

# Animal Behaviour

## Predation risk effects on intense and routine vigilance of Burchell's zebra and blue wildebeest --Manuscript Draft--

<b>Manuscript Number:</b>	ANBEH-D-20-00561R2
<b>Article Type:</b>	UK Research paper
<b>Keywords:</b>	Anti-predator behaviour, Dinokeng Game Reserve, landscape of fear, lion, predator-prey dynamics
<b>Corresponding Author:</b>	Sze Wing Yiu University of the Witwatersrand Johannesburg, Gauteng SOUTH AFRICA
<b>First Author:</b>	Sze Wing Yiu, PhD
<b>Order of Authors:</b>	Sze Wing Yiu, PhD Mark Keith, PhD Leszek Karczmarski, PhD Francesca Parrini, PhD
<b>Abstract:</b>	<p>Prey increase vigilance to maximize predator detection, but this comes at the expense of foraging depending on vigilance types: (1) intense vigilance, when all feeding processes are ceased, and (2) routine vigilance, when animals continue chewing (i.e. lower foraging cost). Few studies have distinguished between vigilance types when examining the effects of predation risk and, in the absence of a commonly accepted conceptual framework, the variables used to define predation risk vary greatly between studies. We investigated the relative importance of four predation risk categories (risky place assessed at the landscape and habitat level, vegetation characteristics at foraging site level, prey characteristics and resource availability) in the time spent on intense and routine vigilance by Burchell's zebra (<i>Equus quagga burchellii</i>) and blue wildebeest (<i>Connochaetes taurinus taurinus</i>) under predation risk from reintroduced predators, lions (<i>Panthera leo</i>). The risk categories each represented a different predation risk component and included metrics that defined the component at multiple scales. Intense vigilance responses were scale-dependent, with zebra responding to risky place at landscape level and wildebeest to vegetation characteristics at foraging area scale. Yet both species were able to adjust and balance between time spent on vigilance types. Prey characteristics influenced the intense vigilance of wildebeest by reducing their intense vigilance with an increase in herd size. Both species maintained similar levels of intense vigilance between seasons, despite lower resource availability thus higher foraging costs in the dry season. However, the reduction in grass quality had likely resulted in the increase in routine vigilance by both species during the dry season, as more time was needed to chew grasses with high fibre content. Our findings suggest different underlying mechanisms for the two types of vigilance behaviours, influenced by the ecology of the species, and demonstrate the importance of distinguishing vigilance types in predation risk studies.</p>

**TITLE**

Predation risk effects on intense and routine vigilance of Burchell's zebra and blue wildebeest

**ABSTRACT**

Prey increase vigilance to maximize predator detection, but this comes at the expense of foraging depending on vigilance types: (1) intense vigilance, when all feeding processes are ceased, and (2) routine vigilance, when animals continue chewing (i.e. lower foraging cost). Few studies have distinguished between vigilance types when examining the effects of predation risk and, in the absence of a commonly accepted conceptual framework, the variables used to define predation risk vary greatly between studies. We investigated the relative importance of four predation risk categories (risky place assessed at the landscape and habitat level, vegetation characteristics at foraging site level, prey characteristics and resource availability) in the time spent on intense and routine vigilance by Burchell's zebra (*Equus quagga burchellii*) and blue wildebeest (*Connochaetes taurinus taurinus*) under predation risk from reintroduced predators, lions (*Panthera leo*). The risk categories each represented a different predation risk component and included metrics that defined the component at multiple scales. Intense vigilance responses were scale-dependent, with zebra responding to risky place at landscape level and wildebeest to vegetation characteristics at foraging area scale. Yet both species were able to adjust and balance between time spent on vigilance types. Prey characteristics influenced the intense vigilance of wildebeest by reducing their intense vigilance with an increase in herd size. Both species maintained similar levels of intense vigilance between seasons, despite lower resource availability thus higher foraging costs in the dry season. However, the reduction in grass quality had likely

resulted in the increase in routine vigilance by both species during the dry season, as more time was needed to chew grasses with high fibre content. Our findings suggest different underlying mechanisms for the two types of vigilance behaviours, influenced by the ecology of the species, and demonstrate the importance of distinguishing vigilance types in predation risk studies.

## **KEYWORDS**

Anti-predator behaviour, Dinokeng Game Reserve, landscape of fear, lion, predator-prey dynamics

## **INTRODUCTION**

Predator avoidance strategies are fundamental in shaping predator-prey dynamics (Abrams & Matsuda, 1997; Abrams, 2000). Antipredator behaviour can be reactive, when prey respond to direct predator encounter (Courbin et al., 2015; Martin & Owen-Smith, 2016), or proactive, when prey respond to perceived predation risks (Creel, Winnie, Maxwell, Hamlin & Creel, 2005; Creel, Schuette & Christianson, 2014). Prey adjust their behavioural responses based on a “landscape of fear” according to the level of perceived predation risk (i.e. fear) in different areas (Laundré, Hernández & Altendorf, 2001; Laundré, Hernández & Ripple, 2010). Behavioural changes resulting from the fear of predation are energetically costly for prey and typically represent a trade-off in foraging that could cascade into population changes (Boyce, 2018; Fortin et al., 2005; Lind & Cresswell, 2005; Laundré et al, 2001; White, Proffitt & Lemke, 2012). The level of fear and thus the behavioural responses of prey are strongly driven by the spatial behaviour of the predator and different environmental factors, which are multi-dimensional and vary across spatial and temporal scales (Moll et al, 2017). An understanding of antipredator behaviour in response to

predation risks at different scales and contexts is therefore crucial for assessing the ecological consequence of non-lethal impacts of predators on prey.

Vigilance behaviour is a commonly used indicator in assessing the non-lethal impact of predation risk on prey (Brown & Kotler 2004; Creel et al, 2014; Hunter & Skinner 1998). It is often assumed to be performed at the expense of foraging time, thus reducing food intake rate (Houston et al, McNamara & Hutchinson, 1993; Illius & Fitzgibbon, 1994; Stears, Schmitt, Wilmers & Shrader, 2020). However, Fortin, Boyce, Merrill & Fryxell (2004a) suggested that herbivores could possibly maintain their food intake rate because of their ability to chew while being vigilant, which has been rarely addressed in vigilance studies. Food intake rate is limited by the time required to search for and handle (cropping, chewing and swallowing) food (Spalinger & Hobbs, 1992). When foraging is handling-limited (i.e. when the next bite can only be taken after the current bite is chewed), the chewing time can be used for other activities, such as vigilance, with minimal foraging cost (Fortin et al, 2004a and Fortin, Boyce & Merrill, 2004b). It is therefore important to distinguish between two types of vigilance behaviour when assessing predation risk effects: routine vigilance with minimal foraging costs, when prey monitor the environment during chewing; and intense vigilance with higher foraging costs, when prey cease feeding and respond to external stimuli (Blanchard & Fritz, 2007). Routine vigilance is often used for both social monitoring and threat detection while intense vigilance serves mainly for the latter purpose (Beauchamp, 2015). Périquet et al (2012) applied this definition and found that the presence of lions increased the intense vigilance of zebra while having no effect on their routine vigilance.

Physiology is also an essential factor influencing vigilance-foraging trade-offs in large herbivores. Ruminants are able to extract and absorb nutrients from grasses efficiently through foregut fermentation and are adapted to a selective diet (Demment & van Soest, 1985). In comparison, non-ruminants, or hindgut fermenters, have a less efficient digestive system and therefore forage more constantly to maximize food consumption and passage rate (Bodenstein, Meissner & van Hoven, 2000). This gives ruminants an advantage over non-ruminants during the wet season when grass quality is high. However, in dry season, grasses become more fibrous and slow down the passage rate in the rumen. Ruminants thus need to spend more time with their heads down searching for specific grass species to reduce fibre intake and maintain daily nutritional requirements (Shrader, Owen-Smith & Ogutu 2006; Van Soest 1994 & 1996). In contrast, hindgut fermenters are able to process grasses with high fibre content to maintain nutritional needs. In addition, body size also plays a role. Larger animals have to maintain a higher daily food consumption in order to meet their metabolic requirement compared to smaller body sized animals (Bodenstein et al, 2000; Demment & van Soest, 1985; Kleynhans, Jolles, Bos & Olff, 2011). The immediate foraging costs associated with intense vigilance is therefore potentially higher for non-ruminants than for ruminants, season-dependent, and for larger body sized herbivores than for smaller ones (Owen-Smith 2002 & 2019). Consequently, both the type of vigilance and the physiology of prey are important in assessing the impacts of predation risk.

We examined the impact of reintroduced lions (*Panthera leo*) on the routine and intense vigilance behaviour of Burchell's zebra (*E. quagga burchelli*), a non-ruminant, and blue wildebeest (*Connochaetes taurinus*), a slightly smaller herbivore than zebra ( $\approx 216\text{kg}$  vs.  $\approx 137\text{kg}$ , see Gallivan & Horak, 1997; Mentis & Duke, 1976; Young, Wagener & Bronkhorst 1969) and a ruminant, in a fenced reserve in South Africa. When prey are unable to avoid

predation by moving to a different area, they would have to rely heavily on vigilance behaviour as an antipredator strategy (Hayward & Kerley, 2009; Tambling & du Toit, 2005). Adapting the conceptual framework of Moll et al. (2017), which suggested the use of a multi-scale analytical approach in predation risk studies, we quantified the landscape of fear by categorizing predation risk metrics as follows: 1) risky places, defined as those areas within a lion home range calculated from actual GPS locations of the predator (Hebblewhite, Merrill & McDonald, 2005; Hebblewhite & Merrill, 2007), representing predation risk at landscape scale, and as predicted probabilities of occurrence of lions calculated from GPS locations and lion resource selection, representing predation risk at habitat scale; 2) vegetation characteristics as a proxy of visibility, using grass height and tree density (foraging area scale; Davies, Tambling, Kerley & Asner, 2016; Loarie, Tambling & Asner, 2013); 3) prey characteristics, using herd size and presence/absence of calves as a measure of the influence of herd structure on vigilance behaviour (Liley & Creel, 2008; Li et al., 2012); and 4) resource availability, using annual seasons, wet and dry, as an indication of the potential trade-off between vigilance and foraging (Creel et al, 2014; Smith & Cain III, 2009). Different metrics were used for each category such that inferences of predation risk could be drawn from multiple ecological aspects and spatial scales. We then tested the relative importance of these four risk categories on the routine and intense vigilance of zebra and wildebeest.

We hypothesized that risky places, relating directly to predator distribution, and resource availability, relating directly to trade-offs in foraging, would be more influential than habitat and prey characteristics on the intense vigilance for both species. We expected this influence to be less prominent in zebra than wildebeest, particularly during the wet season, due to the higher immediate foraging costs associated with being non-ruminants and having

a larger body size. As routine vigilance functions for both social monitoring and predator detection, we hypothesized this vigilance type to be influenced by all of the four categories to a similar extent for both zebra and wildebeest.

## **METHODS**

### *Study area*

The study was conducted in Dinokeng Game Reserve (DGR), situated in the Gauteng and Limpopo Provinces of South Africa, from July 2012 to September 2013. Dinokeng Game Reserve is entirely fenced in an area of 185 km<sup>2</sup>, with altitudes ranging between 1100 m and 1200 m above sea level. Vegetation is dominated by mixed Bushveld, Kalahari thornveld and sourish mixed Bushveld (Rutherford, Mucina & Powrie, 2006). Average annual precipitation is 674 mm that falls mainly during the wet season from October to April; the dry season typically spans from May until the end of September (New, Lister, Hulme & Makin, 2002).

There are more than 20 species of large herbivores in DGR; the most common species are blue wildebeest and impala (*Aepyceros melampus*) (about 1000 individuals each), followed by Burchell's zebra and blesbock (*Damaliscus dorcas phillipsi*) (about 600 individuals each) ("DGR aerial census data", 2012). Eight lions, four males and four females, were introduced to DGR in October and November 2011, which comprised the entire lion population during our one-year study period starting from September 2012. Leopards (*Panthera pardus*) and brown hyaena (*Parahyaena brunnea*) were the only natural occurring large carnivores in the reserve before lion reintroductions, but sightings were exceptionally rare ("Contour Project Managers CC unpublished report", 2009). We focused on the vigilance behaviour of wildebeest and zebra as these two species are important prey species for lions (Hayward & Kerley, 2005).

### *Data collection*

Random transects were driven in the reserve at 20-30 km/h within 3 hours of sunrise and sunset, when predators were most active (Hayward & Hayward, 2006; Yiu, Keith, Karczmarski & Parrini, 2015). When feeding herds of either wildebeest or zebra were located, we parked the vehicle and turned the engine off to observe the herd members. To eliminate potential effects associated with the presence of other prey species (see Schmitt, Stears & Shrader, 2016), data were collected from single species herds only. To prevent pseudo-replication of vigilance observations, transects were driven in different parts (the northern and southern part of the reserve are separated by a main public road, see Fig. A1 for study area map) of the reserve for sunrise and sunset survey sessions in the same day. Data collection started after 5 minutes of turning the engine off, to allow the animals to habituate to the presence of the research vehicle. We used focal animal sampling (Altmann, 1974) to collect vigilance data on one randomly selected female in each herd. Each focal sample lasted five minutes, based on the average duration before the herd would move off as observed in preliminary observations, or until the focal animal was no longer visible. Samples less than 4 minutes were discarded in the analyses. Data were collected from only one individual of the same herd during each session, because the herds generally moved away before the observation on a second animal could be completed. During each focal sampling, we recorded the duration and type of each vigilance bout. An animal was defined as being vigilant when it kept its head above the shoulder while standing still (Hunter & Skinner, 1998). We distinguished between intense vigilance, when the animal was scanning the environment without chewing, and routine vigilance, when the animal was chewing while being vigilant (Beauchamp, 2015; Périquet et al, 2012). We calculated the GPS location of the focal animal by triangulation, using the location of the vehicle recorded by Garmin



60CS handheld GPS receiver and the compass bearing and distance of the focal animal from the vehicle measured by Nikon COOLSHOT Laser Rangefinder. We also recorded herd size, the presence or absence of a calf following the movement of the focal individual, grass height (below knee, between knee and belly or above belly), and tree density in the area (0-20, 21-40, 41-60, 61-80, 81-100%). Grass height was measured in relation to the height of the animals, in order to get an estimate of visibility from the animal perspective. Tree density was visually estimated in a 100 m radius from the animal in the centre of the herd. We had also recorded the position of the focal animal in the herd (centre, edge), but this factor was insignificant in our preliminary analyses thus was discarded for further analyse. A total of 178 focal samples were obtained, consisting of 88 wildebeest samples and 90 zebra samples across the 12 months of survey (see Table A1 for details).

#### *Data analyses*

For each focal sample, we calculated the proportion of time the focal animal spent on intense and routine vigilance behaviour. We grouped seven risk metrics into four categories: risky places, vegetation characteristics, prey characteristics and resource availability (Table 1; adapted from Moll et al, 2017). Risky places were defined using home range (HR) locations and predicted probabilities of occurrence of the lions (PPO), which captured the landscape and habitat scale predation risk from the predator respectively. The HR were constructed and the PPO were calculated in a previous study, for each season, thus accounting for any temporal variation in predation risk (see Yiu, Parrini, Karczmarski & Keith, 2017 and Yiu, Karczmarski, Parrini & Keith, 2018). The home ranges represented 95% utilisation distribution of the lions and predation risk at a landscape level (Hebblewhite & Merrill, 2007; Theuerkauf & Rouys, 2008). We defined predation risk as high when the

locations of the observed prey animals were within the lion home ranges and as low when they were outside the home ranges. Lions had been absent for more than a century before introduction to the study area, therefore areas falling outside the lion home ranges had not had predators for a long time and acted as a good indicator of low predation risk areas.

The predicted probabilities of occurrence of the lions were calculated based on preferences of the lions for different habitat features (elevation, slope, rivers, dams, vegetation density and types, roads and buildings) at 30 m resolution using the resource selection function models derived in Yiu et al (2018), representing predation risks at a habitat level. To associate each vigilance observation with the HR and PPO metrics, GPS locations of the focal animal were overlaid with the maps of each metric in ArcGIS 10.2 (ESRI, Redlands, Calif.). Vegetation characteristics were defined using grass height and tree density collected from the field, which represented predation risk at a foraging area scale. Tall grasses and dense bushes provide concealment for lions to ambush their prey and hinder visibility of prey. These two metrics could therefore influence predation risk and predator detection, thus vigilance behaviour (Makin, Chamaillé-Jammes & Shrader, 2018; Underwood, 1982).

Prey characteristics were defined using herd size and the presence of calves. Herd size could affect vigilance behaviour through many-eyes effect, in which herd members improve predator detection thus reducing individual vigilance (Burger, Safina & Gochfeld, 2000; Childress & Lung, 2003), and dilution and confusion effect, both of which lower individual predation risk (Beauchamp, 2017; Lehtonen & Jaatinen, 2016). Females with calves could potentially have higher vigilance due to fitness cost in losing an offspring (Gochfeld & Burger, 1994). Lastly, we defined resource availability using season, with the dry season

having lower resource availability compared to the wet season because of the reduction in rainfall thus grass quality and quantity (Owen-Smith, 2008).

We built a set of 15 *a priori* models under the information-theoretic approach and interpreted the results using multimodel inference (Burnham & Anderson, 2002; Burnham, Anderson & Huyvaert, 2011). Models were built using combinations of the four risk categories excluding interactions between individual metrics, since the purpose of our study was to understand the relative importance of these risk categories on the two types of vigilance behaviour (Table 1). The metrics of each category described different ecological effects of risks and represented different spatial scales, and were thus always included in the same model. Multi-collinearity between independent variables was tested using the variance inflation factor (VIF) with a cut-off value of 2 (Zuur, Leno & Elphick, 2010). We used generalized linear model with beta distribution to model the vigilance proportions, which are percentage values within standard unit interval (0, 1), using R 3.4.4 (R Core Team, 2018) and R package “betareg” (Cribari-Neto & Zeileis, 2009). The corrected Akaike information criterion (AICc), delta AICc ( $\Delta AICc$ ), Akaike weight ( $\omega_i$ ) and evidence ratios ( $\omega_1/\omega_i$ ) were computed for each model and compared. To assess the relative importance of risk categories, we calculated and ranked the Akaike weight of each category by summing the Akaike weights of all models that include that specific category (Burnham & Anderson, 2002).

To understand whether the prey species adjusted the ratio of time spent in the two types of vigilance in response to predation risk at landscape scale, we first tested the correlation between the two using the Kendall rank correlation test. We then calculated and tested the

effects of lion home range location (inside or outside) on the total proportion of time spent on vigilance using beta regression.

#### *Ethical note*

The study was conducted in compliance with the ethical standard set by the Department of Environmental Affairs and Tourism (DEAT) and Gauteng Department of Agriculture, Conservation and Environment (GDACE). None of the animals were handled physically in the study. To minimize disturbance and stress to the animals, the research vehicle was parked and behavioural observations conducted at least 50 m away from the zebra and wildebeest herds. We terminated our data collection and drove away, when the animals did not show any sign of habituation after the engine was switched off for 5 minutes.

## **RESULTS**

#### *Relative importance of risk categories*

The relative importance of risk categories was the same for both intense and routine vigilance of zebra, with risky places receiving the most support, followed by resource availability, prey characteristics and vegetation characteristics (Table 2). Prey characteristics was the most influential category on the intense vigilance of wildebeest, followed by risky places, vegetation characteristics and resource availability, but all categories had similar weighting in the models (Table 2). In contrast, routine vigilance of wildebeest was, as for zebra, influenced mostly by risky places, followed by resource availability, prey characteristic, and vegetation characteristics (Table 2).

### *Zebra*

Intense vigilance was best explained by the model containing variables from the risky places category only ( $\omega = 0.492$ ), in which intense vigilance was lower outside the home ranges of lions and when the predicted probabilities of occurrence of lions increased (Table 3, Fig. 1). However, the effects of the latter were not prominent. The second best supporting model included variables from both risky places and resource availability categories ( $\omega = 0.161$ ), while the third best supporting model included resource availability only ( $\omega = 0.152$ ; Table 3). However, intense vigilance was similar between the dry and the wet season (Table 3; Fig. 1). The effects of the prey characteristics variables (i.e. herd size and presence of calf) were not notable.

The best supporting model for routine vigilance included variables from the risky places and resource availability categories ( $\omega = 0.446$ ). Routine vigilance was higher with lower predicted probabilities of occurrence and in the dry season compared to the wet season (Table 4, Fig. 1). Opposite to intense vigilance, zebra showed higher routine vigilance outside lion's home ranges. The second best model included only the risky places category, while the third and fourth model included both risky places and prey characteristics with the fourth included resource availability as well. Routine vigilance increased with herd size, and with the presence of calf, but the effects of the variables were not prominent (Table 4, Fig. 1).

### *Wildebeest*

Intense vigilance was best supported by the prey characteristics model, but the weight of the model was relatively low (0.251; Table 5). Intense vigilance decreased with an increase in herd size and was higher in the presence of calf than in the absence of calf (Table 5, Fig.

2). The second best model contained only the resource availability category, followed by the model containing risky places and vegetation characteristics categories (Table 5). Contrary to zebra, wildebeest maintained similar intense vigilance inside and outside of the lion home ranges, but increased vigilance with an increase in predicted probabilities of occurrence of lions (Table 5, Fig. 2). Seasons did not have prominent effects on intense vigilance. Intense vigilance appeared to increase when grass height was above belly height. Response to tree density showed interesting patterns, in which intense vigilance increased from 21-40% to 41-60%, but decreased steadily from 61% to 100% (Table 5, Fig. 2).

The best supporting model for routine vigilance of wildebeest included resource availability only ( $\omega = 0.229$ ; Table 6), and routine vigilance was higher during the dry season compared to the wet season (Fig. 2). The second and third best supporting models included the risky places and prey characteristic category respectively (Table 6). Similar to zebra, the routine vigilance of wildebeest was higher outside lions' home range than inside and increased as the predicted probabilities of occurrence of lions decreased (Table 6; Fig. 2). Routine vigilance of wildebeest decreased with an increase in herd size and the presence of calf, but the effect of herd size was not prominent (Table 6; Fig. 2). Two further models received Akaike weights  $> 0.10$  and evidence ratios  $< 4.00$ : the fourth model consisting of risky places and prey characteristics and the fifth model of risky places and resource availability (Table 6). Routine vigilance of wildebeest was lower in the wet season compared to the dry season (Table 6, Fig. 2).

#### *Relationship between vigilance types*

Intense vigilance was negatively correlated to routine vigilance for both species (zebra:  $p > 0.01$ ,  $\tau = -0.225$ ; wildebeest:  $p < 0.01$ ,  $\tau = -0.321$ ). However, both of the species spent

similar amount of time on vigilance (regardless of vigilance type) inside and outside of the home ranges of lions (Table 7).

## DISCUSSION

The intense vigilance responses of zebra and wildebeest indicate a fundamental difference in the anti-predator behaviour of the two species. The greater influence of prey characteristics suggests that wildebeest relied more on herd size as anti-predator strategy (safety in numbers), as reflected in the inverse relationship between their herd size and intense vigilance, similarly to other studies (Burger et al, 2000; Childress & Lung, 2003; Creel et al, 2014; Djagoun, Djossa, Mensah & Sinsin, 2013; Pays et al, 2009; Périquet et al, 2010; Scheel, 1993). This was not seen in zebra. Resembling Makin, Chamailé-Jammes & Shrader's (2017) observations in the Tswalu Kalahari Reserve, South Africa, wildebeest in our study area often form larger groups ( $21 \pm 14$ , mean  $\pm$  SD) than zebra ( $11 \pm 8$ , mean  $\pm$  SD). Wildebeest could, therefore, take better advantage of the dilution and many-eyes effects and spend less time on intense vigilance compared to zebra under high predation risk (Rieucou & Martin, 2008). This could also result in the wildebeest being less responsive to long-term lion predation risk and depend more on reactive anti-predatory behaviour instead. For example, wildebeest are known to have a longer fleeing distance than zebra and bunch together more often under immediate predation risk (Dannock, Pays, Renaud, Maron & Goldizen 2019; Testroote, 2018).

Furthermore, the intense vigilance behaviour of the two prey species indicated a scale-dependent response: zebra were more sensitive to predation risk at landscape level and wildebeest at foraging area level. Zebra responded to the distribution of lions by increasing their intense vigilance in area where there was a higher chance in encountering the

predator. In contrast, wildebeest seemed negligent to the spatial distribution of the lions, and rather adjusted their intense vigilance based on the density of vegetation as they foraged. Lions hunt by ambushing and make more successful kills in dense vegetation (Davies et al, 2016; Loarie et al, 2013). The taller the grasses and the denser the bush, therefore, the higher the probability of being captured by lions. Dense vegetation, at the same time, reduces visibility thus predator detection efficiency, and therefore could contribute to the increase in intense vigilance by wildebeest (Riginos & Grace, 2008; Riginos, 2015). One interesting pattern we observed though is that, despite an increase from tree density at 21% to 41-60%, the intense vigilance gradually decreased again from 61-100%. This might suggest that once tree density reaches a threshold, the benefits of provision of protective cover outweigh the reduction in visibility. This scale-dependent response could potentially incur higher foraging costs for wildebeest, when they increase intense vigilance in areas with dense vegetation yet low chance of encountering a lion. However, as a ruminant, wildebeest might be able to afford this foraging cost at the foraging area scale better than zebra, a non-ruminant, therefore resulting in the differences in response between the two species.

Intense vigilance of zebra was, unexpectedly, influenced by resource availability to a greater extent than that of wildebeest. However, both species spent similar amount of time on intense vigilance between the two seasons. This might suggest that the animals were able to compensate for the high foraging costs of intense vigilance in dry season by using other behavioural strategies. For example, a shift in habitat use could allow the animals to search for food with better quality or quantity. In Kruger National Park, wildebeest are known to move away from grazing lawns (i.e. short-grass plains with high food quality during wet seasons, but that deplete during dry seasons), and spend more time in seep-zone grasslands



as the season progresses from wet to dry (Owen-Smith, 2019; Yoganand & Owen-smith, 2014). Similarly, zebra were observed in other studies to relocate to areas with higher grass biomass during the dry season, which had allowed the zebra to obtain higher food quantity (Groom and Harris 2009). Stears et al (2020) suggested that zebra could reduce intra-herd food competition by maintaining consistent herd size across seasons despite drastic changes in resource availability. This is consistent with the similar herd sizes between seasons for zebra in our study (wet season:  $9 \pm 4$ , dry season:  $12 \pm 7$ , mean  $\pm$  SD).

The routine vigilance responses of both species were surprising and reveal an inverse relationship between the two vigilance types: routine vigilance was reduced as intense vigilance increased in high predation risk areas while total time spent on vigilance remained constant. Despite being multifunctional, routine vigilance is less effective than intense vigilance in predator detection as chewing obstructs hearing (Fortin et al, 2004b). Routine vigilance also reduces the amount of time an animal can spend on searching for the next bite while chewing, and on moving within the foraging patch (Blanchard & Fritz, 2007). Balancing between intense and routine vigilance can therefore maximize predator detection while minimizing foraging costs of using both vigilance types under high predation risk. This is an important insight into the understanding of vigilance behaviour, as routine vigilance was reported to be affected only by group size and forage quality in previous studies (Pays et al, 2012; Périquet et al, 2012).

The prominent influence of season and minimal effects of group size on routine vigilance, contrary to our expectations, suggest that foraging constraints prevail over social monitoring in limiting routine vigilance. In the dry season, foraging is not only affected by low forage quality, but also high grass fibre content (Mbatha & Ward, 2010), which lowers

the efficiency and lengthens the time of chewing before the next bite can be taken (Georgiadis & McNaughton, 1990; Knox et al, 2011). This likely increases the amount of 'spare time' the zebra and wildebeest can use for routine vigilance in the dry season. Our results complement the foraging constraint of routine vigilance identified by Pays et al (2012), in which impala increased their routine vigilance in areas with higher grass heights due to an increase in bite sizes.

Our findings reveal different underlying forces driving the intense and routine vigilance behaviour of two large herbivores. The ecology of the species affects how they adjust their level of intense vigilance, with zebra, a non-ruminant with greater foraging time constraints, directing their response specifically to predation risk at landscape scale, while wildebeest, a ruminant, responding to predation risk related to vegetation structure at foraging area scale and relying more on herd protection. Yet, both species showed behavioural plasticity as they balanced their time spent on the two vigilance types to reduce foraging costs under high predation risk. Zebra and wildebeest were able to maintain similar levels of intense vigilance between seasons, possibly by using other behavioural strategies to compensate for the higher foraging costs incurred during the dry season. Our study underscores the importance of differentiating between vigilance types when inferring predation risk effects on prey behaviour and its foraging costs.

## References

- Abrams, P.A. (2000). The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology, Evolution, and Systematics*, 31, 79-105.
- Abrams, P.A., & Matsuda, H. (1997). Prey adaptation as a cause of predator-prey cycles. *Evolution*, 51, 1742-1750.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227-267.
- Beauchamp, G. (2015). *Animal vigilance: monitoring predators and competitors*. London, U.K.: Academic Press.
- Beauchamp, G. (2017). Disentangling the various mechanisms that account for the decline in vigilance with group size. *Behavioural Processes*, 136, 59-63.
- Blanchard, P., & Fritz, H. (2007). Induced or routine vigilance while foraging. *Oikos*, 116, 1603-1608.
- Bodenstein, V., Meissner, H.H., & Van Hoven, W. (2000). Food selection by Burchell's zebra and blue wildebeest in the Timbavati area of the Northern Province Lowveld. *South African journal of wildlife research*, 30, 63-72.
- Boyce, M.S. (2018). Wolves for Yellowstone: dynamics in time and space. *Journal of Mammalogy*, 99, 1021-1031.
- Brown, J.S., & Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7, 999-1014.

- 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. (2<sup>nd</sup> ed.). New York, U.S.: Springer-Verlag.
- Burnham, K.P., Anderson, D.R., & Huyvaert, K.P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, 65, 23-35.
- Childress, M.J., & Lung, M.A. (2003). Predation risk, gender and the group size effect: does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, 66, 389-398.
- Courbin, N., Loveridge, A.J., Macdonald, D.W., Fritz, H., Valeix, M., Makuwe, E.T., & Chamailé-Jammes, S. (2015). Reactive responses of zebras to lion encounters shape their predator-prey space game at large scale. *Oikos*, 125, 829-838.
- Creel, S., Winnie, J., Maxwell, B., Hamlin, K., & Creel, M. (2005). Elk alter habitat selection as an antipredator response to wolves. *Ecology*, 86, 3387-3397.
- 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.
- Cribari-Neto, F., & Zeileis, A. (2009). Beta regression in R. *Journal of Statistical Software*, 34, 1-24.

- Dannock, R.J., Pays, O., Renaud, P.C., Maron, M., & Goldizen, A.W. (2019). Assessing blue wildebeests' vigilance, grouping and foraging responses to perceived predation risk using playback experiments. *Behavioural Processes*, *164*, 252-259.
- Davies, A.B., Tambling, C.J., Kerley, G.I., & Asner, G.P. (2016). Effects of vegetation structure on the location of lion kill sites in African thicket. *PloS one*, *11*, e0149098.
- Demment, M.W., & Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, *125*, 641-672.
- Djagoun, C.A., Djossa, B.A., Mensah, G.A., & Sinsin, B.A. (2013). Vigilance efficiency and behaviour of Bohor reedbuck *Redunca redunca* (Pallas 1767) in a savanna environment of Pendjari Biosphere Reserve (Northern Benin). *Mammal Study*, *38*, 81-89.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., & Mao, J.S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*, 1320-1330.
- Fortin, D., Boyce, M.S., Merrill, E.H., & Fryxell, J.M. (2004a). Foraging costs of vigilance in large mammalian herbivores. *Oikos*, *107*, 172-180.
- Fortin, D., Boyce, M.S., & Merrill, E.H. (2004b). Multi-tasking by mammalian herbivores: overlapping processes during foraging. *Ecology*, *85*, 2312-2322.
- Gallivan, G.J., & Horak, I.G. (1997). Body size and habitat as determinants of tick infestations of wild ungulates in South Africa. *South African Journal of Wildlife Research*, *27*, 63-70.
- Georgiadis, N.J., & McNaughton, S.J. (1990). Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. *Journal of Applied Ecology*, *27*, 623-634.

- Gochfeld, M., & Burger, J. (1994). Vigilance in African mammals: differences among mothers, other females, and males. *Behaviour*, *131*, 153-169.
- Groom, R., & Harris, S. (2009). Factors affecting the distribution patterns of zebra and wildebeest in a resource-stressed environment. *African Journal of Ecology*, *48*, 159-168.
- Hayward, M.W., & Hayward, G.J. (2006). Activity patterns of reintroduced lion *Panthera leo* and spotted hyaena *Crocuta crocuta* in the Addo Elephant National Park, South Africa. *African Journal of Ecology*, *45*, 135-141.
- Hayward, M.W., & Kerley, G.I. (2005). Prey preferences of the lion (*Panthera leo*). *Canadian Journal of Zoology*, *267*, 309-322.
- Hayward, M.W., & Kerley, G.I. (2009). Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biological Conservation*, *142*, 1-13.
- Hebblewhite, M., & Merrill, E.H. (2007). Multiscale wolf predation risk for elk: does migration reduce risk?. *Oecologia*, *152*, 377-387.
- Hebblewhite, M., Merrill, E.H., & McDonald, T.L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos*, *111*, 101-111.
- Houston, A.I., McNamara, J.M., & Hutchinson, J.M. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *341*, 375-397.
- Hunter, L.T.B., & Skinner, J.D. (1998). Vigilance behaviour in African ungulates: the role of predation pressure. *Behaviour*, *135*, 195-211.

- Illius, A.W., & Fitzgibbon, C. (1994). Costs of vigilance in foraging ungulates. *Animal Behaviour*, *47*, 481-484.
- Kleynhans, E.J., Jolles, A.E., Bos, M.R., & Olf, H. (2011). Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos*, *120*, 591-600.
- Knox, N.M., Skidmore, A.K., Prins, H.H., Asner, G.P., van der Werff, H.M., de Boer, W.F., van der Waal, C., de Knegt, H.J., Kohi, E.M., Slotow, R., & Grant, R.C. (2011). Dry season mapping of savanna forage quality, using the hyperspectral Carnegie Airborne Observatory sensor. *Remote Sensing of Environment*, *115*, 1478-1488.
- Laundré, J.W., Hernández, L., & Altendorf, K.B. (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. *Canadian Journal of Zoology*, *79*, 1401-1409.
- Laundré, J.W., Hernández, L., & Ripple, W.J. (2010). The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, *3*, 1-7.
- Lehtonen, J., & Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, *70*, 449-458.
- Li, C., Jiang, Z., Li, L., Li, Z., Fang, H., Li, C., & Beauchamp, G. (2012). Effects of reproductive status, social rank, sex and group size on vigilance patterns in Przewalski's gazelle. *Plos one*, *7*, e32607.
- Liley, S., & Creel, S. (2008). What best explains vigilance in elk: characteristics of prey, predators, or the environment?. *Behavioral Ecology*, *19*, 245-254.
- Lima, S.L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. *Animal Behaviour*, *49*, 11-20.

- Lind, J., & Cresswell, W. (2005). Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, *16*, 945-956.
- Loarie, S.R., Tambling, C.J., & Asner, G.P. (2013). Lion hunting behaviour and vegetation structure in an African savanna. *Animal Behaviour*, *85*, 899-906.
- 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.
- Makin, D.F., Chamaillé-Jammes, S., & Shrader, A.M. (2018). Changes in feeding behavior and patch use by herbivores in response to the introduction of a new predator. *Journal of Mammalogy*, *99*, 341-350.
- Martin, J., & Owen-Smith, N. (2016). Habitat selectivity influences the reactive responses of
- Mbatha, K.R., & Ward, D. (2010). The effects of grazing, fire, nitrogen and water availability on nutritional quality of grass in semi-arid savanna, South Africa. *Journal of Arid Environment*, *74*, 1294-1301.
- Mentis, R.R. (1976). Carrying capacities of natural veld in Natal for large wild herbivores. *South African Journal of Wildlife Research*, *6*, 65-74.
- Moll, R.J., Redilla, K.M., Mudumba, T., Muneza, A.B., Gray, S.M., Abade, L., Hayward, M.W., Millspaugh, J.J., & Montgomery, R.A. (2017). The many faces of fear: a synthesis of the methodological variation in characterizing predation risk. *Journal of Animal Ecology*, *86*, 749-765.



- New, M., Lister, D., Hulme, M., & Makin, I. (2002). A high-resolution data set of surface climate over global land areas. *Climate Research*, *21*, 1-25.
- Owen-Smith, N. (2002). *Adaptive Herbivore Ecology. From resources to populations in variable environments*. Cambridge: Cambridge University Press.
- Owen-Smith, N. (2008). Changing vulnerability to predation related to season and sex in an African ungulate assemblage. *Oikos*, *117*, 602-610.
- Owen-Smith, N. (2019). Ramifying effects of the risk of predation on African multi-predator, multi-prey large-mammal assemblages and the conservation implications. *Biological conservation*, *232*, 51-58.
- Pays, O., Goulard, M., Blomberg, S.P., Goldizen, A.W., Sirot, E., & Jarman, P.J. (2009). The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behavioral Ecology*, *20*, 469-477.
- 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.
- Périquet, S., Valeix, M., Loveridge, A.J., Madzikanda, H., Macdonald, D.W., & Fritz, H. (2010). Individual vigilance of African herbivores while drinking: the role of immediate predation risk and context. *Animal Behaviour*, *79*, 665-671.
- Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., Pays, O., Fortin, D., Madzikanda, H., Fritz, H., Macdonald, D.W., Loveridge, A.J. (2012). Influence of

immediate predation risk by lions on the vigilance of prey of different body size.

*Behavioral Ecology*, 23, 970-976.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.

Rieucou, G., & Martin, J.G.A. (2008). Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. *Oikos*, 117, 501-506.

Riginos, C., & Grace, J.B. (2008). Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. *Ecology*, 89, 2228-2238.

Riginos, C. (2015). Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology*, 84, 124-133.

Rutherford, M.C., Mucina, L., & Powrie, L.W. (2006). Biomes and bioregions of southern Africa. The vegetation of South Africa, Lesotho and Swaziland. *Strelitzia*, 19, 30-51.

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.

Shrader, A.M., Owen-Smith, N., & Ogutu, J.O. (2006). How a mega-grazer copes with the dry season: food and nutrient intake rates by white rhinoceros in the wild. *Functional ecology*, 20, 376-384.

- Smith, S.M., & Cain III, J.W. (2009). Foraging efficiency and vigilance behaviour of impala: the influence of herd size and neighbour density. *African Journal of Ecology*, 47, 109-118.
- 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., Schmitt, M.H., Wilmers, C.C., & Shrader, A.M. (2020). Mixed-species herding levels the landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, 287, 20192555.
- Tambling, C.J., Du Toit, J.T. (2005). Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *Journal of Applied Ecology*, 42, 431-441.
- Testroote, E. (2018). Vigilance and flight behaviour in herds of three different ungulate species: zebra, wildebeest and impala. MSc thesis. Wageningen University & Research. Netherlands.
- Theuerkauf, J., & Rouys S. (2008). Habitat selection by ungulates in relation to predation risk by wolves and humans in the Białowieża Forest, Poland. *Forest Ecology and Management*, 256, 1325-1332.
- Underwood, R. (1982). Vigilance behaviour in grazing African antelopes. *Behaviour*, 79, 81-107.
- Van Soest, P. J. (1994). Nutritional ecology of the ruminant (2nd ed). Cornell University Press.
- Van Soest, P. J. (1996). Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. *Zoo Biology*, 15, 455-479.

- White, P.J., Proffitt, K.M., & Lemke, T.O. (2012). Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist*, *167*, 174-187.
- Yiu, S.W., Keith, M., Karczmarski, L., & Parrini, F. (2015). Early post-release movement of reintroduced lions (*Panthera leo*) in Dinokeng Game Reserve, Gauteng, South Africa. *European Journal of Wildlife Research*, *61*, 861-870.
- Yiu, S.W., Parrini, F., Karczmarski, L., & Keith, M. (2017). Home range establishment and utilization by reintroduced lions (*Panthera leo*) in a small South African wildlife reserve. *Integrative Zoology*, *12*, 318-332.
- Yiu, S.W., Karczmarski, L., Parrini, F., & Keith, M. (2018). Resource selection in reintroduced lions and the influence of intergroup interactions. *Journal of Zoology*, *307*, 111-124.
- Yoganand, K., & Owen-Smith, N. (2014). Restricted habitat use by an African savanna herbivore through the seasonal cycle: key resources concept expanded. *Ecography*, *37*, 969-982.
- Young, E., Wagener, L.J.J., & Bronkhorst, P.J.L. (1969). The blue wildebeest as a source of food and by-products: The production potential, parasites and pathology of free living wildebeest of the Kruger National Park. *The Journal of the South African Veterinary Association*, *40*, 315-318.
- Zuur, A.F., Leno, E.N., & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3-14.

## Tables

**Table 1.** Categories and levels of the risk metrics (i.e. independent variables) and the a priori models for the vigilance responses of zebra and wildebeest.

Risk category	Risk metrics
Risky places (RP)	Home ranges of lions (HR; inside*, outside), predicted probabilities of occurrence of lions (PPO)
Vegetation characteristics (VC)	Grass height (below knee*, between knee and belly, above belly), tree density (0-20%*, 21-40%, 41-60%, 61-80%, 81-100%)
Prey characteristics (PC)	Herd size, calf (no*, yes)
Resource availability (RA)	Season (dry*, wet)
Combination of risk categories	Model
1 RP	HR + PPO
2 VC	Grass height + Tree density
3 PC	Herd size + Calf
4 RA	Season
5 RP + VC	HR + PPO + Grass height + Tree density
6 RP + PC	HR + PPO + Herd size + Calf
7 RP + RA	HR + PPO + Season
8 VC + PC	Grass height + Tree density + Herd size + Calf
9 VC + RA	Grass height + Tree density + Season
10 PC + RA	Herd size + Calf + Season

11	RP + VC + PC	HR + PPO + Grass height + Tree density + Herd size + Calf
12	RP + VC + RA	HR + PPO + Grass height + Tree density + Season
13	RP + PC + RA	HR + PPO + Herd size + Calf + Season
14	VC + PC + RA	Grass height + Tree density + Herd size + Calf + Season
15	RP + VC + PC + RA	HR + PPO + Grass height + Tree density + Herd size + Calf + Season

---

\* indicates reference level for categorical metrics.

**Table 2.** The relative importance and Akaike weights (in bracket) of risk categories on the vigilance response of zebra and wildebeest.

Relative importance	Zebra		Wildebeest	
	Intense	Routine	Intense	Routine
1	Risky places (0.758)	Risky places (0.930)	Prey characteristics (0.561)	Risky places (0.537)
2	Resource availability (0.369)	Resource availability (0.601)	Risky places (0.412)	Resource availability (0.484)
3	Prey characteristics (0.190)	Prey characteristics (0.345)	Vegetation characteristic (0.364)	Prey characteristics (0.448)
4	Vegetation characteristics (0.004)	vegetation characteristics (0.037)	Resource availability (0.349)	Vegetation characteristics (0.090)

**Table 3.** Intense vigilance response of zebra. Models of evidence ratio ( $\omega_1/\omega_i$ ) < 5 are presented.

Model	Risk metric	Coefficient	SE	$\Delta AICc$	$\omega$ ( $\omega_1/\omega_i$ )
RP	HR: outside	-0.5102	0.2161	0	0.492 (1)
	PPO	-0.4878	0.4592		
RP + RA	HR: outside	-0.5045	0.2357	2.239	0.161 (3.06)
	PPO	-0.4811	0.4729		
	Season: wet	-0.0141	0.2092		
RA	Season: wet	-0.1699	0.1937	2.350	0.152 (3.24)

Risky place = RP, resource availability = RA, lion home range = HR, predicted probabilities of occurrence = PPO. Reference levels of categorical risk metrics: HR = inside, season = dry.



**Table 4.** Routine vigilance response of zebra. Models of evidence ratio ( $\omega_1/\omega_i$ ) < 5 are presented.

Model	Risk metric	Coefficient	SE	$\Delta AICc$	$\omega$ ( $\omega_1/\omega_i$ )
RP + RA	HR: outside	0.5509	0.1998	0	0.446 (1)
	PPO	-0.3629	0.4033		
	Season: wet	-0.3765	0.1770		
RP	HR: outside	0.3478	0.1854	1.799	0.181 (2.46)
	PPO	-0.5477	0.4007		
RP + PC	HR: outside	0.3611	0.1881	2.175	0.150 (2.97)
	PPO	-0.3691	0.4071		
	Herd size	0.0277	0.0125		
	Calf: yes	-0.0423	0.1783		
RP + PC + RA	HR: outside	0.4917	0.2062	2.621	0.120 (3.72)
	PPO	-0.2758	0.4124		
	Herd size	0.0202	0.0132		
	Calf: yes	-0.0174	0.1765		
	Season: wet	-0.2724	0.1873		

Risky place = RP, prey characteristics = PC, resource availability = RA, lion home range = HR, predicted probabilities of occurrence = PPO. Reference levels of categorical risk metrics: HR = inside, season = dry, calf = no.

**Table 5.** Intense vigilance response of wildebeest. Models of evidence ratio ( $\omega_1/\omega_i$ ) < 3 are presented.

Model	Risk metric	Coefficient	SE	$\Delta AICc$	$\omega$ ( $\omega_1/\omega_i$ )
PC	Herd size	-0.0090	0.0072	0	0.251 (1)
	Calf: yes	0.3921	0.2030		
RA	Season: wet	-0.0545	0.1825	1.446	0.122 (2.06)
RP + VC	HR: outside	-0.0959	0.2138	1.749	0.105 (2.39)
	PPO	1.1955	0.5222		
	Grass height:				
	below belly	0.5589	0.2122		
	below shoulder	0.6342	0.3161		
	Tree density:				
	21-40%	-0.4354	0.2914		
	41-60%	0.4800	0.2577		
	61-80%	0.0300	0.2897		
	81-100%	-0.1331	0.2851		
	PC + RA	Herd size	-0.0082		
Calf: yes		0.4023	0.2042		
Season: wet		-0.0748	0.1907		

Risky place = RP, vegetation characteristics = VC, prey characteristics = PC, resource

availability = RA, lion home range = HR, predicted probabilities of occurrence = PPO.

Reference levels of categorical risk metrics: Calf = no, season = dry, HR = inside, grass height = below knee, tree density = 0-20%.

**Table 6.** Routine vigilance response of wildebeest. Models of evidence ratio ( $\omega_1/\omega_i$ ) < 3 are presented.

Model	Variable	Coefficient	SE	$\Delta\text{AICc}$	$\omega$ ( $\omega_1/\omega_i$ )
RA	Season: wet	-0.0977	0.1766	0	0.229 (1)
RP	HR: outside	0.1929	0.1845	0.289	0.199 (1.15)
	PPO	-0.4158	0.5022		
PC	Herd size	-0.0038	0.0071	0.610	0.169 (1.36)
	Calf: yes	-0.1967	0.2042		
RA + PC	HR: outside	0.3831	0.1997	1.000	0.139 (1.65)
	PPO	-0.1253	0.5119		
	Herd size	-0.0070	0.0074		
	Calf: yes	-0.2825	0.2064		
RP + RA	HR: outside	0.3158	0.2103	1.376	0.115 (1.99)
	PPO	-0.2520	0.5203		
	Season: wet	-0.2258	0.2031		

Risky place = RP, prey characteristics = PC, resource availability = RA, lion home range = HR, predicted probabilities of occurrence = PPO. Reference levels of categorical risk metrics:

Season = dry, HR = inside, calf = no.

**Table 7.** Coefficients for the effect of lion home range location on the proportion of total vigilance of zebra and wildebeest.

Species	Coefficient	SE	Z-value	p-value
Zebra	-0.0337	0.1643	-0.205	0.838
Wildebeest	0.1355	0.1637	0.828	0.408

Reference level of lion home range location: inside.

**Table A1.** Sample sizes of vigilance focal observation for each categorical risk metric.

Species	Zebra	Wildebeest
<i>Season</i>		
Wet	47	47
Dry	43	41
<i>Risk</i>		
High	47	56
Low	43	32
<i>Calf</i>		
Yes	30	32
No	60	56
<i>Grass height</i>		
Below knee	32	35
Below belly	48	44
Below shoulder	10	9
<i>Tree density</i>		
0-20%	18	30
21-40%	11	14
41-60%	30	13
61-80%	15	15
81-100%	16	16

## Figure legends

**Figure 1.** Intense and routine vigilance proportion (%) of zebra in relation to (a) the location of lion's home range, and (b) season. Simple means and 95% confidence interval are presented in the graph. Horizontal line indicates significant difference in the beta coefficients in beta regression models when other variables were controlled.

**Figure 2.** Intense and routine vigilance proportion (%) of wildebeest in relation to (a) the location of lion's home range, (b) tree density, (c) season, (d) grass height, (e) presence of calf, and (f) herd size. Simple means and 95% confidence interval are presented in the graph. Horizontal line indicates significant difference in the beta coefficients in beta regression models when other variables were controlled.

**Figure A1.** Study area map, Dinokeng Game Reserve, South Africa.

## **Acknowledgements**

This work was supported by The Rufford Small Grants for Nature Conservation (grant number 13035-1) and The University of Hong Kong Postgraduate Research Travel Award.

We thank the Dinokeng Management Association for the permission to conduct the research and access to the lion data. We are grateful to Kwalata Game Ranch, Mongena Game Lodge, Pride of Africa and landowners for their assistance in the field and for allowing the fieldwork to be undertaken in their properties. We thank T. Keith, C. Pretorius and T. Higgs for the logistic support throughout. Mark Keith acknowledges the support provided by the Eugène Marias Chair for Wildlife Management, University of Pretoria.

Figure 1

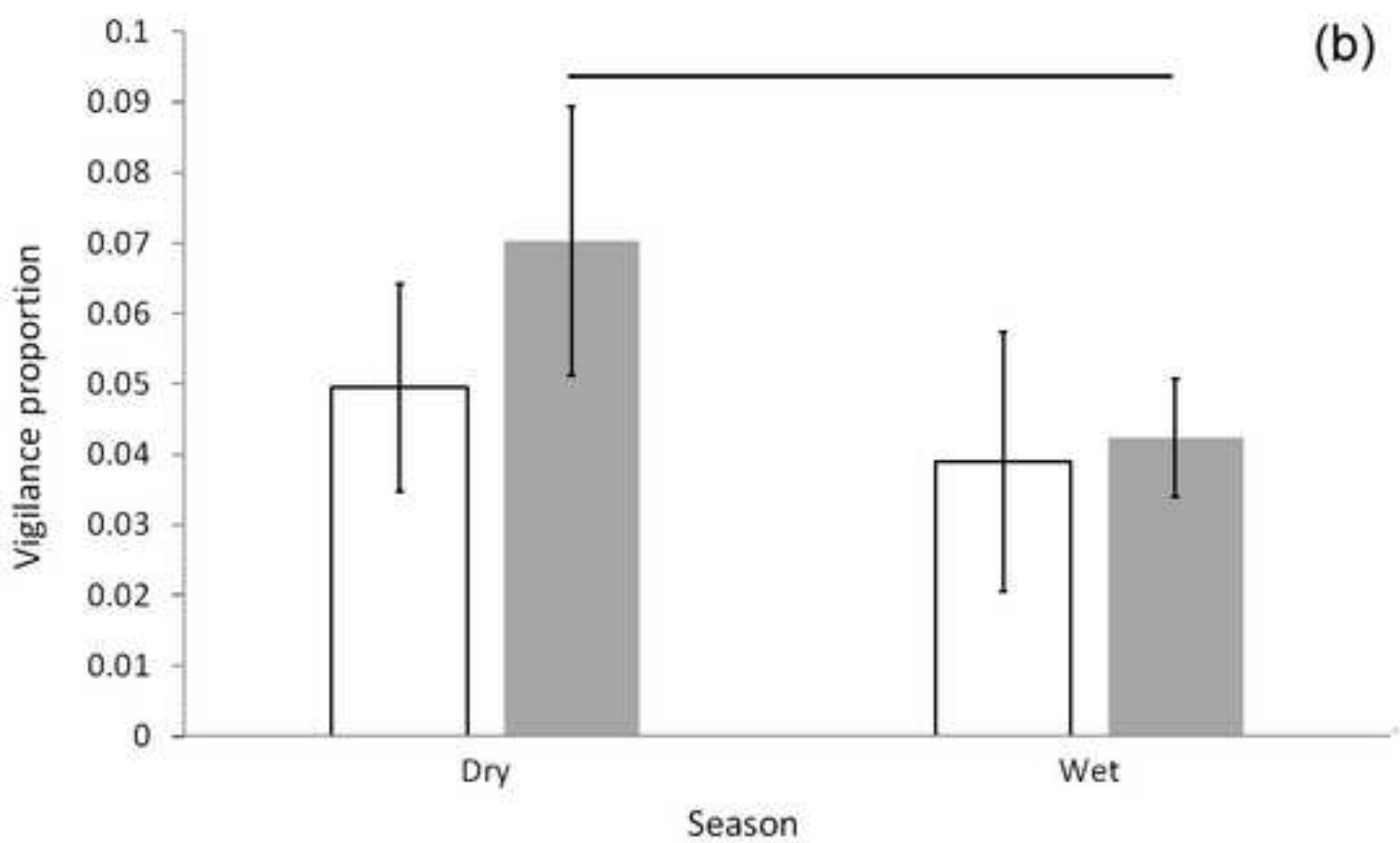
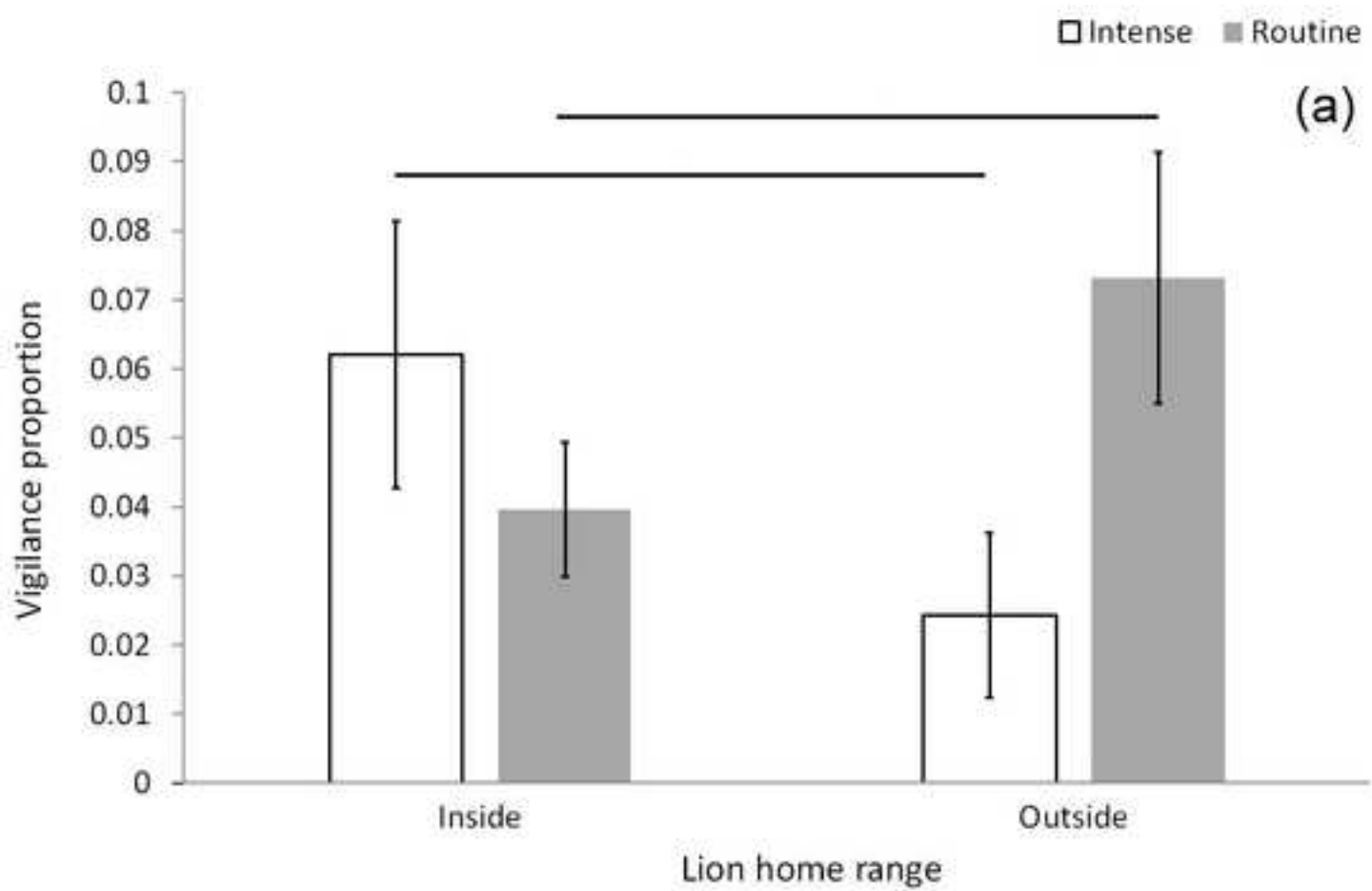


Figure 2

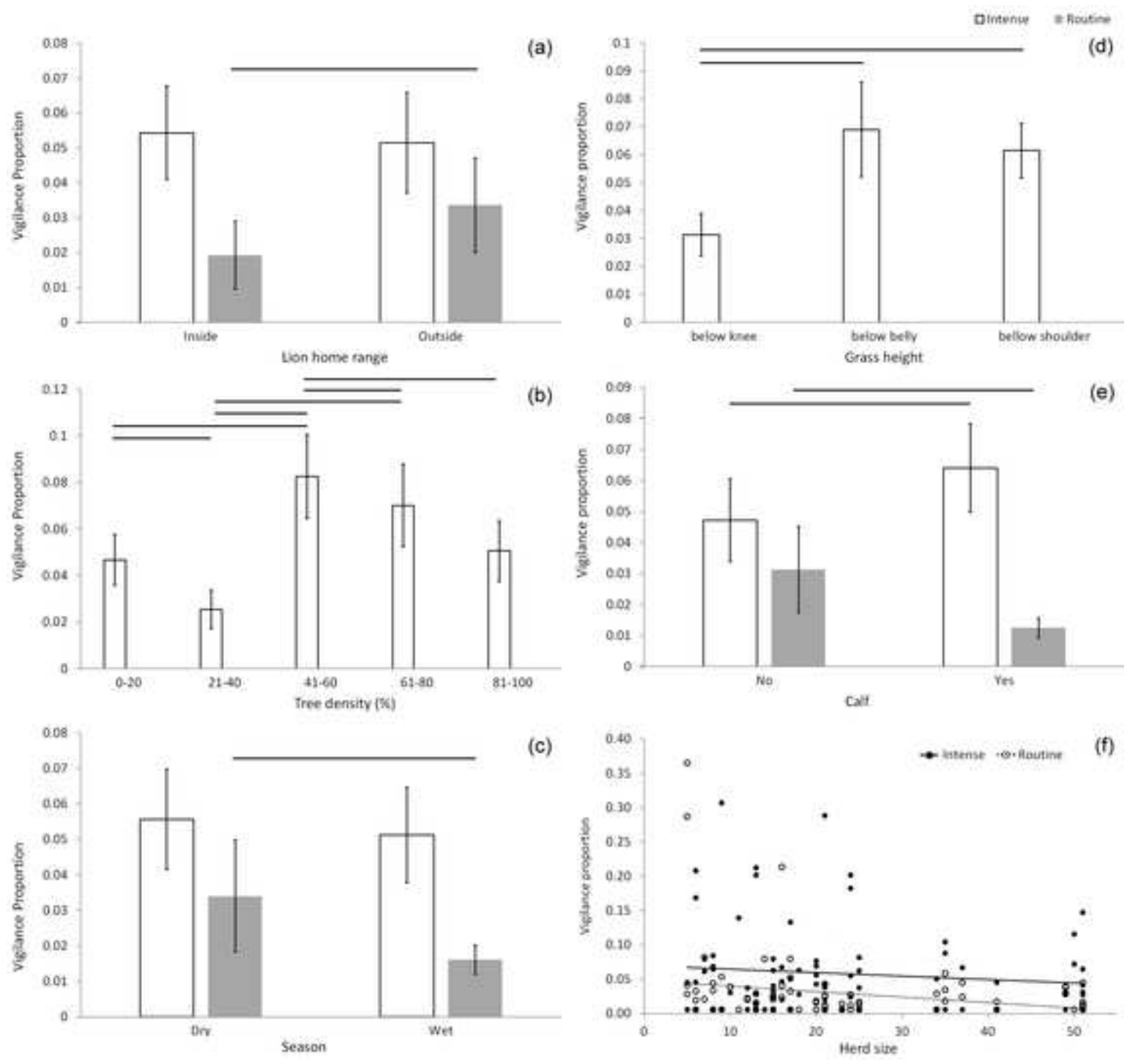
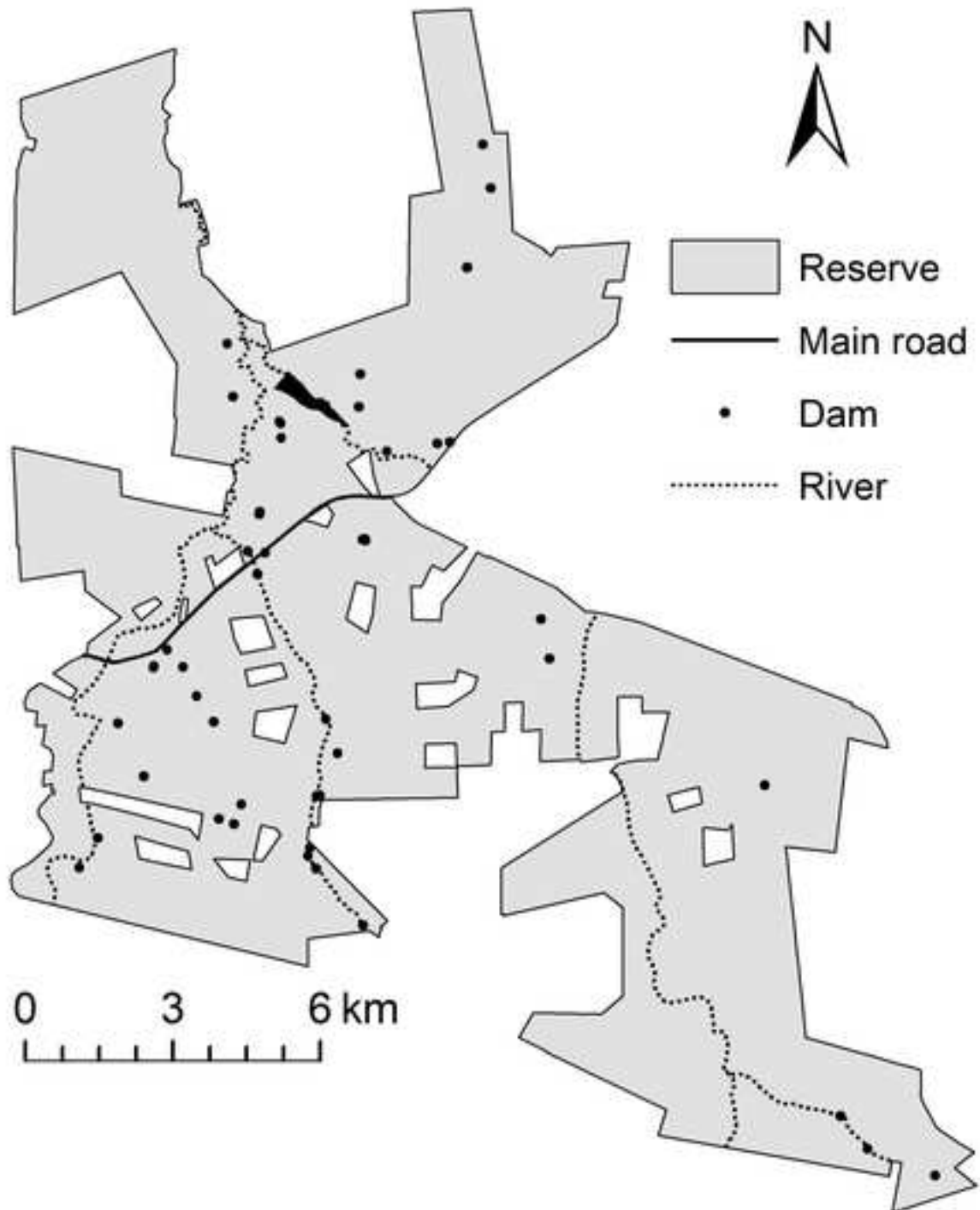




Figure A1



### **Ethical note**

The study was conducted in compliance with the ethical standard set by the Department of Environmental Affairs and Tourism (DEAT) and Gauteng Department of Agriculture, Conservation and Environment (GDACE). None of the animals were handled physically in the study. To minimize disturbance and stress to the animals, the research vehicle was parked and behavioural observations conducted at least 50 m away from the zebra and wildebeest herds. We terminated our data collection and drove away, when the animals did not show any sign of habituation after the engine was switched off for 5 minutes.

### **Animal Utilization Proposal or Research Protocol No.**

There is no official animal utilization proposal or research protocol no., because research approval is not required when the method does not involve the handling of animals. However, approval was acquired from the Dinokeng Management Association prior the research was conducted.