippos, they hunt solitarily and therefore would require more living area per animal. This was evident in the differences between the numbers of crocodiles observed between the two sites, which were no more than 3 at Behobeho and upwards of 7 at a time in Lake Tagalala.

Interspecific Competition

Guild members, such as the grazing ungulates or the hippos and crocodiles, can reduce interspecific competition by dividing the available resources. MacArthur and Levins (1967) have shown that the degree of overlap in resource use was positively related to the intensity of competition between species. As well, ecological similarities between

species increases the potential for interspecific competition, such as similar body size and patterns of resource use seen in the zebra and wildebeest (Sinclair, 1977 as cited in Grange et al., 2004). This follows that there is a limit to the number of competing species that can coexist as the number of species would be regulated by the amount of available resources (Fryxell et al., 1988). However, recently Winemiller et al. (2004) utilized the model of species packing to demonstrate that a reduction in interspecific competition occurred as a result of decreasing overlap in resource use.

While Sinclair (1985) found a high degree of overlap between all species, the advent of the migrating wildebeest herd caused other grazers to shift their diet preferences to other vegetative types so as to minimize competition with the numerous wildebeests. As a result, there was a decrease in the degree of overlap between the other grazers (Sinclair, 1985). This was also evident in Yoshiyama and Roughgarden (1977) who showed that when two species were utilizing different resources, smaller separation distances occurred between the competitors. Therefore, an increase in potential resource options will allow for the coexistence of more species, thereby increasing species diversity. As species packing increases with heightened species diversity, this allows for increased potential associations between species.

Habitat Selection

Although species coexistence may be regulated by competition, such coexistence can also be regulated by noncompetitive mechanisms. In a study of coral reef fishes, habitat separation occurred as a result of competitive interactions; however this segregation was attributed to the differences in the habitat adaptations between the reef fishes (Sano, 1990). Furthermore, in other studies on marine reef fishes, Holbrook and Schmitt (1989) showed that low overlap occurred between species due to the slightly different foraging adaptations of each species towards their different habitats, and not as a consequence of competition.

In any interactions between species, Rosenzweig (1981) showed that species were either in competition, or experiencing exploitation or mutualism. However, competition between species was found to have disappeared altogether when species occupied completely separate habitats (MacArthur et al., 1966). Consequently, a species' choice of habitat would be influenced by its interactions with other species around it. Chesson and Rosenzweig (1991) demonstrated this in two species that varied in their competitive abilities between habitats, which resulted in a strong segregation between the two species. Habitat selection is a species' optimal choice and may be influenced by density dependent factors (Chesson and Rosenzweig, 1991) or other factors such as interspecific and/or intraspecific competition (Rosenzweig, 1981). As competition varies among habitats, differential habitat selection plays an important role in increasing the probability of species to coexist and is a major contributor to the coexistence of species (Morris, 1999).

Sinclair (1985) found that a high similarity in vegetation choice exists between species which contributes to a high overlap in their food habitat and consequently their habitat use. Most species are eating the same food in the same habitats and this in itself would increase the probability of species associations among species that eat the same food such as was often seen with the ungulates in this study. The percentage coincidence of species being found together was the result of a preference for vegetation types (Jarman, 1972) and other studies have shown that such species associations were not the result of random associations with vegetation (Simberloff, 1983; Sinclair, 1985). Since most species prefer the same foods and habitats, Sinclair (1985) notes that individuals of all species are usually found in the optimum habitat of short grasslands and open savannahs at moderate distances from water; and this was true for most of the ungulates observed in the game reserve.

Predation

Guilds that show a high degree of overlap are usually comprised of herbivores subjected to extreme predation pressure. Roughgarden and Feldman (1975) hypothesized that complete niche overlap was possible when predation pressure was strong enough to suspend the effects of competition among prey species, allowing for more coexisting species. A mathematical model was used to establish a relationship between the predators and niche separation distances in the prey guild which suggested that predation pressure contributed to the extensive overlapping among prey species and was a primary cause of prey species diversity (Roughgarden and Feldman, 1975). Aggregative responses by prey to predators have been observed (Turchin and Kareiva, 1989), and it has been determined that the effects of predation causes species to converge for protection (Hamilton, 1971). Furthermore it has been determined that larger groups of gazelles detect approaching predators at greater distances than smaller groups (FitzGibbon, 1990), and that nearly all species were observed closer together than expected, which suggests that predation has resulted in ungulate species assembling together for mutual protection in multi-species herds (Sinclair, 1985).

Since wildebeest are the preferred prey of all large carnivore species (Schaller, 1972), the zebra and other ungulates species could reduce the risk of predation on themselves by staying close to the wildebeest and this was observed in gazelles and impalas who preferred to remain within 300m of wildebeest herds (Sinclair, 1985). In fact, the zebra exhibits a "dual strategy" of either staying close to or staying away from the wildebeest as the wildebeest imparts both a cost and benefit to the zebra (Sinclair, 1985). While the wildebeest affords protection from predation, they are also a source of competition, so that in the dry season the zebra actually changes their food preference to decrease the potentials of competition (Sinclair, 1985). However this increases the predation rate on the zebra so that they are consumed by lions on average 63% of the time as compared to

wildebeests which are consumed on average 35% of the time (Schaller, 1972). Therefore the zebra are mainly regulated by predators and as a consequence, such predation pressure influences the behaviour of ungulates which results in the mixed species herds.

However, both food resources and predation have been shown to regulate populations as Sinclair and Arcese (1995) found that when food becomes limiting, animals take greater risks to obtain more food which results in a heightened exposure to predation. Sinclair et al. (2003) has determined that a threshold occurs at prey body size of approximately 150kg, above which predator limitation switches to food limitation, in which ungulate species have few natural predators and are regulated by the availability of resources. Thus, in diverse species communities, both predation pressure and resource limitation acts simultaneously to regulate sympatric populations, and it appears that predation plays as important a role as interspecific competition in structuring animal communities (Sinclair, 1985; Sinclair and Arcese, 1995). Therefore the study of habitat dependent interactions as well as an understanding of complex behavioural responses by grazers to species interactions, including predator-prey interactions, can improve our understanding of the distribution and abundance of species, as well as provide valuable insights into the ecological dynamics and interrelationships of African ungulates. Such understanding may be essential for the successful conservation of diverse and species-rich communities.

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Figures

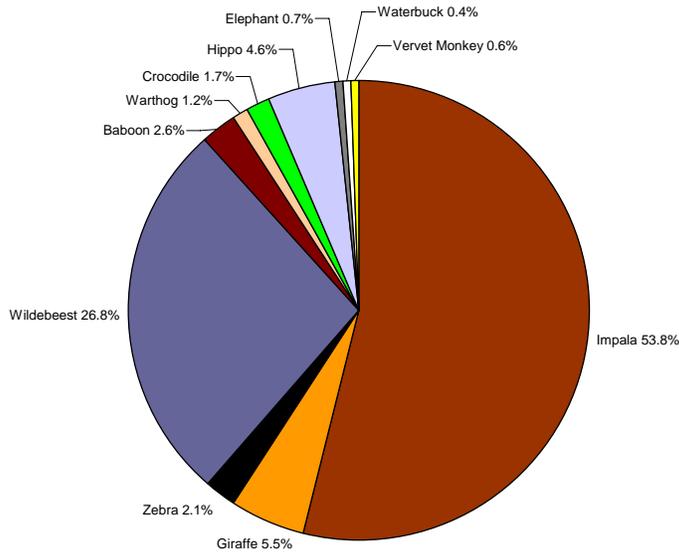


Figure 1. Frequency of animal species observed over a two week period in the Selous game reserve. Each piece represents the percentage of that species out of all animals sighted, with the carnivores omitted.

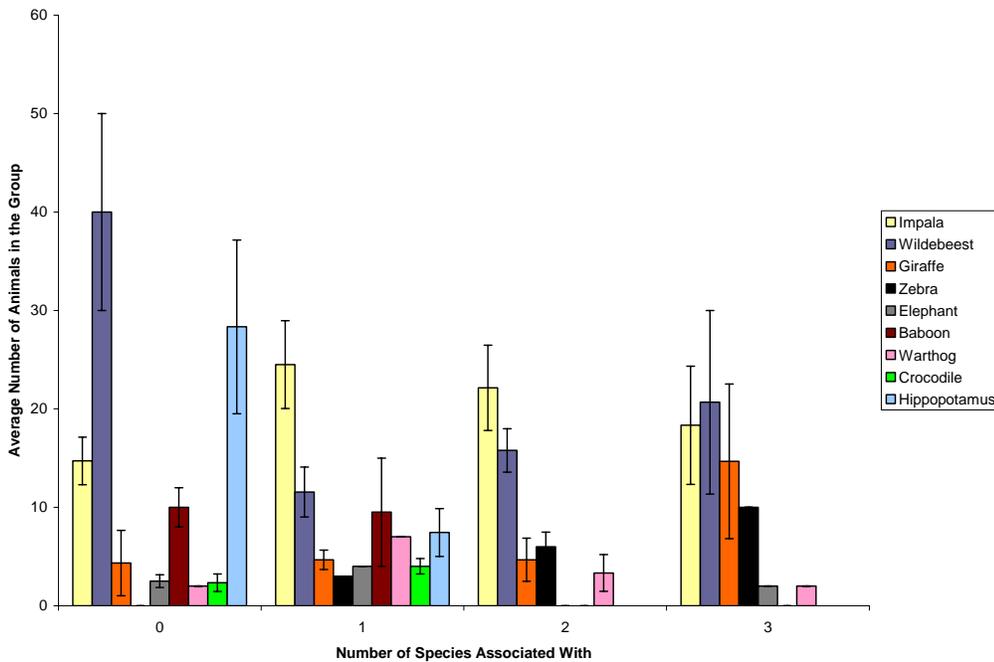


Figure 2. The effects of species association on group size. The average group size of each species either increases or decreases with increasing number of species associations. Bars represent the mean and error bars represent the standard errors. Bars without error bars consisted of one observation only. No significant differences were observed although two approached significance, impala group size increased from being alone to with one other species ($p = 0.063$) and hippo group size decreased ($p = 0.06$).

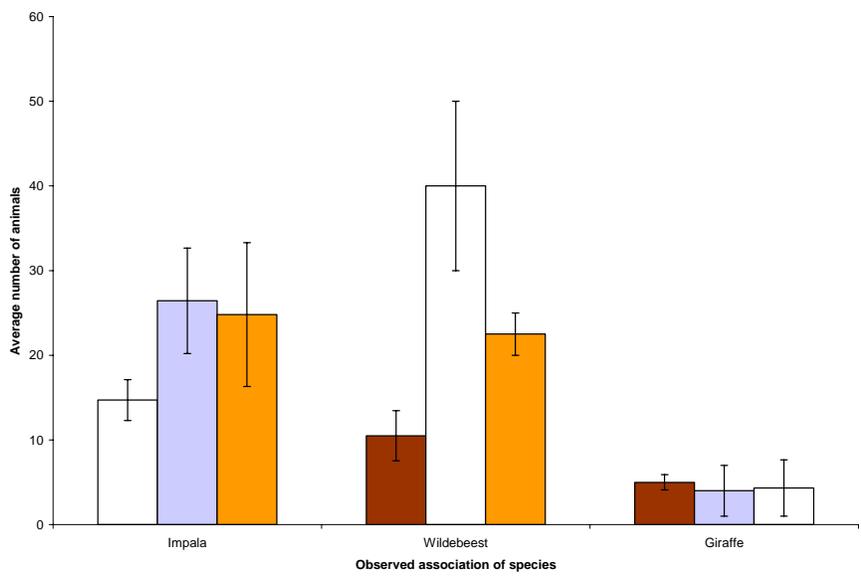


Figure 3. The effects of species association on group size in animals that were frequently observed. White bars = no association (alone), blue bars = associated with wildebeest, orange bars = associated with giraffe, brown bars = associated with impala. Bars represent the mean and error bars represent standard errors.

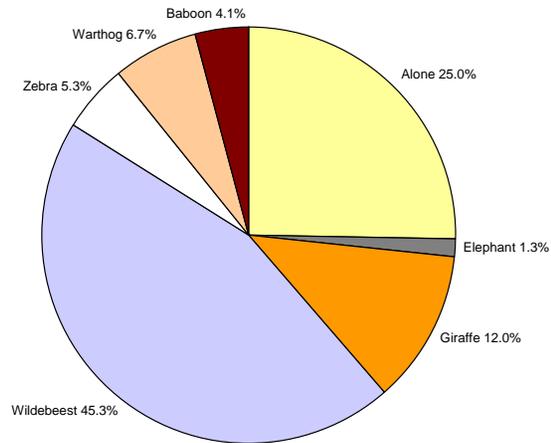


Figure 4. Impala

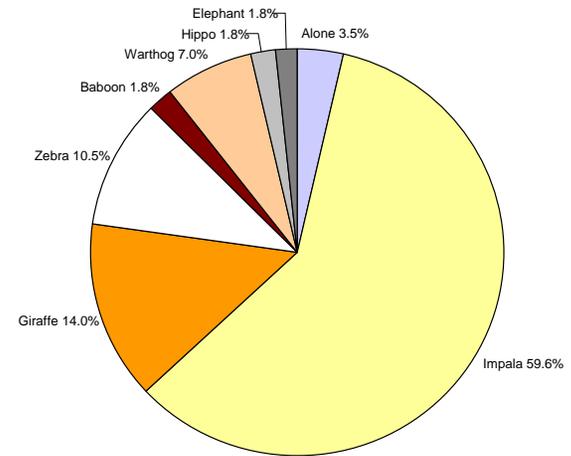


Figure 5. Wildebeest

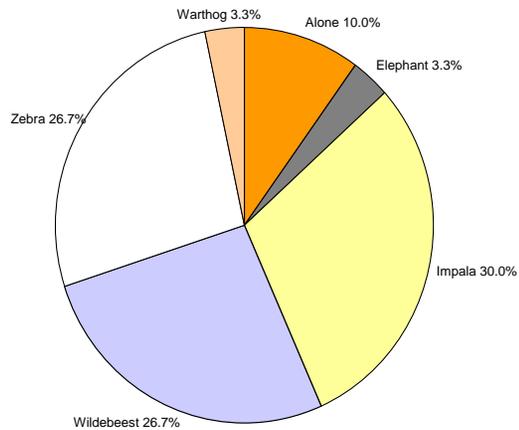


Figure 6. Giraffe

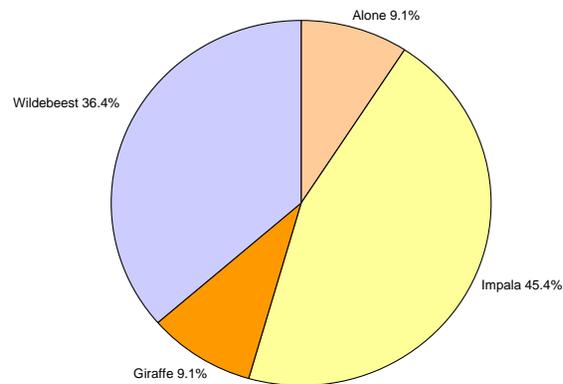


Figure 7. Warthog

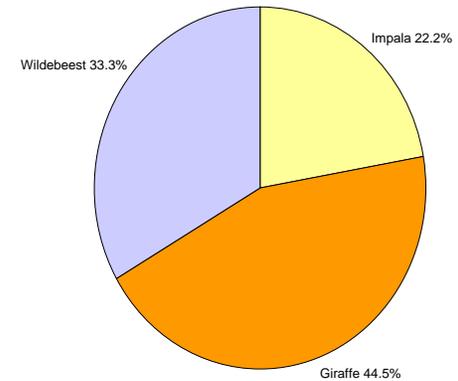


Figure 8. Zebra

Figures 4 – 8. Each representation displays the frequency of each animal observed, whether alone or in association with other animals. Species are represented by the different colours and also labeled including the percentage of association corrected for the frequency of animals over all observed associations.

TABLE 1. Results from t-tests comparing the means of the average number of animals observed alone or with other species. Only species with two or more observations (either alone or with other species) were included. The chi-square analysis (below) tested for a difference in whether animals associated specifically with different types of species or randomly. Cells with expected counts < 10 were omitted for the second chi-square analysis. A single asterisk denotes significance at < 0.05, and a double asterisk denotes significance at < 0.0005.

Species Group(s)	Associating Species Group(s)	T-value	Degrees of Freedom	P-value	Significance
Impala Alone	Wildebeest Alone	-2.46	1	0.25	
	Giraffe Alone	2.52	4	0.065	
	Baboon Alone	1.50	5	0.19	
	Impala with Wildebeest	-1.75	16	0.099	
	Impala with Giraffe	-1.14	4	0.32	
	Impala with Baboon	-0.51	1	0.70	
Wildebeest Alone	Giraffe Alone	-3.38	1	0.18	
	Baboon Alone	2.94	1	0.21	
	Wildebeest with Impala	2.83	1	0.22	
	Wildebeest with Giraffe	1.70	1	0.34	
Giraffe Alone	Baboon Alone	-1.46	2	0.28	
	Giraffe with Impala	-0.19	2	0.86	
	Giraffe with Wildebeest	0.07	2	0.95	
Baboon Alone	Baboon with Impala	0.09	1	0.95	
Impala with Wildebeest	Wildebeest with Impala	2.31	18	0.033	*
	Impala with Giraffe	-0.15	8	0.88	
	Impala with Baboon	0.55	1	0.68	
Impala with Giraffe	Giraffe with Impala	2.32	4	0.081	
	Impala with Baboon	0.37	2	0.75	
Impala with Baboon	Baboon with Impala	0.92	1	0.53	
Wildebeest with Giraffe	Giraffe with Wildebeest	-4.74	1	0.13	
	Wildebeest with Impala	-3.10	4	0.036	*
Giraffe with Impala	Giraffe with Wildebeest	0.32	1	0.80	
Crocodile Alone	Hippo Alone	-2.93	2	0.099	
	Crocodile with Hippo	-1.41	5	0.22	
Hippo Alone	Hippo with Crocodile	2.07	2	0.17	
Crocodile with Hippo	Hippo with Crocodile	-1.75	6	0.13	
Chi-square	$\chi^2 = 423.12$		81	< 0.0005	**
	$\chi^2 = 74.85$		20	< 0.0005	**

TABLE 2. Results from t-tests comparing the means of the average number of animals observed with more than one other species. Only species with two or more observations (either alone or with other species) were included. All t-tests showed no significance. Below, the chi-square analysis tested for a difference between the expected and observed values for all associating species, while correcting for the frequency of animals and using the percentage of observed associations over all recorded associations.

Species Group(s)	Associating Species Groups	T-value	Degrees of Freedom	P-value
Impala Alone	Impala with Wildebeest & Zebra	-0.99	1	0.50
	Impala with Wildebeest & Warthog	-0.05	2	0.97
Impala with Wildebeest & Zebra	Impala with Wildebeest & Warthog	0.79	2	0.51
Wildebeest Alone	Wildebeest with Impala & Zebra	1.70	1	0.34
	Wildebeest with Giraffe & Zebra	2.18	1	0.27
	Wildebeest with Impala & Warthog	2.92	1	0.21
Wildebeest with Impala & Zebra	Wildebeest with Giraffe & Zebra	1.41	2	0.29
	Wildebeest with Impala & Warthog	3.13	2	0.089
Wildebeest with Giraffe & Zebra	Wildebeest with Impala & Warthog	1.97	2	0.19
Giraffe Alone	Giraffe with Wildebeest & Zebra	-0.37	2	0.75
Zebra with Impala & Wildebeest	Zebra with Wildebeest & Giraffe	1.79	1	0.32
Chi-square	$\chi^2 = 927.38$	$df = 81$	P-value < 0.0005 **	

TABLE 3. Results from regressions of the number of animals in a group based on the number of species the animal was observed to be associated with in the same area. Number of species associated with ranged from none to 3. An asterisk denotes significance at < 0.05.

Animal Regressed	Regression equation	R ²	P-value	Significance
Impala	Y = 18.4 + 2.42x	1.6%	0.403	
Wildebeest	Y = 16.5 - 0.78x	0.2%	0.792	
Giraffe	Y = 2.17 + 3.17x	21.2%	0.085	
Baboon	Y = 11.0 - 3.50x	29.4%	0.345	
Warthog	Y = 4.12 - 0.37x	2.0%	0.789	

Zebra	$Y = -0.83 + 3.50x$	48.2%	0.126	
Elephant	$Y = 2.73 - 0.091x$	0.8%	0.864	
Crocodile	$Y = 2.33 + 1.67x$	16%	0.252	
Hippopotamus	$Y = 28.3 - 20.9x$	52.4%	0.008	*
