

Vigilance and flight behaviour in herds of three different ungulate species: zebra, wildebeest and impala



MSc Thesis Report

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Abstract

The majority of wild animals deal with predation on a daily basis. To escape or avoid predation, prey species have adopted a large number of anti-predator strategies e.g. being vigilant and fleeing. Vigilance and flight behaviour can indirectly be influenced by factors such as age, sex, body weight, position in the group, distance to cover, food density and quality, season, weather, time of the day, etc. Although a lot of research about vigilance and flight behaviour has already been done, only few studies looked at more than one species. The aim of this study was to determine how vigilance and flight behaviour differ over group size, group composition, sex, habitat type and part of the day, in three different African ungulate species. These three species comprise of plains zebra, blue wildebeest and impala. The study was performed in Welgevonden Game Reserve in the Limpopo Province of South Africa. Behavioural observations were done to measure individual vigilance in terms of scan frequency, mean scan duration and scan proportion, and group vigilance as group scan level and group vigilance level. Furthermore groups of animals were approached to measure alert distance (AD) and flight initiation distance (FID). Various explanatory variables were tested for a significant influence by using ANOVA on linear mixed models. All seven final models contained different explanatory factors. Where present in the final model, group size negatively influenced vigilance and FID, and habitat openness negatively influenced vigilance, but positively influenced FID. Time of the day and sex did not significantly influence vigilance and flight behaviour at all, and were thus not in any of the final models. The factors species and group composition did have a significant influence in some of the final models. However, these factors did not show consistency in how they influenced the different measures of vigilance and flight behaviour, it being either positive or negative. Although, it was confirmed that some of the studied variables indirectly influence vigilance and fleeing behaviour in plains zebra, wildebeest and impala, it still remains difficult to fully explain how animals adjust their strategies to escape predation and other disturbances.

Introduction

The majority of all animals deal with predation on a daily basis. These animals have adopted a large number of anti-predator strategies in order to escape or avoid this threat. However, the use of these anti-predator strategies leads to a decrease in time available for foraging, which has negative consequences for fitness. Therefore, it is important for animals to balance their time between foraging (eating) and anti-predator strategies (not getting eaten). A well-studied anti-predator strategy is vigilance. Vigilance is mostly characterised as the action or state of keeping watch for possible danger by actively scanning the surroundings while lifting the head and tilting the ears. It can also be expressed by snorting, stomping, and alarm calling. A well-known attribute of vigilance is the “group-size effect”, whereby the frequency and duration of head-raising decreases in individuals as group size increases (Elgar, 1989; Lima, 1990; Lima, 1995; Pulliam, 1973). Individuals benefit from living in a group. They can spend more time foraging, but still have the tendency to spot predators earlier. Even if each individual is looking less frequent or less long (Lima, 1990; Pulliam, 1973). Secondly the “dilution effect” decreases the chance of being caught when predators actively attack (Dehn, 1990). The “group-size effect” has been confirmed in the following animals, elk, *Cervus elaphus* (Childress & Lung, 2003), greater flamingo, *Phoenicopterus roseus* (Beauchamp & McNeil, 2003),

springbok, *Antidorcas marsupialis* (Bednekoff & Ritter, 1994), impala, *Aepyceros melampus* (Hunter & Skinner, 1998; Matson et al., 2005), wildebeest, *Connechaetes taurinus* (Hunter & Skinner, 1998; Underwood, 1982), zebra, *Equus burchellii*, reedbuck, *Redunca arundium*, and common eland, *Taurotragus oryx* (Underwood, 1982), as well as a great deal of other mammals and birds (Elgar, 1989 review). Besides predators, vigilance helps animals escape or avoid human-induced disturbances, such as hunting or poaching. Even leisure activities such as hiking, mountain biking or safari and villages nearby animals’ habitats can already be a factor of disturbance (Manor & Saltz, 2005; Recarte et al., 1998; Schultz & Bailey, 1978; Setsaas et al., 2007; Stankowich, 2008).

There are a number of additional factors that could affect an animal’s sense of safety and thereby affect their vigilance, namely: age, sex, body weight, position in the group, distance to cover, food density and quality, season, weather, and time of day (Elgar, 1989). A lot is already known about how these factors cause animals to change their vigilance according to how safe they feel. However, a lot still remains unknown and/or unclear. Hence, this study. For example, it is likely that animals foraging at the periphery of a group are often more vigilant than animals in the centre, as they are at greater risk of being attacked (Bednekoff & Ritter, 1994; Hunter & Skinner, 1998; Matson et al., 2005; Underwood, 1982). Researchers have found it difficult to explain

the influence of sex on vigilance levels, and results often conflict with one another. For example, Childress & Lung (2003) found females of elk to have a higher scan frequency and longer scan duration than males and Barnier et al. (2016) found the opposite effect in zebra, namely that males scan more regularly with longer scans than females. Matson et al. (2005) found that females have a higher frequency of scanning, but that males spend higher proportion of time scanning. Hunter & Skinner (1998) found the difference between male and female vigilance to be somewhat dependent on predation pressure and prey species. An effect of body weight in different species was found by Underwood (1982) who saw that proportion of time spent being vigilant and the rate of vigilance events decreased as species increased in body size. As smaller species are easy targets for attack and are more top-down regulated by several predator species, they need to scan for danger more regularly and for longer periods of time (Sinclair et al., 2003; Underwood, 1982). Vigilance levels can also differ in other habitat types. This is linked to openness of vegetation and distance to cover. Goldsmith (1990) and Underwood (1982) saw that animals had lower frequency and proportion of scanning in open habitat types. They explained these observations by referring to lower visibility in closed habitats. Furthermore, some predators use an ambush-technique, sneaking up to their prey as close as possible. So prey need to be more aware of this. Bednekoff & Ritter (1994) found vigilance levels to be higher near trees compared to in the open and also linked this to predators hiding in tree clumps. The differences between animal vigilance at various times of the day have very rarely been studied, predominantly due to the difficulties associated with night-time observations. Bednekoff & Ritter (1994) looked at diurnal and nocturnal vigilance in springbok (*Antidorcas marsupialis*). They found that vigilance is performed longer in late mornings compared to early mornings and afternoons. Furthermore, they found that vigilance during the night was performed longer than during the day. Makin et al. (2017) found that zebra and wildebeest had a greater sense of safety during the day than during crepuscular periods and during the night. Longer vigilance at crepuscular periods and at night is probably linked to nocturnal activity of predators in the area (Bednekoff & Ritter, 1994; Makin et al., 2017). Matson et al. (2005) compared vigilance levels in impala between morning and afternoon and found that vigilance levels were higher in the afternoon than in the morning.

A second type of anti-predator strategy is flight-behaviour, where the prey animal actually runs from its predator. In situations where the danger gets too close and the risk of getting caught is too high, it might be a good option to flee from the intruder. However fleeing is energetically costly and it reduces the time spent foraging (Ydenberg & Dill, 1986). Furthermore, initiating a flight might cause the predator to start a chase and this creates a risk for the fleeing individual to be killed. So it might be advantageous to wait until a group member or the predator itself starts to run. The flight initiation distance (FID), the distance at which a threshold to flee between the animals and the threat has been reached, can indirectly be affected by several different factors, e.g. group size, sex, age, season, habitat, and hunting pressure. The effect of group size on flight distance shows quite some contradictions in literature. Larger groups may flee at greater distance, because they might be able to detect disturbances earlier (many-eyes hypothesis; Lima, 1990). On the other hand, larger groups might flee at shorter distances, because they have a larger sense of safety and individuals are less likely to be caught in larger groups (dilution effect; Dehn, 1990). De Boer et al. (2004) found larger groups to have a greater flight distance, but Matson et al. (2005) found smaller groups to have a greater flight distance. Manor & Saltz (2005) even found no significant effect of group size. Stankowich (2008) found a weak effect of larger groups to show a greater flight distance. Several studies found an increased flight initiation distance for animals that live in areas with hunting and increased human presence (Altmann, 1958; Crosmar et al., 2001; Manor & Saltz, 2005; Setsaas et al., 2007; Stankowich, 2008). However Stankowich (2008) found several studies to report an effect of habituation in animals that often get exposed to human activity, resulting in smaller flight initiation distances over time. The indirect effect of sex on flight distance shows, just as the indirect effect of sex on vigilance, no consistent results about one sex to have greater flight distance. However Recarte et al. (1998) and Stankowich (2008) found a trend towards females fleeing at greater distance than males. Females with offspring always flee at greater distances than males and other females (Altmann, 1958; Recarte et al., 1998; Stankowich, 2008). Altmann (1958) and Stankowich (2008) both found animals to have a longer FID in open habitat types. This longer distance is linked to several factors. Animals have a higher visibility in open habitats. Moreover, animals have

more space to run in open areas. Furthermore, cover is less and distance to refuge is greater in open areas, which may lead to an increased risk. This can cause animals to initiate flight earlier (Stankowich, 2008). A factor that might also affect an animal's suspicion, and thereby the flight distance is the way an approacher behaves and the way it looks. A more threatening approach (faster and more direct) and bright colours will cause greater flight distances (Stankowich, 2008). This suggests that animals pay attention to differences in the behaviour of intruders to judge the relative level of threat (Ydenberg & Dill, 1986).

In this study, the following question will be addressed: How does vigilance and flight behaviour differ over group size, group composition, sex, habitat type and part of the day, in three different African ungulate species? For vigilance behaviour of individual animals, sex will also be taken into account as explanatory factor. The study question was answered by testing the following hypotheses and expectations: (1) The "group-size effect" describes the relationship between an animal's sense of safety and the herd size. Therefore, it is expected that individuals living in smaller herds will each have more frequent and longer vigilance scans, resulting in a longer total duration of vigilance per individual than animals living in large herds. They will also have a longer FID than animals in large herds. (2) Smaller species are easier targets and are more top-down regulated by several predator species than larger species (Sinclair et al., 2003; Underwood, 1982). It is, therefore, expected that individuals of smaller animal species (impala in my study) will each have more frequent and longer vigilance scans, resulting in a longer total duration of vigilance per individual than individuals of large species (zebra, wildebeest). Furthermore individuals of smaller species will have a longer FID. (3) There is no consistency about either males or females having a higher sense of safety. However, Stankowich's (2008) meta-analysis showed a trend towards females being more skittish. So, in this study it is expected that female individuals will each have more frequent and longer scans, resulting in longer total duration of vigilance per individual than male individuals. Mostly female groups will therefore show the same pattern for higher vigilance levels than mixed or mostly male groups. FID will also be longer in mostly female groups. (4) Openness of vegetation and distance to cover describe the relationship between anti-predator strategies and different habitat types. Thus, it is expected that individuals in open habitat will each have a lower scan frequency and shorter scans,

resulting in shorter total duration of vigilance per individual than individuals in closed habitat. FID will be longer in open habitat than in closed habitat. (5) A prey's sense of safety is linked to activity of predators in the area. Therefore, it is expected that individuals will each have a lower scan frequency and shorter scans, resulting in shorter total duration of vigilance per individual in the afternoon compared to the morning. FID will be longer in the morning than in the afternoon.

Material & method

Study site & study species

This research was conducted within a 1200 ha fenced area, hencefore referred to as "the breeding camp", on Welgevonden Game Reserve (24°14'S, 27°46'E). The reserve is located in the Waterberg area in the Limpopo Province of South Africa. Field data were collected from September till November, covering the hot dry season and the beginning of the wet season. The vegetation in the area of the breeding camp mostly consists of *Burkea africana* woodland mixed with vegetation dominated by *Diplorhynchus condylocarpon* and *Terminalia sericea*. In the north-eastern top of the study area some grassland can be found. The Waterberg area is a stone-rich area and is one of three major mountain ranges in the Limpopo Province (UNESCO, 2016). The rocks form plateaus and thereby cause a difference in height. The breeding camp is located on a hill-slope, with the altitude increasing from the North to the South. See figure 1 for a map of the breeding camp.

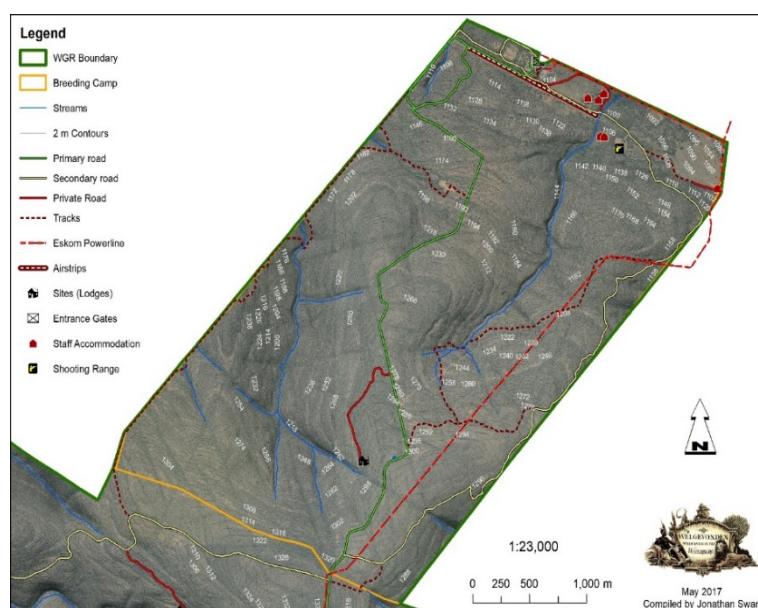


Figure 1. Map of the breeding camp of Welgevonden Game Reserve (WGR). ©Jonathan Swart, research ecologist of WGR

This study focussed on three African ungulate species namely plains zebra, *Equus burchellii*, blue wildebeest, *Connochaetes taurinus*, and impala, *Aepyceros melampus*. The plains zebra is a medium sized equid, weighs 175 to 385 kg (Grubb, 1981) and is spread throughout south-eastern Africa. This grazing animal prefers open grasslands, open woodlands and open scrublands. Zebras tend to live in permanent family groups comprised of one male and one to six females plus the young. Bachelors can form groups of up to sixteen individuals. The animals primarily graze on grass, which comprises 90% of the diet. Though sometimes also herbs, leaves and twigs are eaten. Plains zebra is preyed by lions, *Panthera leo*, spotted hyena, *Crocuta crocuta*, cheetah, *Acinonyx jubatus*, and leopard, *Panthera pardus* (Colvin & Nihranz, 2009). Blue wildebeest is common in Eastern and Southern Africa. Its habitat comprises of a wide variety from dense bush to open woodland floodplains, but the animal prefers savannahs. It can weigh 118 to 270 kg. Herds are mostly made up of about eight females with calves and bulls are known to wander amongst these herds. Wildebeest are grazers who mostly eat rapidly growing grasses. When grass is sparse leaves of shrubs and trees are eaten. Blue wildebeest is mostly preyed by lion, cheetah and spotted hyena (Geraci, 2011). The impala is a medium sized antelope. Males mostly weigh 60 to 65 kg while females weigh between 40 and 45 kg. The species ranges over much of Southern and Eastern Africa (Matson et al., 2005) and can be found in woodland with little undergrowth and low to medium grassland. The animals form different social structures depending on the season. The average size of a female herd is about fifteen to 100 animals, depending on available space. During the wet season different group formations can be found namely: males with and without females, bachelor herds, and breeding herds of females and juveniles. During the dry season, males can be found grouped together or mixed with females. Impala is a mixed feeder eating grass in the wet season and browse in the dry season (Lundrigan & Sproull, 2000).

As part of a bigger project, some individuals of these three species were given a tagged neck collar with an integrated GPS logger and accelerometer. See table 1 for an overview of how many animals of each species and sex have received a collar. In this study the collars were solely used for the number and colour of the tag as a measure of animal identity.

Table 1. Overview of distribution of collars			
	total	males	females
zebra	30	10	20
wildebeest	34	15	19
impala	33	13	20

Data collection

Animals were observed for their behaviour during the morning (7-9 AM) and afternoon (3-5 PM) from two towers at different locations, by car or from the tented camp within the study area. Behaviour was scored with a Samsung tablet, using the "Behavioral Observation Tool" application. It was assumed that herd size and composition remained constant over several days. In order to check for this, herds were followed and monitored during the duration of the study period.

Different measurements were recorded for each group of animals encountered, namely: species, group size, group composition (juvenile/adult and sex class), date, time of day, collar number, and level of vigilance. Vigilance was seen as the action or state where animals actively scan the area for possible danger and thereby raise the head. One to three focal collared animals within a group were observed for 10 minutes, unless animals moved away or became distracted/disturbed. The following was measured for the focal animals: scan frequency (number of vigilance events per minute, #/min), the average duration of each event (seconds) and the proportion of total observing time spent vigilant (time scanning/time observed). The sex of the focal animals was also noted. Furthermore, when possible, a total group scan was performed to determine the vigilance level of the group as a whole. For group vigilance, herds were observed 20 times using a fixed-interval, time-point rule. Each fixed-point intervals lasted 15 seconds for groups up to fifteen individuals, adding one second for every additional individual. During these intervals, the vigilant individuals were counted. Group scan level was estimated as: the average percentage of animals in the group displaying vigilant behaviour during the scan. Group vigilance was estimated as: the proportion of intervals where a minimum of one animal was vigilant (Childress and Lung, 2003). Group scans were also performed on herds that did not contain animals equipped with a collar. Furthermore, for every day, weather conditions, cloud cover and vegetation type were noted, since these factors can also affect animal behaviour.

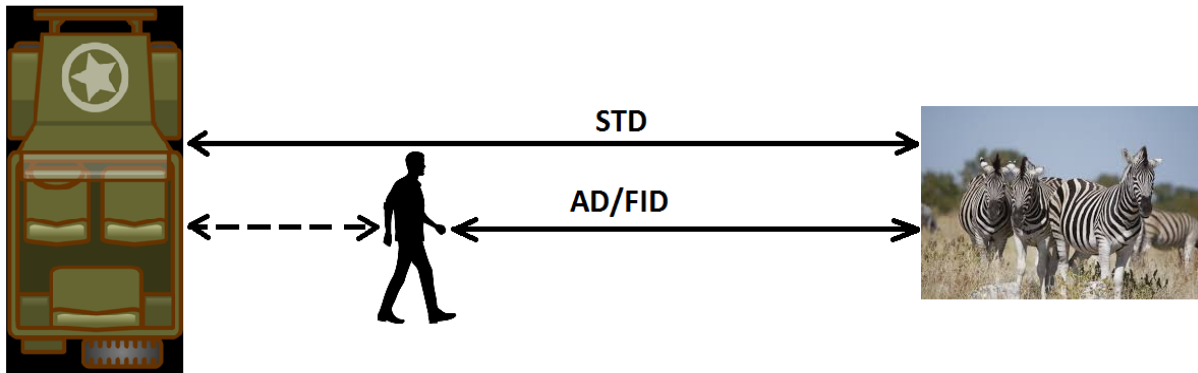


Figure 2. Visualisation of how starting distance (STD), alert distance (AD) and flight initiation distance (FID) were measured. First STD was measured, then a person started walking towards the animals and once they reacted (vigilance or fleeing) distance from the person to the nearest animals was measured. This distance was represented by either AD or FID.

Following the method of Setsaas et al. (2007), recordings of flight behaviour were performed, focussing on the flight initiation distance. For these recordings, groups of animals, either with or without collars, were approached to measure the following: alert distance (AD), which is the distance a person can approach animals at which they become alert or start to show higher vigilance, and flight initiation distance (FID), which is the distance to which a person can approach animals up until they flee. Again, species, group size, group composition, vegetation type, date, time of the day, weather conditions and cloud cover were noted if individual or group vigilance had not been recorded before. The starting distance (STD) from the vehicle to the position of the nearest animals was measured using a laser range finder. Then the observer started to walk towards the animals in a straight line. Pace of walking was about one step per second and was the same for and during each recording. It was assumed that the observer approaching the animals is a proxy for how the animals deal with a threat. The observer recorded the distance between him/herself and the nearest animals once all animals in the herd displayed “alert” behaviour. This was done with the range-finder. The person continued to walk until the animals fled. At that point the observer stopped walking and recorded the distance between him/her and the nearest animals using the range-finder. See also figure 2.

Data analysis

Analyses were done using R 3.4.3. The packages used in R were the lme4, lmerTest, and multcomp packages. All data were tested for normality. The three different measures for individual vigilance were scan frequency (#/min), mean scan duration (s) and proportion scanning of total observed time. The different measures for vigilance of the herd as a

whole were group scan level (mean percentage of individuals scanning during an interval) and group vigilance level (proportion of intervals with at least one individual scanning), and the measures of flight behaviour were AD and FID. Since the same individuals and groups were observed several times during three months, data are repeated measurements. Analysis of how all dependent variables are influenced by all independent factors was performed using linear mixed models. Fixed factors in the linear mixed models were either species (zebra, wildebeest, impala), group composition (mostly-females, mostly-males, mixed), sex (male, female), the time of day (morning, afternoon), and/or habitat type (bush, mixed savannah, open grassland). Group size as number of individuals was a covariate. Certain interaction effects of the fixed factors were also tested. Interaction effect were expected and tested between group size and group composition, group size and species, species and the time of the day, species and sex, species and group composition, and species and habitat type. Random factors in the models were individual or group identity, weather conditions (sunny, cloudy, rainy), and cloud cover.

The focus was not on finding the best fitting model, but on finding the model that included all independent variables which significantly influenced the dependant variables. The first step in this, was creating a linear mixed model for every of the dependant variables, with all five or six independent variables included. The models for measures of individual vigilance included species, group composition, sex, time of day, group size and habitat type. The models for measures of group vigilance and flight behaviour included species, group composition, time of day, habitat type, and group size. Significance of the independent variables was tested by using an ANOVA for each of the created models. Variables that

did not significantly influence the dependant variables were removed from the model. After this, each of the interaction effects was added one at a time. Again, ANOVAs were used on the models to test for significance of the interaction effects. So in the end every model contained only those independent variables and interaction effects that significantly influence the dependant variables (see table 3).

For the independent variables that did show significance, a post-hoc Tukey test was performed to find differences between different levels of the variable. I used each of the final mixed models (as shown in table 3) to predict values of the dependant variables with each possible combination of values for the other fixed factors. This was done to see the effect of each independent variable and interaction effect separately.

Results

Individual vigilance behaviour

There was a significant difference in the frequency of scanning between the three species ($F=5.75$, $p<0.01$) (table 2 and 3). Wildebeest has a lower frequency of scanning than zebra and impala, when all other variables are equal (figure 3A). Vegetation cover has a significantly positive effect on scan frequency ($F=8.96$, $p<0.001$), with highest values in bushy areas (figure 3C and table 2 and 3). Scan frequency is significantly different between different group compositions ($F=5.63$, $p<0.01$) (table 2 and 3). Scan frequency is highest for herds comprising of mostly males and lowest for mixed herds (figure 3B). The difference in mean scan duration between the species is not significant, but shows a trend ($F=2.73$, $p=0.07$). Other fixed factors have no significant effect on the duration of scanning (table 2 and 3, figure 4).

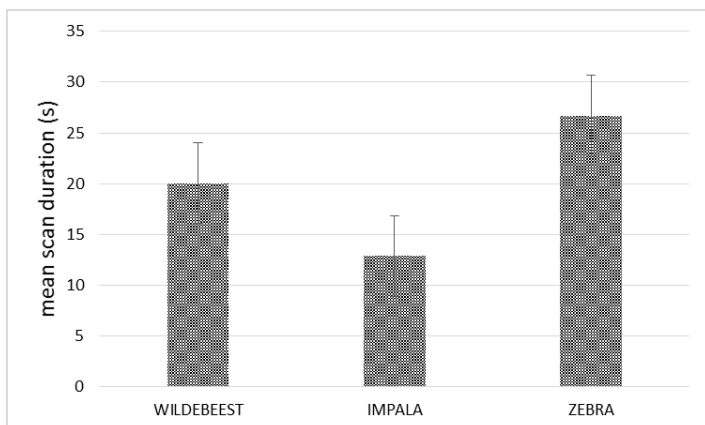


Figure 4. Differences in duration of scanning, indicated as the average duration of a head raise performed by an individual, between the three studies species. Values were predicted in R, using the linear mixed model. Error bars represent standard error. N=157

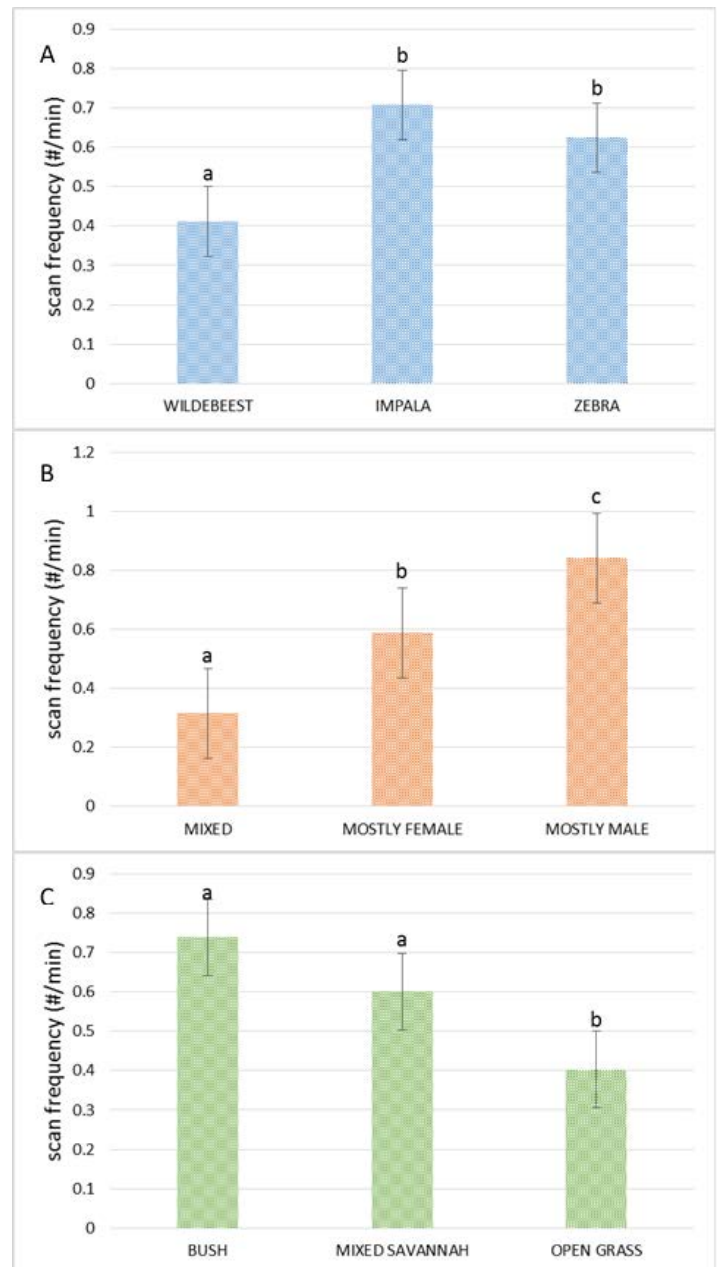


Figure 3. Differences in frequency of scanning, indicated as the number of head raises performed by an individual per minute, between A) the three studies species, B) ungulate group composition, and C) habitat type. Values were predicted in R, using the linear mixed model. Error bars represent standard error. N=157

Species has a significant effect on proportion of time spent scanning ($F=6.56$, $p<0.01$). Zebra has a higher proportion of scanning than wildebeest. Vegetation cover has a positive effect on the proportion of time spent scanning ($F=5.13$, $p<0.01$), with highest values in bushy areas. Bushy vegetation shows a higher proportion of scanning than mixed savannah and open grass. Scan proportion changes significantly over group size, but this effect depends on group composition due to a significant interaction ($F=2.95$, $p=0.03$). For mixed groups and herds comprising of mostly females, group size has a negative effect on the proportion of time spent scanning. For herds comprising of mostly males, group size has a positive

effect on the proportion of time spent scanning (table 2 and 3, figure 5A-C).

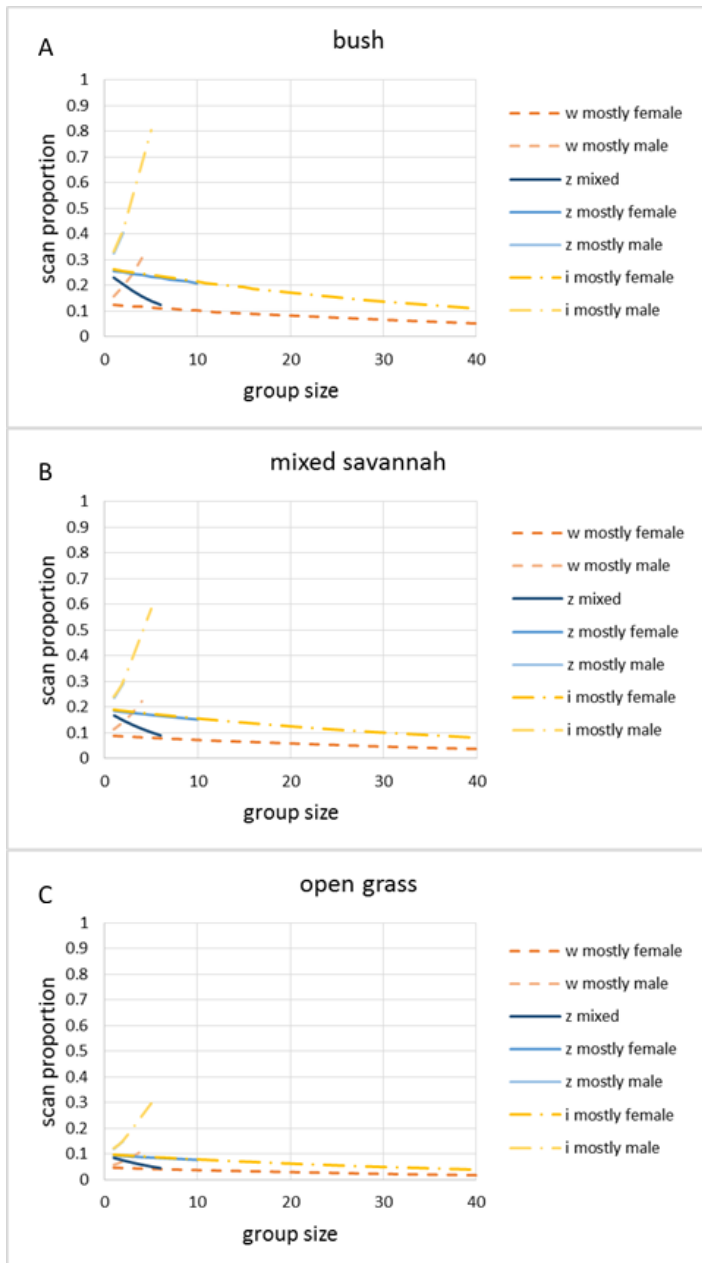


Figure 5. The effect of ungulate group size and group composition on the scan proportion, indicated as the proportion of observed time spent scanning the area by an individual, in plains zebra (z) and wildebeest (w) and impala (i) in A) bushy habitat, B) mixed savannah habitat and C) open grass habitat. Values were predicted in R, using the linear mixed model. Lines stop at the maximum observed group

Group vigilance behaviour

Group size has a significantly negative effect on the group scan level ($F=4.71$, $p=0.05$). Furthermore, overall group scanning is significantly affected by group composition ($F=6.08$, $p=0.03$). It is higher in mixed groups than in groups comprising of mostly females (table 2 and 3, figure 6). The difference in group vigilance level between mixed groups and mostly-female groups is not significant, but shows a trend ($F=3.27$, $p=0.09$) (figure 7, table 2 and 3).

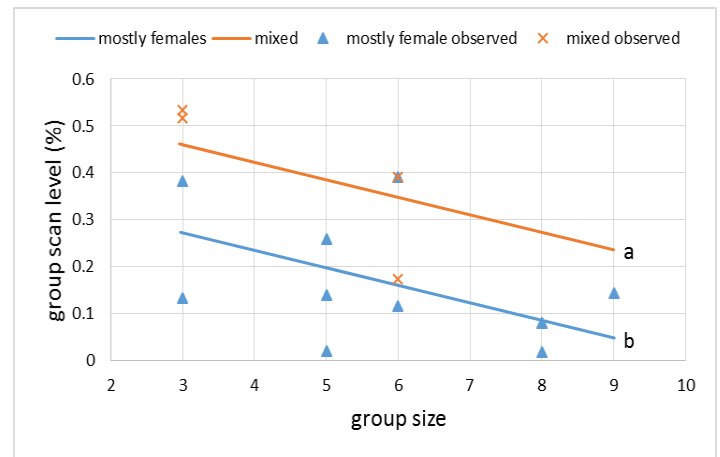


Figure 6. The effect of ungulate group size and group composition on the group's scan level, indicated as the average proportion of animals performing a head raise during a 15s-scan. Values were predicted in R, using the linear mixed model. Triangles and crosses are observed values. $N=15$

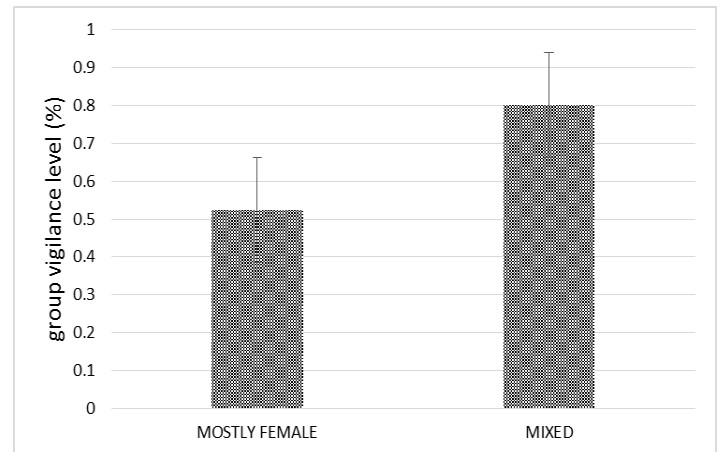


Figure 7. Differences in ungulate group vigilance level, indicated as the proportion of 15s-scans with at least one individual being vigilant, between mostly-female groups and mixed groups. Values were predicted in R, using the linear mixed model. Error bars represent standard error. $N=15$

Flight behaviour

None of the tested fixed factors have a significant effect on the alert distance (AD) (table 2 and 3). The flight initiation distance (FID) changes significantly over group size, but this effect depends on species due to a significant interaction ($F=14.44$, $p<0.01$). Group size has a negative effect on the FID for both wildebeest and zebra, but this effect is stronger for zebra. Vegetation cover has a negative effect on the FID ($F=21.51$, $p<0.01$). The distance at which animals flee is shorter in bushy vegetation than in mixed savannah areas and in open grass areas. Furthermore, FID is significantly different in different group compositions ($F=13.35$, $p=0.01$). The distance is shorter for mixed groups than for mostly-female groups and mostly-male groups (table 2 and 3, figure 8A-C).

Table 2. Results of the ANOVAs used to test whether group composition, sex, time of the day, group size and habitat type significantly influence scan frequency, mean scan duration, scan proportion, group scan level, group vigilance level, alert distance and flight initiation distance in plains zebra, wildebeest and impala. For each factor in the linear mixed models, the F- and p-values are given. For group size as covariate, the covariate estimate and standard error are given where the variable was significant. Values of interaction effects are only shown for the ones that were significant. For each model, the applied method of estimation (REML=restricted maximum likelihood) and the sample size (n) are given. Dashes (--) indicate that this variable was not tested in the model. An overview of the final models is given in table 3.

model no.		1	2	3	4	5	6	7
independent variables	statistics	scan frequency (#/min)	mean scan duration (s)	scan proportion	group scan level (%)	group vigilance level (%)	alert distance (m)	flight initiation distance (m)
species	F	5.75	2.73	6.56	1.16	0.99	0.10	0.93
	p	< 0.01	0.07	< 0.01	0.45	0.46	0.76	0.37
group composition	F	5.63	1.02	1.99	6.08	3.27	3.19	13.35
	p	< 0.01	0.36	0.15	0.03	0.09	0.11	0.01
sex	F	0.70	1.64	1.39	--	--	--	--
	p	0.41	0.20	0.24	--	--	--	--
time of day	F	2.48	0.42	0.02	2.32	1.38	2.79	2.02
	p	0.09	0.66	0.98	0.18	0.27	0.14	0.20
group size	F	2.13	1.02	2.34	4.71	0.18	0.03	14.99
	p	0.15	0.31	0.13	0.05	0.70	0.86	0.02
covariate estimate					-0.037			-3.648
s.e.					0.017			2.128
vegetation/habitat type	F	8.96	0.57	5.13	1.67	0.75	1.03	21.51
	p	< 0.001	0.57	< 0.01	0.31	0.52	0.40	< 0.01
group composition x group size	F			2.95				
	p			0.03				
species x group size	F							14.44
	p							< 0.01
estimation method		REML	REML	REML	REML	REML	REML	REML
n		157	157	157	15	15	15	15

Table 3. Overview of linear mixed models. Crosses (x) indicate that the variable was significant (x indicates $p \leq 0.05$, xx indicates $p \leq 0.01$, xxx indicates $p \leq 0.001$). Dots (°) indicate that the variable showed a trend towards significance ($p < 0.1$). Dots with lines (°) indicate that the two variables showed a significant interaction. Empty boxes indicate that the variable was not significant and thus excluded from the model. For each model, the sample size (n), the value of the AICc, and the marginal R squared (R^2_m) and conditional R squared (R^2_c) are given. F- and p-values of each variable are given in table 2.

model no.	1	2	3	4	5	6	7
	scan frequency (#/min)	mean scan duration (s)	scan proportion (%)	group scanning (%)	group vigilance (%)	alert distance (m)	flight initiation distance (m)
species	xx	°	xx				°
group composition	xx		°	x	°		xx
group size			°	x			x°
sex							
habitat type	xxx		xx				xx
time of day							
n	157	157	157	15	15	15	15
AICc	176.20	1458.45	-52.59	5.38	17.92	100.17	96.23
R^2_m	0.156852	0.034776	0.154392	0.537639	0.189299	0.641637	0.784083
R^2_c	0.255194	0.089935	0.154392	0.537639	0.189299	0.745586	0.930053

Table 4. Correlations between the independent variables for each of the different linear mixed models.								
model		intercept	wildebeest	zebra	mostly-females	mostly-males	mixed savannah	
1: scan frequency	wildebeest	-0.474	--	--	--	--	--	
	zebra	-0.662	0.687	--	--	--	--	
	mostly-females	-0.702	-0.055	0.165	--	--	--	
	mostly-males	-0.575	-0.123	0.201	0.780	--	--	
	mixed vavannah	-0.196	0.040	-0.010	-0.100	-0.124	--	
	open grass	-0.264	0.241	0.202	-0.235	-0.246	0.585	
2: mean scan duration		intercept	wildebeest					
	wildebeest	-0.783	--					
	zebra	-0.828	0.731					
3: scan porportion		intercept	wildebeest	zebra	mixed savannah	open grass	mostly-females: group size	mostly-males: group size
	wildebeest	-0.816	--	--	--	--	--	--
	zebra	-0.834	0.806	--	--	--	--	--
	mixed savannah	-0.308	0.004	-0.024	--	--	--	--
	open grass	-0.473	0.149	0.120	0.575	--	--	--
	mixed: group size	-0.236	0.133	-0.025	0.120	0.268	--	--
	mostly-females: group size	-0.590	0.494	0.542	-0.042	-0.095	0.147	--
	mostly-males: group size	-0.272	0.147	0.319	-0.159	-0.133	0.036	0.366
4: group scan level		intercept	mostly-females					
	mostly-females	-0.236	--					
	group size	-0.783	-0.339					
5: group vigilance level		intercept						
	mostly-females	-0.856						
7: flight initiation distance		intercept	mostly-females	mostly-males	mixed savannah	open grass	group size	
	mostly-females	-0.163	--	--	--	--	--	
	mostly-males	-0.605	0.202	--	--	--	--	
	mixed savannah	-0.611	-0.107	0.386	--	--	--	
	open grass	-0.611	-0.242	0.381	0.732	--	--	
	group size	-0.509	-0.582	0.234	0.430	0.430	--	
	group size: zebra	0.281	0.448	-0.126	-0.610	-0.432	-0.679	

Discussion

The aim of this study was to determine how vigilance and flight behaviour in three different African ungulate species were affected by group size, group composition, sex, habitat type and part of the day. For individual vigilance, I looked at the number of scans per minute, the mean duration of each scan and the proportion of total observed time spent scanning. For vigilance of the whole herd, I looked at the average proportion of individuals looking up during a 15s-scan and the proportion of 15s-scans with at least one individual being vigilant. In terms of flight behaviour I looked at the alert distance (AD) and the flight initiation distance (FID). Overall, I found that group

size negatively influenced vigilance and FID and that habitat openness negatively influenced vigilance and positively influenced FID. Time of the day and sex did not significantly influence vigilance and flight behaviour at all. Furthermore, the factors species and group composition did not show consistency in how they influenced measures of vigilance and flight behaviour.

It is well-known that animals spend less time on anti-predator strategies and more time on foraging when living in large herds compared to small herds. This is the so-called "group-size effect" (Elgar, 1989; Lima, 1990; Lima, 1995; Pulliam, 1973). I also found a significantly negative effect of group size, i.e. for the

proportion of time spent scanning, for group scanning and for FID. Many studies found that vigilance levels in individuals decrease as size of the herd increases. For example Childress & Lung (2003) found this effect for elk (*Cervus elaphus*), Beauchamp & McNeil, 2003 found it in greater flamingos (*Phoenicopterus ruber*), Bednekoff & Ritter (1994) found it in springbok (*Antidorcas marsupialis*), Matson et al. (2005) found it for impala and Hunter & Skinner (1998) found the effect in impala and wildebeest. For individual vigilance, I found the effect of group size to be dependent on the composition of the observed herds. For mixed herds and mostly-female groups I indeed found the scan proportion to decrease with increasing group size. However, for mostly-male groups I found the proportion of scanning to increase in larger groups. Childress & Lung (2003) also found this interaction effect between group composition and group size, as they found females and yearlings to reduce time spent scanning with increasing group size, while they did not find an effect of group size on male groups. Mostly-male groups, which are bachelor herds most of the time, may have higher vigilance levels with increasing group size because they are looking for females to mate with or because they are on the lookout for competitors. However, in this study the effect of group size for mostly-male groups can also be caused by a low sample size (N=21). The effect of group size for the herd as a whole was found before by Childress & Lung (2002) and by Underwood (1982). It can probably best be explained by comparing a small and a large herd in their ability to detect possible danger. If it takes, for example, three individuals to spot possible danger early on, in a smaller herd automatically a larger proportion of the animals need to scan their surroundings than in a large herd. So in smaller groups almost all individuals need to constantly check the surroundings, while the animals in a large group can all take turns and alternate between scanning and eating. Furthermore, Childress & Lung (2002) found that group vigilance level (intervals with at least one scanning animal) goes up with increasing group size. With that they suggest that animals in larger groups have a possible benefit of detecting predators early. However, I did not find an effect of group size on group vigilance, so I cannot make the same conclusion. Matson et al. (2005) and Altmann (1958) found similar results for flight initiation distance in impala and moose, as I did in zebra and wildebeest. On the contrary de Boer et al. (2004) and Aastrup (2000) reported larger groups of roe deer, fallow deer and caribou to have a greater

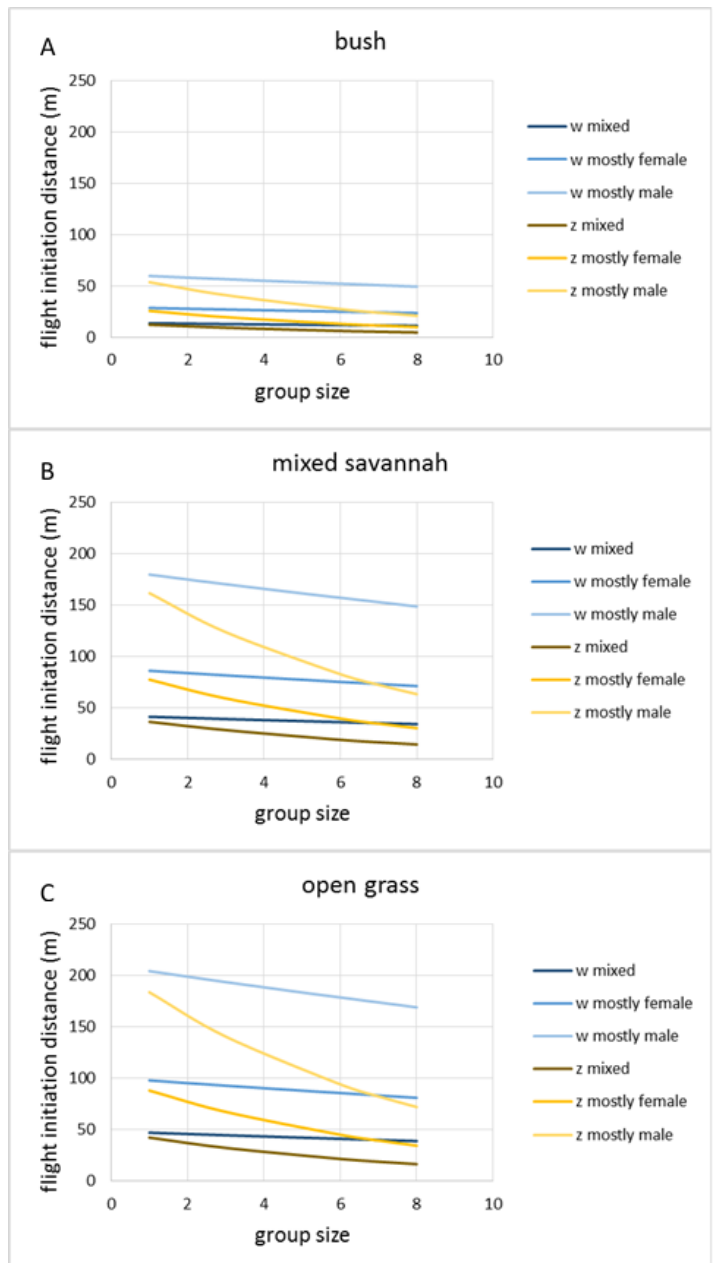


Figure 8. The effect of ungulate group size and group composition on the flight initiation distance, indicated as the distance to which an observer can approach before animals flee, in plains zebra (z) and wildebeest (w) in A) bushy habitat, B) mixed savannah habitat and C) open grass habitat. Values were ln transformed and predicted in R, using the linear mixed model. N=15

FID. Stankowich (2008) found a slightly bigger proportion of literature to report increasing FID with increasing group size, but also found that there is a lot of difference in these results between studies. This shows the contradictions in literature in the effect of group size on flight initiation distance. My findings of decreasing FID in larger groups contributes to the dilution effect of larger groups fleeing at shorter distances due to a greater sense of safety (Dehn, 1990). The fact that I found both vigilance levels and the distance at which animals flee to decrease with group size confirms the “group-size effect”.

For the three species studied in this thesis, I found some significant differences in their individual vigilance behaviour. Though, these results were not consistent. Looking at the study by Underwood (1982) it was expected that zebra would have lowest levels of vigilance and that impala would have highest levels of vigilance. However, I found wildebeest to have a lower scan frequency and scan proportion than zebra. Makin et al. (2017) also compared these two species, but did not find a difference between their proportion of time spent scanning. Although it was expected that impala would have greater vigilance levels than zebra, I did not find any significant difference between these two species at all. The results that I found for vigilance levels of the different species, might be caused by an effect of group size. Of impala I mostly observed large groups (10+ individuals) and of wildebeest I observed a few very large herds of up to 40 individuals, while the largest group of zebra consisted of ten individuals. So maybe impala and wildebeest do indeed have higher levels of vigilance than zebra, but in this study the effect of body weight might be cancelled out by the group-size effect due to an artefact of the observations. Due to an insufficient range of herd size observations for each of the species, my models might have had difficulties to distinguish between some of the herd sizes. The models might have picked up some incidental patterns for the group sizes with only few samples available, and drawn these patterns out of proportion. It is thus questionable how trustworthy the results of the predictions are for the group sizes that only had few observations.

Hunter & Skinner (1998) also found the effect of decreasing vigilance levels with increasing body size and body weight by comparing impala and wildebeest. Though not significant, impala did show highest values for frequency (figure 5A) and proportion of scanning (figure 5C), which could still suggest that my hypothesis is true. The flight initiation distance has not been compared between species before. I found that FID is greater in wildebeest than in zebra. This could again be linked to the effect of body weight found by Underwood (1982). Since zebras are heavier than wildebeests, we can probably suggest that wildebeests are an easier target. This might explain why they are more vigilant and thus also have a longer FID than zebras. However, I found wildebeest to have lower vigilance levels than zebra, so that contradicts with the previous suggestion. The difference in flight initiation distance might also be caused by a difference in predator-escape strategy used by both species.

While I did not find any significant effect of sex, I did find an effect of group composition. Since I only made a division of group composition based on the number of males and females in the group and did not take the presence of juveniles and mothers into account, it can basically be said that the group composition represents differences between sexes. In literature, results about the effect of sex are often conflicting. Some find females to have higher vigilance levels (Childress & Lung, 2003) and some find males to have higher vigilance levels (Barnier et al., 2016). Matson et al. (2005) found that females scan more frequently, but that males have a higher proportion of scanning. This shows that different measures of vigilance may even vary within the same sex. Matson et al. (2005) linked this pattern to a difference in the way the sexes escape predation or engage in social vigilance. Males of some African ungulate species are more vulnerable to natural predation and trophy hunting. Furthermore, males might display vigilance as a result of seasonal rivalry with other males. Hunter & Skinner (1998) found the difference between male and female vigilance to be dependent on prey species and predation pressure. For vigilance of individuals I found that the scan frequency and the scan proportion were lowest in mixed groups and highest in mostly male groups. Since the mixed groups have an approximately equal amount of male and female individuals, I would expect that this group type has intermediate values of vigilance. I can thus not make any clear statement whether males or females cause either an increase or a decrease in vigilance. However, the male groups that I encountered were very small, with a maximum of five individuals for impala. The effect of high scan frequency and proportion in males might thus also be due to a “group-size effect”. Besides, I only observed few mostly-male groups, so this effect could also be an artefact of small sample size. Because of these small sample sizes and the small group sizes for male groups, the model might again have had difficulties in distinguishing between male groups of different sizes. So, the trustworthiness of these results for mostly-male groups is quite low. For both group scan level and group vigilance level I found opposite effects of group composition as for individual vigilance. In both cases I namely found mostly female groups to have lower vigilance levels than mixed groups. This in turn could indicate that females have lower vigilance levels than males. Childress & Lung (2003) also found that group vigilance was different between different group compositions. They found levels to be highest in

groups containing mothers and lowest in mostly male groups. They did however not find a difference between mixed groups and mostly female groups, where I did. Since I have only a limited amount of observations for vigilance of the group as a whole, the higher vigilance levels for mixed groups might be an artefact of the small sample size. I am thus also not able to make any clear conclusions about the effect of group composition on vigilance of the whole group. Recarte et al. (1998) and Stankowich (2008) reported females to have a longer FID than males, which corresponds with my results that mostly female groups have a longer FID than mixed groups (which indicates that male presence shortens the FID). However, I found mostly male groups to have an even greater FID than mixed and mostly female groups, which is in contrast with other literature. This could be due to the fact that the only record of a mostly male group was a solitary male. The model could, therefore, not distinguish between male groups of different group sizes, which makes the outcome untrustworthy. This male "group" is thus best ignored. If we leave the mostly male groups aside and only look at the results of individual vigilance, we see that individuals of mostly female groups have higher vigilance levels than mixed groups. This implies that, regardless of species, the sense of safety decreases when more females are present. Possibly because females are more vulnerable than males and because females often have a young they need to protect. In this study I did not take the presence of juveniles and mothers into account, which makes it hard to correctly compare to other literature. Other studies have namely shown that mothers are even more vigilant than other females (Childress & Lung, 2003; Hunter & Skinner, 1998). Furthermore, Altmann (1958), Burger & Gochfeld (1994), Hunter & Skinner (1998), Rowe-Rowe (1974) and Stankowich (2008) all found FID to be greater when young were present. For future research it might thus be good to make a more broad division also looking at mothers and/or juveniles.

For the variable habitat type, i.e. habitat openness, I found the expected effects. Both scan frequency and scan proportion were highest in closed bushy vegetation. These same results were found for different ungulate species by Goldsmith (1990), Underwood (1982) and Bednekoff and Ritter (1994). Bednekoff & Ritter (1994) looked at animals near trees versus out in the open, but this could be compared to closed versus open habitat. On the other hand, Matson et al. (2005) found the proportion of

scanning to be higher in impalas that were far from cover. In this study zebra and wildebeest both showed a longer FID in open areas compared to closed bushy areas. This effect was also seen by Altmann (1958) and Stankowich (2008). The findings that ungulates become more vigilant and have shorter FID in closed habitat might be caused by several factors. Firstly, a lower visibility in these closed habitat types. Higher visibility in open areas allows animals to spot an intruder earlier, which can increase FID. Secondly, animals have more space to run in open areas than in bushy areas when they do spot an intruder. They might thus choose to flee earlier, thereby increasing the chance to outrun the predator. This can again increase FID. Furthermore, little cover and greater distance to refuge in open areas may lead to an increased risk, causing animals to initiate flight more quickly and thereby increasing FID (Stankowich, 2008). However, some predators use an ambush-technique and tend to hide in cover, so prey species need to be more wary in closed vegetation (Bednekoff & Ritter, 1994). Looking at the habitat types where the three studied species are mostly found, an interaction effect between species and habitat type would be expected. Zebra and wildebeest are namely grazers who prefer grasslands (Colvin & Nihraz, 2009; Geraci, 2011), while impala is a mixed feeder who can mostly be found in woodland with little undergrowth (Lundrigan & Sproull, 2000). However, I did not find this interaction to be significant, and thus cannot say anything about species-specific behaviour in any type of habitat.

Of all the variables that were tested, I did not find a significant effect of sex and time of the day on vigilance levels and FID. When looking at other studies, no consistency in results can be found for vigilance levels and FID either being greater or smaller due to these variables. This might imply that both variables do indeed not affect vigilance and flight behaviour. However, the fact that I did not find a significant effect of time of the day can also be caused by the division I made. Bednekoff & Ritter (1994) namely found that vigilance levels were not different between early morning and afternoon, but that levels were higher in the late morning. I only looked at morning versus afternoon. So, for future research it could be better to look at more different parts of the day. What was also interesting is that the alert distance was not significantly affected by any of the dependant variables. I find it hard to properly explain this result. I wrote down the AD once all individuals in the herd were showing alertness by raising their head.

Though, the animals might have already been alert while still foraging and thus keeping their heads low. It is also possible that members of the herd rely on the one or two individuals that raise their heads early on. Waiting on all individuals to raise their head, might thus have led to a misinterpretation of alertness within the herd.

For several variables I only had a few observations, leading to low statistical power. For future research, observations could be extended to a longer period of time or to a larger area. This makes it possible to collect more replicates, also in different seasons. Because I couldn't find clear results for the effects of group composition and time of the day, it might be needed to divide these variables into different and/or more categories in the future. Furthermore, at times it was difficult to differentiate between 'head-raising' and 'standing' in the animals, since animals would sometimes keep their heads held high while switching between gazing off into the distance and actively scanning. Matson et al. (2005) also observed animals ruminating with their head raised for a long period of time, mostly toward the warmer hours of the middle of the day. This could have led to a wrong count of head-raising events.

To recap, I did indeed find that vigilance levels were higher and FID were longer in small herds and that vigilance levels were lower and FID was greater in open habitat types. The results for the effects of species, group composition, sex and time of the day were either inconsistent or absent. So further research is needed to get more clarity on the effects of these factors. Although I confirmed that some of the studied variables affect vigilance and fleeing behaviour in plains zebra, wildebeest and impala, many more factors are also important in this relationship. Thus it still remains difficult to fully explain how animals adjust their strategies to escape predation and other disturbances.

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