Predation risk and herd position influence the proportional use of antipredator and social vigilance by impala

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Highlights

- Animals divide the time they are vigilant between antipredator and social vigilance.
- Yet, it is unclear how central and edge individuals prioritize these vigilance types.
- We found impala at the edge of herds had higher total and antipredator vigilance.
- As risk increased, edge individuals sacrificed social for antipredator vigilance.
- Yet, central individuals sacrificed antipredator for social vigilance.

Abstract

Vigilance is just one of the many fitness enhancing activities that animals do each day. However, as vigilance is used for both predator detection and obtaining social information, individuals must decide how to divide their time between these two vigilance types. Yet, it is unclear, 1) how prey species living in the centre and edge of groups prioritise their use of these different vigilance types, and 2) how this prioritisation varies with increasing risk. To explore this, we focused on the degree to which impala (*Aepyceros melampus*), a herd-living antelope, adjusted their antipredator (looking out from the herd) and social (looking at herd members) vigilance across three sites with different predator guilds and predator densities. We found that as predator types and densities increased, herd size increased, but that impala did not adjust the total time they spent vigilant (antipredator plus social vigilance). Thus, they did not sacrifice other fitness enhancing activities (e.g. foraging) to increase vigilance. Yet, overall, within the herds, edge individuals displayed greater total vigilance (antipredator plus social) and showed a greater proportional use of antipredator vigilance compared to central individuals. With increasing predator numbers, edge individuals maintained and ultimately increased their proportional use of antipredator vigilance. In contrast, central individuals reduced their use of antipredator vigilance and increased social vigilance. As suggested elsewhere, this adjustment may have been related to these individuals trying to increase foraging efficiency and cohesion benefits. However, they may have also monitored conspecifics to detect threats, while obtaining both short (e.g. less time spent in a vulnerable head-down position) and long-term (e.g. reduced daily foraging time allowing more time for less vulnerable activities) antipredator benefits. Ultimately, our results highlight that herd position and predator differences can influence overall vigilance levels and how individuals adjust their use of antipredator and social vigilance.

Key words: fitness enhancing activities, herd size, social information, spatial position

A key way in which prey species can reduce predation risk is via predator detection (i.e. vigilance; Pulliam, 1973; Fairbanks & Dobson, 2007; Beauchamp, 2019). Moreover, by associating with conspecifics, individuals benefit from the vigilance of other group members (i.e. the “many-eyes” effect; Pulliam, 1973). Nevertheless, despite the overall antipredator benefits of group-living, predation risk varies depending on where an individual is within the group. Specifically, individuals on the edge of groups tend to face greater risk compared to central individuals, as predators generally target edge individuals (Hunter & Skinner, 1998; Lingle, 2001; Quinn & Cresswell, 2006). Thus, central individuals tend to be sheltered from predators by the surrounding group members (i.e. smaller domains of danger; Hamilton, 1971). Therefore, in an attempt to reduce predation risk, edge individuals may maintain higher levels of antipredator vigilance compared to central individuals (i.e. the edge effect; Bednekoff & Ritter, 1994; Di Blanco & Hirsch, 2006; Blanchard, Sabatier, & Fritz, 2008; Faveau, Goldizen, & Pays, 2010).

While vigilance is often related to antipredator behaviour, it can also serve as a means of monitoring other group members and thus obtaining social information (termed social vigilance from here on; Beauchamp, 2001; Pays, Dubot, Jarman, Loisel, & Goldizen, 2009a; Pays et al., 2009b). Social information provides animals with access to additional information about their environment such as the location of food patches, overall habitat quality, and the risk of competition from other group members (Valone & Templeton, 2002; Favreau et al., 2010; Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010). For example, central individuals can monitor the foraging of group members around them, and then join these individuals at their patches (i.e. scrounging; Caraco & Giraldeau, 1991; Vickery, Giraldeau, Templeton, Kramer, & Chapman, 1991).

Nevertheless, social vigilance directed at group members may also help reduce predation risk if, 1) monitoring other group members increases the likelihood of detecting approaching predators (Barta & Giraldeau, 2000; Barta, Liker, & Monus, 2004), 2) predators avoid attacking scanning individuals (i.e. predator selectivity effect; Packer & Abrams, 1990; Lima, 1994), 3) monitoring other group members reduces the limits of collective detection (e.g. scanning individuals are vigilant non-detectors that observe other group members reacting to predators; Lima, 1994; Lima & Zollner, 1996; Pays et al., 2012), or 4) scanning reduces the amount of time that an individual spends looking for food in a vulnerable head-down position (Lima & Bednekoff, 1999; Tisdale & Fernández-Juricic, 2009).

As individuals divide their time between a range of fitness enhancing activities such as foraging, obtaining mates, and other social interactions, they are limited with regards to the total amount of time that they may remain vigilant (McNamara & Houston, 1992; Sirot & Touzalin, 2009; Blanchard, Pays, & Fritz, 2017; Ota, 2018). Thus, the time they do allocate to vigilance tends to be divided between predator detection and the social monitoring of other group members (Favreau et al., 2010; Pays et al., 2012). How individuals make this split, will likely depend on a number of factors including an individual's age and sex, the level of perceived risk, and position in the group (Bednekoff & Ritter, 1994; Pays et al., 2012; Lung & Childress, 2006). Despite an understanding of this adjustment, it is unclear, 1) how prey species living in the centre and edge of groups prioritise their proportional use of antipredator and social vigilance, and 2) how this prioritisation varies with different levels of predation.

To address this knowledge gap, we recorded both antipredator and social vigilance of three populations of free-ranging impala (*Aepyceros melampus*), a herd-living antelope, that differed with regards to the predators and predator densities they were exposed to. As adjustments of group/herd size is primarily a proactive response to high-risk areas (Creel, Schuette & Christianson, 2014), we predicted that impala would move in larger herds in sites containing a greater diversity and density of predators. Yet, despite adjustments to vigilance tending to be a reactive response to the close proximity of predators (Creel et al., 2014), it is also possible that prey species, especially individuals at the edge of a herd, maintain greater levels of overall vigilance with increasing risk. However, to do this, prey species would need to sacrifice time spent on other fitness enhancing activities to increase the total time they spent vigilant. In contrast, prey species may allot a specific amount of time for vigilance and thus any adjustments to their vigilance would be done by adjusting the proportional use of antipredator and social vigilance. With this in mind, we predicted that due to the greater risk they experience (e.g. Lingle, 2001), edge individuals would allot a greater proportion of time towards antipredator vigilance compared to central individuals, and that this difference would become greater as risk increased (Edge_1 in Fig. 1). However, as vigilance is not the only fitness enhancing activity that impala display, it is possible that edge individuals constantly maintain maximum levels of antipredator vigilance irrespective of risk and thus their use of antipredator vigilance would remain relatively stable despite increasing risk (Edge_2 in Fig. 1).

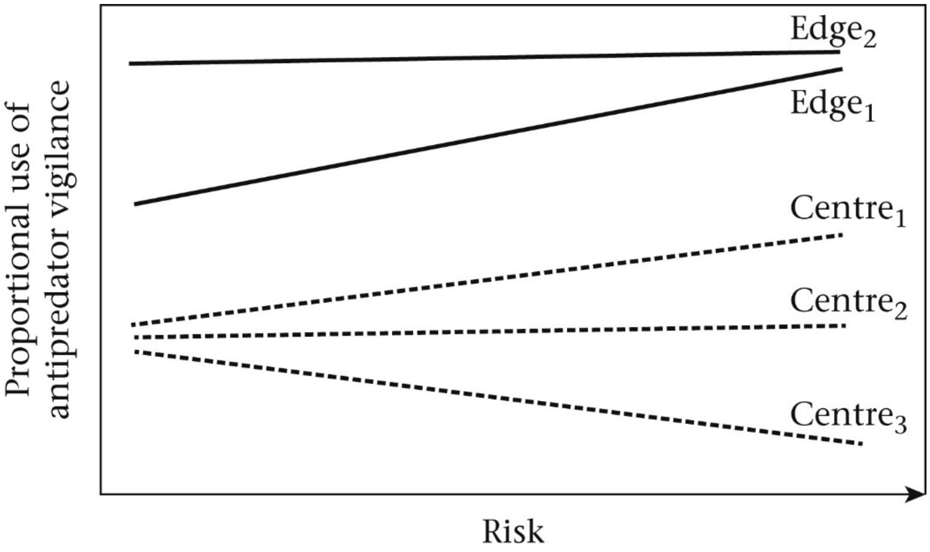

Figure 1. Predictions about how impala at the centre (Centre_1, Centre_2, Centre_3) and edge (Edge_1, Edge_2) of herds may adjust their proportional use of antipredator vigilance in response to increasing predation risk. As adjustments are to the proportional use of antipredator vigilance, an increase in the use of antipredator vigilance reflects and decrease in the use of social vigilance and vice versa.

As central individuals tend to experience lower predation risk compared to edge individuals (e.g. Blanchard et al., 2008), and thus have more time to obtain social information, we expected them to display lower overall levels of antipredator vigilance compared to individuals on the edge of the herd (Fig. 1). Yet, there are a number of ways in which they may adjust their use of antipredator vigilance in response to increasing levels of risk (Fig. 1). First, if, despite their smaller domains of danger, risk to central individuals increases as overall predation risk increases, then we predicted that central individuals should increase their use of antipredator vigilance with increasing risk (Centre_1 in Fig. 1). However, if the probability of attack of central individuals is not affected by changes in overall predation risk, then we predicted that vigilance levels would remain constant despite increasing risk (Centre_2 in Fig. 1). Finally, as suggested by previous studies (Ranta, Peuhkuri, Hirvonen, & Barnard, 1998; Bugnyar & Kotrschal, 2002; Barta et al., 2004), if central individuals increase their use of social vigilance with increasing predation risk (e.g. for scrounging), there should be a corresponding decrease in the use of antipredator vigilance; Centre_3 in Fig. 1).

METHODS

Ethical Note

All aspects of the research design adhere to the ASAB/ABS Guidelines for the Use of Animals in Research. In addition, the Animal Ethics Committee at the University of Pretoria approved the research protocol and awarded the ethics code: EC030-18.

Study Sites

The study was conducted during the winter dry season (May to October 2018) across three protected areas in South Africa that varied in relation to predator guilds and densities. Madikwe Game Reserve (High number of predator types and density) (680 km^2; 24.817°S, 26.217°E), contained 25 leopard (*Panthera pardus*), 14 wild dog (*Lycaon pictus*), 3 cheetah (*Acinonyx jubatus*), 25 spotted hyena (*Crocuta crocuta*), and 35 lion (*Panthera leo*) (Nel, 2018). This gave an overall predator density of 0.15 predators/km^2. Telperion Nature Reserve (Intermediate number of predator types and density) (110 km^2; 25.708°S, 28.930°E) contained 4 leopards (0.04 predators/km^2; Somers, n.d.), while Groenkloof Nature Reserve (Low predator density) (6 km^2; 25.793°S, 28.204°E) did not contain predators.

Study Species

Impala are a good model species with which to study the proportional use of antipredator and social vigilance as their vigilance is influenced by predation pressure, group size, and spatial position (Lung & Childress, 2006). The main predators of impala, in order of prey preference, are leopard, wild dog and cheetah, with these three predators sharing a strong overlap in their preference for impala (Hayward et al., 2006a; Hayward, Hofmeyr, O'brien, & Kerley, 2006b; Hayward, O'brien, Hofmeyr, & Kerley, 2006c; Hayward & Kerley, 2008). In contrast, impala tend to be avoided by lion (Hayward & Kerley; 2005), and hunted in proportion to availability by spotted hyenas (Cooper, Holekamp, & Smale, 1999; Hayward, 2006). Nevertheless, despite not favouring impala, lion and hyena still pose a threat.

Data Collection

In each site, we recorded impala vigilance from a stationary vehicle using binoculars. To limit our disturbance on the herds, we only recorded data from herds that were >50 m away from the vehicle. To record the detailed action sequence of an observed individual, we used focal sampling and spoke into a portable voice recorder. We then transcribed the recordings to determine the duration of the action sequence to the nearest second. Within each herd, we focused our data collection on two individuals in the centre of the herd and two on the edge (i.e. *N*= 4 individuals per herd; 10-40% of the herd). We did this to ensure we obtained the same amount of data from each herd irrespective of size. Yet, to avoid pseudoreplication, we calculated the mean vigilance for the central and edge individuals separately and thus used herds as our replicates (see Schmitt, Stears, Wilmers, & Shrader, 2014 for similar procedure). In total, we recorded data from 10 herds (range 10-40 individuals) in each of the three sites resulting in 30 herds in total. Observations were split approximately equally between the morning and afternoons in each of the sites (Low predator: four mornings, six afternoons, Intermediate predator: five mornings, five afternoons, High predator: six mornings, four afternoons).

A focal individual was considered to be vigilant when it raised its head above the horizontal with its ears in an upright position (Scheel, 1993; Schmitt et al., 2014). Each observation began when the focal individual was foraging with its head down. As individuals were grazing during the observations, we did not have to differentiate between vigilance and the impala browsing with their heads up. We limited each observation to a two-minute (120 seconds) foraging bout, during which the duration and type of vigilance (antipredator or social) was recorded. We selected 120 seconds because it was the longest length of time that we could consistently observe individuals across all three sites. Nevertheless, we are confident that we were able to gather reliable data during these observations as our observation length sits within the range (i.e. 29-300 seconds) of observations utilised in other vigilance studies of impala (e.g. Burger & Gochfield, 1994; Matson, Goldizen, & Putland, 2005; Blanchard et al., 2008; Pays et al., 2012; van der Meer, Fritz, & Pays, 2015; Blanchard et al., 2017).

We defined antipredator vigilance as an individual looking out away from the herd and social vigilance when individuals looked towards other herd members (Schmitt, Stears, & Shrader, 2016). Despite the wide monocular field of view provided by having their eyes on the side of their heads (Hughes, 1977), impala look directly towards objects (e.g. an approaching predator) when alert and vigilant (Estes, 1991; Shrader pers. obs.). This suggests, that despite their panoramic field of view, impala rely heavily on the small forward-facing region of binocular overlap common in ungulates (Hughes & Whitteridge, 1973; Hughes, 1977; Piggins & Phillips, 1996) to actively view an object of interest. As binocular vision provides better depth perception and thus better estimates of how far away an object is and how fast it is moving (Bishop, 1973), the use of binocular vision likely plays a key role in predator detection and avoidance. As such, we used this intent forward-looking behaviour when the impala were vigilant, to indicate whether an individual was actively looking towards a herd mate or out away from the herd. Lagory (1986) followed the same protocol to determine if white-tailed deer (a species that also has eyes on the side of its head) were focused on specific objects (e.g. conspecifics, approaching researcher). As the impala in the different herds maintained inter-individual distances of ca. 3-6 m, determining where the focal individuals were looking was relatively easy.

One concern, however, is that because central individuals are surrounded by other herd members, they may by chance alone look more frequently at conspecifics (i.e. use social vigilance) compared to edge individuals. To explore this, we took 30 side-on digital images of impala herds while they were feeding (i.e. the same conditions under which we recorded vigilance data) and generated estimates of a central individual's view blocked by other herd members as it looked out away from the herd. We did this by opening the pictures in Microsoft Paint for Windows (version 1903, Microsoft) and counting the number of pixels across each individual impala in front of (i.e. closer to the camera) a randomly selected central individual. To determine the proportion of the central individual's field of view blocked by herd members, we added the pixels measured across the blocking impala and then divided that value by the total number of pixels across the entire herd including the open spaces (i.e. the outer edges of the farthest left and right impala in the herd). If central individuals raised their heads and looked in a random direction, we would then expect their social vigilance to be equal to the proportion of their view blocked by the surrounding herd members. We acknowledge that this method is rather crude but having some quantifiable measure of obstruction as opposed to just making assumptions about the extent to which a central individual's field of view was blocked provides greater insight.

To ensure that we collected data when all the predators were generally active during the day, we made observations within the first three hours after sunrise (06:00-09:00) and the last three hours before sunset (15:00-18:00) (Hayward & Slotow, 2009). To control for the potential effect of vegetation on the landscape of fear (Burger, Safina, & Gochfeld, 2000; Shrader, Brown, Kerley, & Kotler, 2008), we limited our observations to herds that were foraging in open grassland areas >30 m from vegetation clumps. Furthermore, to control for the confounding effects of age and sex, we limited observations to adult females within breeding herds (i.e. one dominant male moving with a herd of females; Jarman, 1974). Owing to the time of year, there were no dependent juveniles within these herds.

Data Analysis

Herd size and predator differences

To determine whether herd size varied in relation to predator differences, we ran a one-way ANOVA with a Tukey Posthoc test to compare herd size across the three sites. Data were log10 transformed to achieve normality and then back transformed for graphical representation.

Total Vigilance

The data for determining the factors influencing the amount of time impala allocated to total vigilance were not normally distributed due to a number of zero values (i.e. individuals that were not vigilant during the two-minute observation period; *N*= 20 out of 122 individuals spread relatively equally across the three sites). Despite some individuals not being vigilant during the observations, there was never an instance when the non-vigilant individuals appeared twice in the same group and position. As such, we were able to gather data from all the observed herds. To deal with these zero values, we employed a two-step procedure. First, we used a chi-square analysis to determine the binomial probability that an individual impala was vigilant or not during the two-minute observation (i.e. 1 being vigilant or 0 being non-vigilant). We ran the chi-square test using the dependent variable as vigilant or not (1 or 0) and the independent variable as either site, position, or herd size. The chi-square test revealed that herd size determined whether an impala was going to be vigilant or not (Pearson chi-square$_{19}$= 34.220, *P*= 0.017). We then removed all zeros from the data set and generated means for those impala that were vigilant

(*N*= 57 mean values) (see Schmitt et al., 2014 for a similar procedure). We then ran a generalized linear model with a Gamma distribution and a log link function, using total time vigilant as the dependent variable, with position within the herd, and site and as independent variables. Herd size was included as a covariate to control for herd size differences. We used the full model including the main effects (position and site) and the interaction of these effects as the ΔAIC between the finite sample corrected Akaike's Information Criterion for the full model (AICc= 442.027) was less than 2 when compared to the model containing only the main effects (AICc= 441.247). Thus, we could not justify removing the interaction (Burnham & Anderson 2002). Data were back transformed for graphical representation.

Proportional use of antipredator and social vigilance

Having determined how total vigilance varied, we then asked, what influences the proportional use of antipredator and social vigilance? The proportional use of social vigilance was calculated by subtracting the amount of antipredator vigilance from the total vigilance. To answer this, we ran a generalized linear model with a binomial distribution and a logit link function using proportional data as the dependent variable, and position within the herd, and site as independent variables. In some observations, individuals did not display social vigilance, yet as this indicated the individual's choice of only using antipredator vigilance, we included these data in the analysis. Once again, we included herd size as a covariate to control for herd size differences. We used the full model including the interaction as it was the most parsimonious model (AICc= 228.093) compared to the main effects only model (AICc= 242.182). We back transformed the data for graphical representation and plotted the marginal means ± SE.

Field of view of central individuals

To determine whether the estimated proportion of the field of view of central individuals blocked by surrounding herd members varied with herd size, we ran a linear regression. Prior to analysis, however, we arcsine transformed the proportions to achieve normality.

Next, to determine whether the proportional use of social vigilance by central individuals was simply an artifact of these individuals being in the centre of the herd (i.e. social vigilance was equal to the proportion of field of view blocked by surrounding herd members), we ran separate chi-square tests for each site. In these tests, we compared our observed split between social and antipredator vigilance (Low predator site: social 0.05, antipredator 0.95; Intermediate predator site: social 0.28, antipredator 0.72; High predator site: social 0.14, antipredator 0.86; see Fig. 3 below) and compared these proportions to the expected proportions where social vigilance was equal to the proportion of view blocked by surrounding herd members (i.e. social 0.41, antipredator 0.59).

RESULTS

Herd size

Herd size significantly increased with increasing predator presence (ANOVA: $F_{2,27}$= 4.488, *P*= 0.021; Fig. 2). Specifically, impala occurred in larger herds in the site with the greatest number of predator types and density compared to the site without predators (*P*= 0.016), while herd size in the intermediate site did not differ to herds in the sites with no (*P*= 0.457), or many predators (*P*= 0.199).

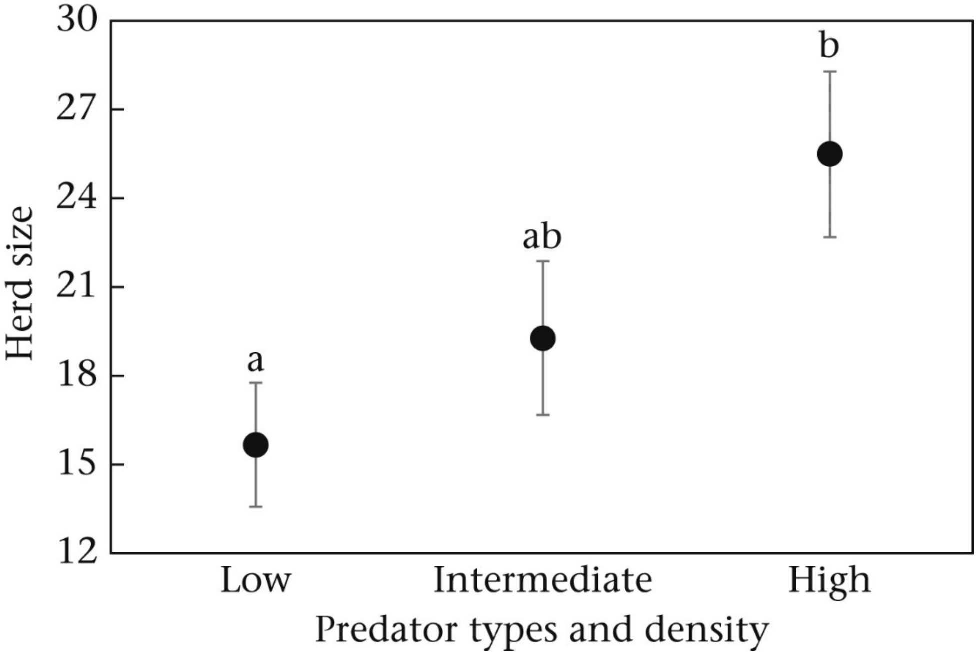

Figure 2. Relationship between herd size (number of individuals per herd) and level of predation risk (i.e. predator types and density). Error bars represent SE.

Total Vigilance

In contrast to our prediction, the overall vigilance of the impala did not differ with increasing predator presence (Generalized Linear Model: Wald chi-square$_2$= 1.135, *P*= 0.567). Rather, individuals at the edge of a herd across all three sites maintained significantly higher levels of total vigilance (23± 3 sec; Mean ±SE) compared to individuals in the centre (15± 2 sec) (Generalized Linear Model: Wald chi-square$_1$= 5.779, *P*= 0.016), while the interaction between these variables was not significant (Generalized Linear Model: Wald chi-square$_2$= 4.704, *P*= 0.095).

Proportional use of antipredator and social vigilance

In all three study sites, impala divided the total time that they were vigilant between antipredator and social vigilance, but consistently displayed a greater use of antipredator vigilance (Fig. 3). Moreover, the impala herds adjusted their overall proportional use of antipredator vigilance in response to site and position in the herd (Table 1). Specifically, antipredator vigilance was higher for individuals at the edge of a herd compared to those in the centre (Fig. 4). Yet, this was only significant in the intermediate ($P<0.001$) and high ($P<0.001$) predator sites. In the site without predators, the proportional use of antipredator vigilance by the impala did not differ between central and edge individuals ($P= 0.123$). Overall, the use of antipredator vigilance by individuals at the edge of herds was high and did not differ between the no predator and intermediate predator sites ($P= 0.543$). However, impala in the site with the greatest number of predators had significantly greater levels of antipredator vigilance compared to the impala in both the no predator ($P= 0.005$) and intermediate predator sites ($P= 0.001$; Fig. 4).

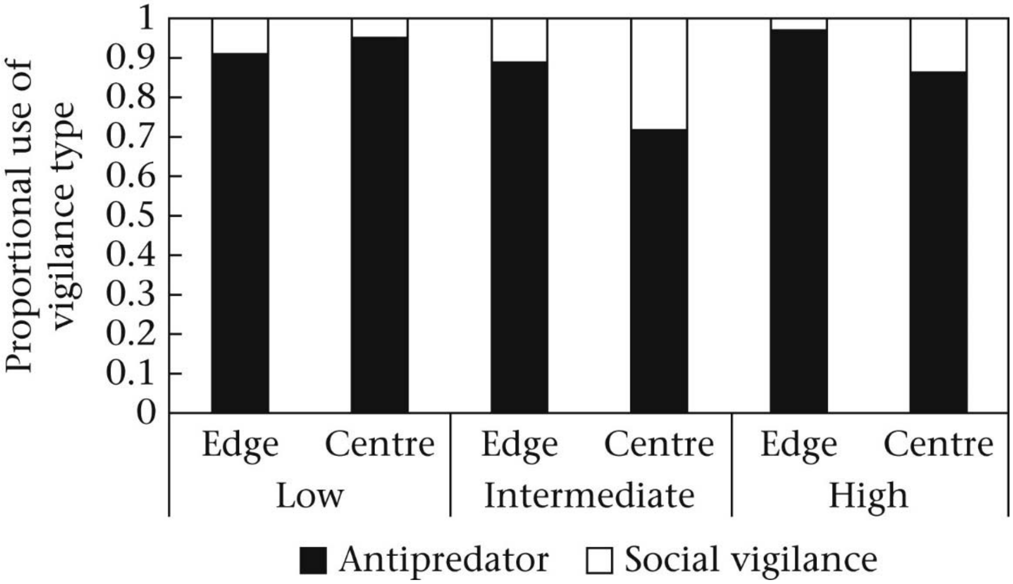

Figure 3. Proportional use of antipredator and social vigilance for individuals at the centre and edge of a herd across different levels of predation risk (i.e. predator types and density).

Table 1. Tests of model effects and variable significance for antipredator vigilance. Bold p-value indicates significance.

Variable	Wald Chi-Square	Degrees of Freedom	*P*-value
Site	25.455	2	**<0.001**
Position	9.440	1	**0.002**
Site x Position	14.923	2	**0.001**

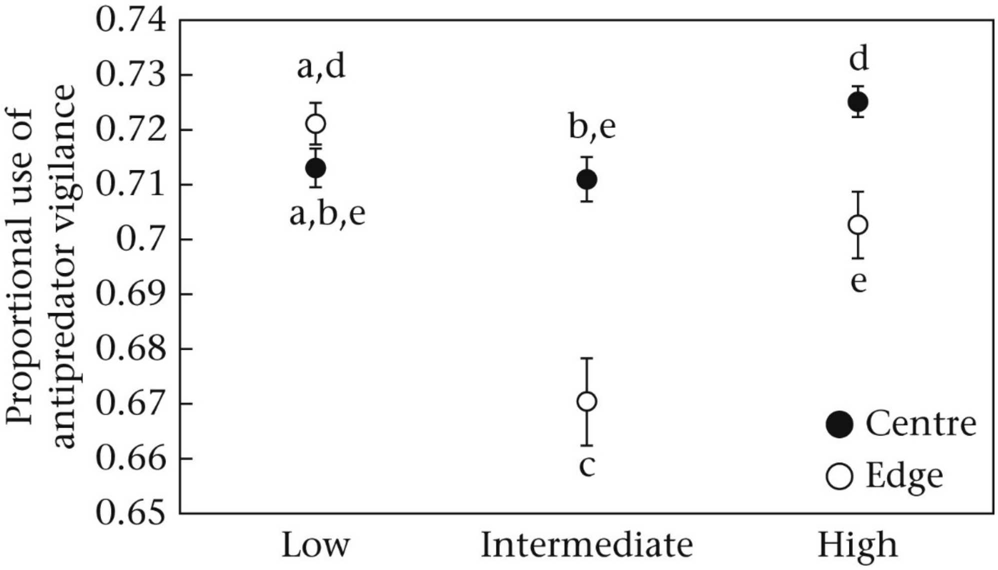

Figure 4. Differences in the proportional use of antipredator vigilance with regards to position within the herd and the level of predation risk (i.e. predator types and density). Marginal means ± SE are plotted.

In contrast, the proportional use of antipredator vigilance by the impala at the centre of the herds was significantly lower in the intermediate and high predator sites compared to the no predator site (low vs. intermediate risk *P*< 0.001; low vs. high risk *P*= 0.007; Fig. 4). Moreover, central individuals in the intermediate site maintained the lowest levels of antipredator vigilance (intermediate vs. high predator site *P*= 0.001; Fig. 4). As a reduction in the proportional use of antipredator vigilance indicates an increase in the use of social vigilance, central impala in the intermediate and high predator sites increased their use of social vigilance at the expense of antipredator vigilance.

Field of view of central individuals

Across the different herds, we found that on average surrounding herd members blocked the field of view of central individuals by a proportion of 0.41 (range 0.20 - 0.67). Yet, this did not change significantly ($R^2 < 0.0001$, $F_{1,29} = 0.001$, $P = 0.979$; Fig 5) as herd size increased ($\beta = 0.005$, $P = 0.979$).

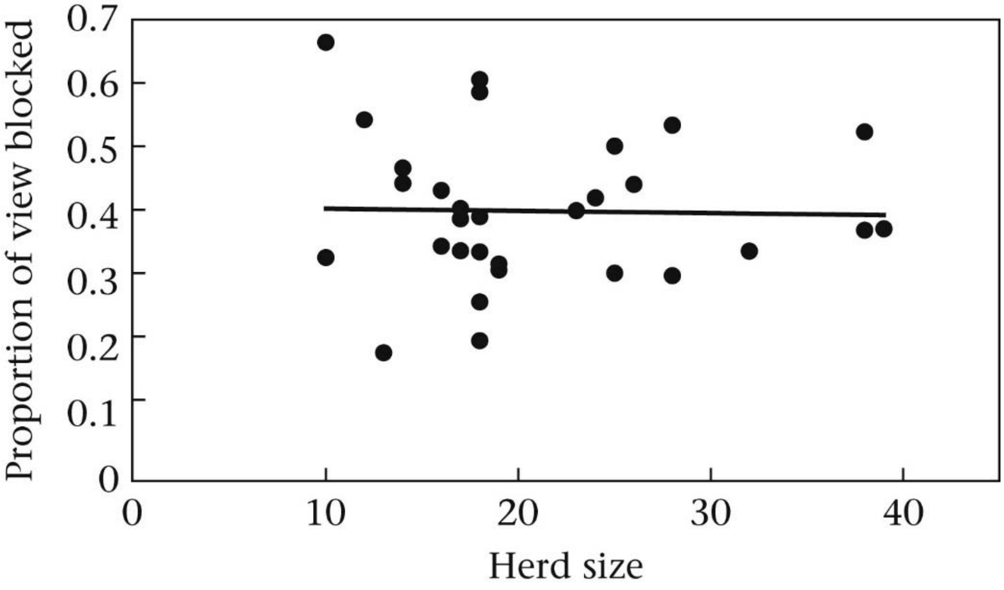

Figure 5. Estimates of the proportion of the field of view of central individuals blocked by surrounding herd mates and how it varies with changes in herd size.

Comparing the expected proportional use of social and antipredator vigilance (0.41 and 0.59 respectively) by central individuals to the observed use of these two vigilance types, we found that central individuals utilised social vigilance less than expected in all three sites (Low: $\chi^2_1 = 0.536$, P<0.001; Intermediate: $\chi^2_1 = 0.070$, $P<0.001$; High predators: $\chi^2_1 = 0.301$, $P<0.001$).

DISCUSSION

As vigilance is just one of the fitness enhancing activities that animals divide their time between, the total time that individuals can remain vigilant is limited (Sirot & Touzalin, 2009; Ota, 2018). As such, individuals will likely need to divide their vigilance between antipredator and social vigilance. Yet, how they do this may vary with predation risk both within groups (e.g. location within the herd) and across sites varying in predation risk (Bednekoff & Ritter, 1994). In this study, we found that as the number of predator types and density increased, impala herd size also increased, but that the impala did not increase the total time that they were vigilant. Rather, individuals at the edge of herds consistently displayed higher total vigilance compared to central individuals across all sites. In addition, edge individuals generally maintained a greater proportion of antipredator vigilance compared to central individuals, while central individuals in the intermediate and high predator sites displayed a greater proportional use of social vigilance compared to those in the no predator site.

With increasing number of predator types and density, we found that impala moved in larger herds, but did not increase their overall vigilance levels. On the surface, this tends to suggest that the impala relied more on proactive measures to reduce potential predation risk across the sites as opposed to reactive responses such as adjusting vigilance levels (Creel, Winnie, Christianson, & Liley, 2008; Broekhuis, Cozzi, Valeix, McNutt, & Macdonald, 2013). Moreover, by not increasing overall vigilance as predator types and density increased, the impala in our study did not sacrifice the time they spent on other fitness enhancing activities. In their study, Creel et al. (2014) recorded larger impala herds in risky open habitats (i.e. far from protective cover) compared to apparently safer closed habitats. As habitat type can be a good indicator of risk (i.e. a landscape of fear; Altendorf, Laundré, López González, & Brown, 2001;

Valeix et al., 2009; Stears & Shrader, 2015), Creel et al. (2014) suggested that the adjustment in impala herd sizes were proactive measures against long-term cues about potential risk. Our results potentially expand these predictions from the habitat scale to the larger landscape scale (i.e. study sites). We too recorded data in an open habitat (i.e. savanna grasslands), but we recorded differences in herd sizes in this habitat type across three separate sites that varied in predator types and density. This suggests that proactive measures such as increasing herd sizes may not be limited to habitat type alone, but rather may also vary with overall differences in predation risk between landscapes (see also Matson et al., 2005). Yet, a limitation in our study is that each level of predation risk (low, intermediate, high) is represented by only one site. Thus, it is possible that other collinear factors may have influenced impala herds sizes. As such, further study is required to determine the full range of spatial scales at which impala may adjust their herd sizes as a proactive measure to reduce predation risk.

Despite changes in vigilance being considered a reactive response to predation risk (Creel et al., 2008; Creel et al., 2014), the fact that impala at the edge of the herds maintained higher total vigilance and generally a greater proportional use of antipredator vigilance across all the sites compared to individuals in the centre (except at the site without predators), suggests that adjustments in vigilance can also be a proactive measure against predators. This 'edge effect' has been recorded in a number of prey species (e.g. Matson et al., 2005; Blanchard et al., 2008; Shi, Li, & Xiao, 2011). For example, Di Blanco and Hirsch (2006) found that ring-tailed coatis (*Nasua nasua*) at the edge of the group were more vigilant than central individuals, but that leading edge individuals maintained the highest vigilance, as they were more likely to be the first to come into contact with ambush predators. In our study, however, edge individuals living without predators still maintained high levels of both total and antipredator vigilance, suggesting an awareness of their potential vulnerability and thus greater precautions taken to limit risk.

In addition to their greater use of total vigilance, impala at the edge of the herds maintained an overall higher proportional use of antipredator vigilance compared to central individuals. Yet, in contrast to our prediction Edge$_2$, we found that the proportional use of antipredator vigilance by edge individuals did not remain stable across the sites, but rather increased in the site with the greatest number of predator types and density. Thus, in line with our prediction Edge$_1$, this suggests that the edge individuals may respond to increasing predator presence by reducing their use of social vigilance to increase their proportional use of antipredator vigilance.

For central individuals, our results suggest that they did not experience greater predation pressure with increasing predator presence (prediction Centre$_1$) or maintain similar levels of antipredator vigilance across the different sites (prediction Centre$_2$). Rather, the lower levels of antipredator vigilance displayed by central herd members in the intermediate and high predator sites compared to the no predator site suggests that they reduced the proportional use of antipredator vigilance to increase their use of social vigilance in these sites (prediction Centre$_3$). Yet, why the impala maintained significantly lower levels of antipredator vigilance in the intermediate site compared to the high predator site is unclear.

The question that remains, however, is why did central individuals increase their proportional use of social vigilance in the sites with predators? As suggested in previous studies (Barta & Giraldeau, 2000; Barta et al., 2004), it could be that they utilised social vigilance for scrounging activities. If this was the case, then they could have increased their feeding efficiency (Caraco & Giraldeau, 1991; Vickery et al., 1991). As intake rate is related to search time and handling time (Holling, 1965; Spalinger & Hobbs, 1992), scroungers may reduce their search time by simply monitoring other individuals that have already found patches. However, it may also have provided central individuals with short-term antipredator benefits such as predator detection via monitoring other group members (Barta & Giraldeau, 2000; Barta et al., 2004), reduced risk via the predator selectivity effect (Packer & Abrams, 1990; Lima, 1994), a decrease in the limits of collective detection by observing surrounding herd members reactions towards predators (Lima & Zollner, 1996; Pays, Beauchamp, Carter, & Goldizen, 2013), and a reduction in the amount of time they spent in a vulnerable head-down position (Lima & Bednekoff, 1999; Tisdale & Fernández-Juricic, 2009).

An increase in the use of social vigilance for antipredator purposes may be expected if surrounding herd members greatly reduced the ability of central individuals to look out from the herd to search for predators. For example, it is possible that the observed increase in the use of social vigilance was due to an increase in group cohesion (i.e. reduction in inter-individual distances) with increasing herd size. If this was the case, then central individuals may have had a larger proportion of their field of view blocked by surrounding herd mates in these larger herds. This then would have been recorded as a larger proportional use of social vigilance.

We did not measure changes in inter-individual distances in the different herds. Yet, we found that central individuals utilised social vigilance less than expected (i.e. social vigilance did not equal the proportion of their view blocked by other herd members). This suggests that the proportional use of social vigilance by central individuals in our study was not simply an artifact of them being in the centre of the herd. Rather, our results suggest that they were able to look out and search for predators and when they lifted their heads and were vigilant, they did so in a specific non-random direction. However, our findings may be influenced by the small number of images (*N*= 30) we had available to estimate the proportion of the view blocked and the method of counting pixels on these images. A better option may have been to use overhead images obtained using a drone and combining these estimates with agent-based computer models to determine how central individuals' field of view changed over time. These, however, were beyond the scope of the study.

It is logical that the view of central individuals would be greatly reduced as herds size increased. Yet, if this was the case, and we underestimated the proportion of view blocked in larger herds, then the difference between the observed and expected values would only become greater, especially for the larger herds in the site with more predators. Thus, this would statistically provide even greater support for our findings. As such, we are confident that the changes in the proportional use of social and antipredator vigilance by central individuals that we recorded reflect decisions made by the impala and were not simply a reflection of the number of individuals in their field of view. This, however, in no way suggests that central individuals did not gain antipredator benefits from their use of social vigilance, but rather that the increase in social vigilance was not driven purely by antipredator benefits.

Central individuals may have also obtained long-term benefits from monitoring other herd members, such as a reduction daily foraging time (i.e. foraging like time minimisers; Bergman, Fryxell, Gates, & Fortin, 2001), which would then allow them to participate in other less-vulnerable head-up fitness enhancing activities (e.g. ruminating while scanning for predators). Unfortunately, recording these different behaviours was beyond our experimental design, thus further study would be required to tease apart the extent to which these potential short and long-term benefits affected the central individuals overall use of social vigilance.

Another possibility is that the impala herds were more compact (i.e. displayed shorter inter-individual distances) while foraging in the site with more predators, as a way to further reduce predation risk. More compact groups has been shown in fiddler crabs (Viscido & Wethey, 2002) and in desert big horn sheep (Mooring, Fritzpatrick, Nishihra, & Reisig, 2004). If the impala herds in our study were more compact, then it is possible that intra-group competition may have been greater in herds living in sites with predators, which could then have prompted an increased use of social vigilance (Treves, 1999; Blanchard et al., 2008). This, however, requires further study.

We acknowledge that our experimental design resulted in us collecting data from a limited number of individuals within a small number of herds at each site. Unfortunately, this has prevented us from drawing definite conclusions about the factors driving the greater use of social vigilance by central individuals in the sites with predators. Nevertheless, despite only focusing on 30 herds, our results highlight how impala within herds and across sites prioritise their use of antipredator and social vigilance. By monitoring these adjustments, we gain valuable insight from the animals' perspective into how they weigh up the importance of different activities under varying levels of potential risk (e.g. Barnier et al., 2014; Makin, Chamaillé-Jammes, & Shrader, 2017). Moreover, as our study is the first to explore the prioritisation of antipredator and social vigilance, we believe that our results make a timely and important contribution to the understanding of vigilance behaviour of individuals living in groups.

In our study, we did not find that impala reduced the amount of time that they spent on other fitness enhancing activities so that they could increase their overall vigilance. Rather, we found that depending on their location within the herd, impala adjusted their use of social and antipredator vigilance in response to differences in predator presence. Yet, as individuals may not maintain the same position with groups over extended periods of time (Krause & Ruxton, 2002; Melletti, Delgado, Penteriani, Mirabile, & Boitani, 2010), adjustments between the use of antipredator and social vigilance are likely being made at both short temporal and spatial scales.

References

Altendorf, K. B., Laundré, J. W., López González, C. A., & Brown, J. S. (2001). Assessing effects of predation risk on foraging behavior of mule deer. *Journal of Mammalogy, 82*, 430-439.

Barnier, F., Valeix, M., Duncan, P., Chamaillé-Jammes, S., Barre, P., Loveridge, A. J., Macdonald, D. W., & Fritz, H. (2014). Diet quality in a wild grazer declines under the threat of an ambush predator. *Proceedings of the Royal Society B: Biological Sciences, 281*, 1785.

Barta, Z., & Giraldeau, L. A. (2000). Daily Patterns of Optimal Producer and Scrounger Use under Predation Hazard: A State-Dependent Dynamic Game Analysis. *The American Naturalist, 155*, 570-582.

Barta, Z., Liker, A., & Monus, F. (2004). The effects of predation risk on the use of social foraging tactics. *Animal Behaviour, 67*, 301-308.

Beauchamp, G. (2001). Should vigilance always decrease with group size? *Behavioral Ecology and Sociobiology, 51,* 47-52.

Beauchamp, G. (2019). On how risk and group size interact to influence vigilance. *Biological Reviews, 94*, 1918-1934.

Bednekoff, P. A., & Ritter, R. (1994). Vigilance in Nxai Pan Springbok, *Antidorcas marsupialis*. *Behaviour, 129*, 1–11.

Bergman, C. M., Fryxell, J. M., Gates, C. C., & Fortin, D. (2001). Ungulate foraging strategies: energy maximizing or time minimizing? *Journal of Animal Ecology, 70*, 289-300.

Bishop, P. O. (1973). Neurophysiology of binocular single vision and stereopsis. In R. Jung (Ed.), *Handbook of Sensory Physiology, vii/3A* (pp. 255-305). Berlin: Springer-Verlag.

Blanchard, P., Pays, O., & Fritz, H. (2017). Ticks or lions: trading between allogrooming and vigilance in maternal care. *Animal Behaviour, 129*, 269-279.

Blanchard, P., Sabatier, R., & Fritz, H. (2008). Within-group spatial position and vigilance: A role also for competition? The case of impalas (*Aepyceros melampus*) with a controlled food supply. *Behavioral Ecology and Sociobiology, 62*, 1863–1868.

Broekhuis, F., Cozzi, G., Valeix, M., McNutt, J. W., & Macdonald, D. W. (2013). Risk avoidance in sympatric large carnivores: reactive or predictive? *Journal of Animal Ecology, 82*, 1098-1105.

Bugnyar, T., & Kotrschal, K. (2002). Scrounging tactics in free-ranging ravens, *Corvus corax*. *Ethology, 108*, 993-1009.

Burger, J., Safina, C., & Gochfeld, M. (2000). Factors affecting vigilance in springbok: importance of vegetative cover, location in herd, and herd size. *Acta Ethologica, 2*, 97–104.

Burnham, K. P., & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach.* New York, NY: Springer-Verlag.

Caraco, T., & Giraldeau, L.-A. (1991). Social foraging: Producing and scrounging in a stochastic environment. *Journal of Theoretical Biology, 153*, 559-583.

Cooper, S. M., Holekamp, K. E., & Smale, l. (1999). A seasonal feast: long-term analysis of feeding behaviour in the spotted hyaena (*Crocuta crocuta*). *African Journal of Ecology, 37*, 149–160.

Creel, S., Schuette, P., & Christianson, D. (2014). Effects of predation risk on group size, vigilance, and foraging behavior in an African ungulate community. *Behavioral Ecology, 25*, 773–784.

Creel, S., Winnie Jr, J. A., Christianson, D., & Liley, S. (2008). Time and space in general models of antipredator response: tests with wolves and elk. *Animal Behaviour, 76*, 1139-1146.

Di Blanco, Y., & Hirsch, B. T. (2006). Determinants of vigilance behavior in the ring-tailed coati (Nasua nasua): The importance of within-group spatial position. *Behavioral Ecology and Sociobiology, 61*, 173–182.

Estes, R. D. (1991). *The behavior guide to African Mammals.* Berkely, CA: University of California Press.

Fairbanks, B., & Dobson, F. S. (2007). Mechanisms of the group-size effect on vigilance in Columbian ground squirrels: dilution versus detection. *Animal Behaviour, 73*, 115–123.

Favreau, F. R., Goldizen, A. W., & Pays, O. (2010). Interactions among social monitoring, anti-predator vigilance and group size in eastern grey kangaroos. *Proceedings of the Royal Society B: Biological Sciences, 277*, 2089–2095.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology and Evolution, 25*, 354–361.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of Theoretical Biology, 31*, 295–311.

Hayward, M. W. (2006). Prey preferences of the spotted hyaena (*Crocuta crocuta*) and degree of dietary overlap with the lion (*Panthera leo*). *Journal of Zoology, 270*, 606–614.

Hayward, M. W., Henschel, P., O'brien, J., Hofmeyr, M., Balme, G., & Kerley, G. I. H. (2006a). Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology, 270*, 298–313.

Hayward, M. W., Hofmeyr, M., O'brien, J., & Kerley, G. I. H. (2006b). Prey preferences of the cheetah (*Acinonyx jubatus*) (Felidae: Carnivora): morphological limitations or the need to capture rapidly consumable prey before kleptoparasites arrive? *Journal of Zoology, 270*, 615–627.

Hayward, M. W., & Kerley, G. I. H. (2005). Prey preferences of the lion (*Panthera leo*). *Journal of Zoology, 267*, 309–322.

Hayward, M. W., & Kerley, G. I. H. (2008). Prey preferences and dietary overlap amongst Africa's large predators. *South African Journal of Wildlife Research, 38*, 93–108.

Hayward, M. W., O'Brien, J., Hofmeyr, M., & Kerley, G. I. H. (2006c). Prey Preferences of the African Wild Dog *Lycaon Pictus* (Canidae: Carnivora): Ecological Requirements for Conservation. *Journal of Mammalogy, 87*, 1122–1131.

Hayward, M. W., & Slotow, R. (2009). Temporal Partitioning of Activity in Large African Carnivores: Tests of Multiple Hypotheses. *South African Journal of Wildlife Research, 39*, 109-125.

Holling, C.S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada, 97*, 5-60.

Hughes, A. (1977). The Topography of Vision in Mammals of Contrasting Life Style: Comparative Optics and Retinal Organisation. In F. Crescitelli (Ed.), *The Visual System in Vertebrates. Handbook of Sensory Physiology, vol 7 / 5* (pp. 615-737). Berlin: Springer.

Hughes, A., & Whitteridge, D. (1973). The receptive fields and topographical organization of goat retinal ganglion cells. *Vision Research* 13, 1101–1114.

Hunter, L. T. B., & Skinner, J. D. (1998). Vigilance Behaviour in African Ungulates : The Role of Predation Pressure. *Behaviour, 135*, 195–211.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour, 48*, 215-267.

Krause, J., & Ruxton, G.D. (2002). *Living in groups.* Oxford: Oxford University Press.

Lagory, K. E. (1986). Habitat, group size, and the behaviour of white-tailed deer. *Behaviour*, *98,* 168-179.

Lima, S. L. (1994). On the personal benefits of anti-predatory vigilance. *Animal Behaviour, 48*, 734-736.

Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? *Animal Behaviour, 58*, 537-543.

Lima, S. L., & Zollner, P. A. (1996). Anti-predatory vigilance and the limits to collective detection: visual and spatial separation between foragers. *Behavioral Ecology and Sociobiology, 38*, 355-363.

Lingle, S. (2001). Anti-Predator Strategies and Grouping Patterns in White-Tailed Deer and Mule Deer. *Ethology, 107*, 295–314.

Lung, M. A., & Childress, M. J. (2006). The influence of conspecifics and predation risk on the vigilance of elk (*Cervus elaphus*) in Yellowstone National Park. *Behavioral Ecology,* 18, 12–20.

Makin, D. F., Chamaillé-Jammes, S., & Shrader, A. M. (2017). Herbivores employ a suite of antipredator behaviours to minimize risk from ambush and cursorial predators. *Animal Behaviour, 127*, 225-231.

Matson, T. K., Goldizen, A. W., & Putland, D. A. (2005). Factors affecting the vigilance and flight behaviour of impalas. *South African Journal of Wildlife Research,* 35, 1–11.

McNamara, J. M., & Houston, A. I. (1992). Evolutionarily stable levels of vigilance as a function of group size. *Animal Behaviour, 43*, 641-658.

Melletti, M., Delgado, M. M., Penteriani, V., Mirabile, M., & Boitani, L. (2010). Spatial properties of a forest buffalo herd and individual positioning as a response to environmental cues and social behaviour. *Journal of Ethology, 28*, 421-428.

Mooring, M. S., Fitzpatrick, T. A., Nishihira, T. T., & Reisig, D. D. (2004). Vigilance, Predation risk and the Allee Effect in Desert Bighorn Sheep. *Journal of Wildlife Management, 68*, 519–532.

Nel, P. (2018). *North West Parks Board Madikwe game audit*. Unpublished raw data.

Ota, K. (2018). Fight, fatigue and flight: narrowing of attention to a threat compensates for decreased anti-predator vigilance. *The Journal of Experimental Biology, 221*, jeb168047.

Packer, C., & Abrams, P. (1990). Should co-operative groups be more vigilant then selfish groups? *Journal of Theoretical Biology, 142*, 341-357.

Pays, O., Beauchamp, G., Carter, A. J., & Goldizen, A. W. (2013). Foraging in groups allows collective predator detection in a mammal species without alarm calls. *Behavioral Ecology, 24*, 1229-1236.

Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. (2012). Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia, 169*, 419-430.

Pays, O., Dubot, A. L., Jarman, P. J., Loisel, P., & Goldizen, A. W. (2009a). Vigilance and its complex synchrony in the red-necked pademelon, *Thylogale thetis*. *Behavioral Ecology, 20*, 22–29.

Pays, O., Goulard, M., Blomberg, S. P., Goldizen, A. W., Sirot, E., & Jarman, P. J. (2009b). The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behavioral Ecology, 20*, 469–477.

Piggins, D., & Phillips, C. J. C. (1996). The eye of the domesticated sheep with implications for vision. *Animal Science, 62,* 301-308.

Pulliam, H. R. (1973). On The Advantages Flocking. *Journal of Theoretical Biology, 38*, 419–422.

Quinn, J. L., & Cresswell, W. (2006). Testing domains of danger in the selfish herd: sparrowhawks target widely spaced redshanks in flocks. *Proceedings of the Royal Society B: Biological Sciences, 273*, 2521–2526.

Ranta, E. S. A., Peuhkuri, N., Hirvonen, H., & Barnard, C. J. (1998). Producers, scroungers and the price of a free meal. *Animal Behaviour, 55*, 737-744.

Scheel, D. (1993). Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Animal Behaviour,* 46, 695–704.

Schmitt, M. H., Stears, K., & Shrader, A. M. (2016). Zebra reduce predation risk in mixed-species herds by eavesdropping on cues from giraffe. *Behavioral Ecology, 27*, 1073–1077.

Schmitt, M. H., Stears, K., Wilmers, C. C., & Shrader, A. M. (2014). Determining the relative importance of dilution and detection for zebra foraging in mixed-species herds. *Animal Behaviour, 96*, 151–158.

Shi, J., Li, D., & Xiao, W. (2011). Influences of sex, group size, and spatial position on vigilance behavior of Przewalski’s gazelles. *Acta Theriologica, 56*, 73–79.

Shrader, A. M., Brown, J. S., Kerley, G. I. H., & Kotler, B. P. (2008). Do free-ranging domestic goats show `landscapes of fear'? Patch use in response to habitat features and predator cues. *Journal of Arid Environments, 72*, 1811-1819.

Sirot, E., & Touzalin, F. (2009). Coordination and Synchronization of Vigilance in Groups of Prey: The Role of Collective Detection and Predators' Preference for Stragglers. *American Naturalist, 173*, 47-59.

Somers, M. (n.d.) [*Predator numbers in Telperion Nature Reserve*]. Unpublished raw data.

Spalinger, D. E., & Hobbs, N. T. (1992). Mechanisms of foraging in mammalian herbivores: new models of functional response. *The American Naturalist, 140*, 325-348.

Stears, K., & Shrader, A.M. (2015). Increases in food availability can tempt oribi antelope into taking greater risks at both large and small spatial scales. *Animal Behaviour, 108*, 155-164.

Tisdale, V., & Fernández-Juricic, E. (2009). Vigilance and predator detection vary between avian species with different visual acuity and coverage. *Behavioral Ecology,* 20, 936-945.

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys. *American Journal of Primatology, 48*, 113–126.

Valeix, M., Loveridge, A. J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., & MacDonald, D. W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: Spatiotemporal variations influence habitat use. *Ecology, 90*, 23-30.

Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: a widespread social phenomenon. *Philosophical Transactions of the Royal Society B: Biological Sciences, 357*, 1549–1557.

van der Meer, E., Fritz, H., & Pays, O. (2015). Anti-predator behaviour of kudu and impala in response to mimicked African wild dog presence: do age and sex matter? *Behaviour, 152*, 1209-1228.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L., & Chapman, C. A. (1991). Producers, Scroungers, and Group Foraging. *The American Naturalist, 137*, 847-863.

Viscido, S. V., & Wethey, D. S. (2002). Quantitative analysis of fiddler crab flock movement: Evidence for 'selfish herd' behaviour. *Animal Behaviour, 63*, 735–741.

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation.* New York, NY: Hafner.