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VIGILANCE BEHAVIOR AND POPULATION DENSITY OF COMMON LARGE HERBIVORES IN A SOUTHERN AFRICAN SAVANNA

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ABSTRACT

The study assessed flight behavioural responses of impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) to human disturbance and compared densities of common large herbivores across Gonarezhou National Park (non-consumptive land use) and the adjacent Malipati Safari Area (consumptive land use) in southeast Zimbabwe. Animal vigilance was measured by flight behaviour and compared in terms of area and group size. Distance sampling method was used to collect data on densities of large herbivores including namely; impala, kudu, zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), waterbuck (*Kobus ellipsiprymnus*), elephant (*Loxodonta africana*), warthog (*Phacochoerus africanus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*) and nyala (*Tragelaphus angasii*), and in both study sites. The vigilance of impala and kudu were higher in Malipati than Gonarezhou ($p < 0.001$). Vigilance in impala was not significantly different with increasing animal group sizes in both Gonarezhou and Malipati ($p > 0.05$). Densities of common large herbivores were marginally different with Gonarezhou having higher animal densities than Malipati ($p \leq 0.05$). Our results suggest that hunting is important in triggering increased vigilance behaviour of herbivores as well as influencing animal densities. Thus, it is important to monitor and reduce negative human activities on animal populations in the study area for enhancing tourism activities and conservation.

Key words: density, herbivore, hunting, sink, source, vigilance, Gonarezhou, Malipati**.**

INTRODUCTION

Animals resort to survival enhancing behaviours to avoid predators with vigilance being one of these behaviours (Lima, 1998; Sirot and Pays, 2011). Vigilance involves animals reacting to the threat posed by predators as animals are thought to make state dependent decisions (Pays *et al.*, 2011). Animal vigilance is an observable trait of behaviour which provides an index of exploitation that would otherwise be difficult to measure (Caro, 2005; Thaker *et al*., 2011). The concept of 'ecology of fear' considers the behavioural responses of prey to stress and fear caused by predators (Benhaniem, 2008; Beauchamp, 2010). It has been shown that both natural predation and anthropogenic disturbances cause similar behaviours such as increased vigilance in herbivores (Lima and Dill, 1990; Papouchis *et al*., 2001). Similarly, hunting activities initiate behavioural responses similar to predation (Janis and Clark, 2002; Périquet *et al*., 2010).

In most of the reported possible mechanisms driving large herbivore populations, reproduction and survival have been central, having direct consequences on recruitment (van Langevelde and Prins, 2008). Recent studies have explored the interplay between environmental gradients, herbivore body size, and predation pressure in several savanna ecosystems (Beauchamp, 2010; Hopcraft *et al.*, 2010; Fritz *et al.*, 2011). These findings support earlier assertions that like resource limitation, predation plays a key role in the limitation of some medium-sized herbivore populations in savanna ecosystems (Grange *et al.*, 2004; Owen-Smith and Mills, 2008).

National Parks are often regarded as refugia for wildlife, whereas, in Zimbabwe mostly legal hunting occurs in surrounding communities having the Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) and Safari Areas. However, illegal hunting to some extent occurs across all the land uses (Gandiwa *et al*., 2013a, 2014). CAMPFIRE is a programme initiated with the goal of alleviating poverty in peripheral rural areas of Zimbabwe that have an abundance of wildlife. This was achieved by granting the communities the right to sustainable use of wildlife through their local Rural District Councils (Gandiwa *et al*., 2013b).

Importance of behavioural studies in conservation biology has been asserted (Sutherland, 1998). Therefore, it is important to establish the extent to which hunting in Safari Areas adjacent to protected areas has impacted animal behaviour. Our study investigated the influence of human hunting on herbivore behavioural responses, estimating vigilance and population density of common herbivores in an area of non-consumptive tourism, southern Gonarezhou National Park (hereafter, Gonarezhou), and a hunting area, Malipati Safari Area (hereafter, Malipati). Specifically, our study objectives were twofold: (i) to compare the impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) vigilance behaviour between southern Gonarezhou and Malipati, and (ii) to determine and compare common large herbivore densities in southern Gonarezhou and Malipati.

MATERIALS AND METHODS

Study area: The study was conducted in the southern region of Gonarezhou National Park (south of railway line) and Malipati Safari Area, south-eastern Zimbabwe (Figure 1). Gonarezhou extends over 5000 km^2 and is located between latitudes 21° 00'-22° 15' S and longitudes 30° 15'-32° 30' E. Southern Gonarezhou occupies two fifth of total Gonarezhou area. Malipati is a hunting safari area, which shares an unfenced border with southern Gonarezhou, along the Mwenezi River, covering an area of 154 km^2. Mean annual precipitation for Gonarezhou and Malipati is about 470 mm, whereas, annual temperature range is 14-33°C (Gandiwa and Kativu, 2009). The climate of Gonarezhou and Malipati, therefore, may be regarded as semiarid (Walker, 1979). The major vegetation type is typical of semi-arid mopane (*Colophospermum mopane*) woodland and is predominantly dry deciduous savanna woodland of varying types. A wide variety of large herbivore species inhabits the Gonarezhou and Malipati ecosystems. These include the African elephant (*Loxodonta africana*), hippopotamus (*Hippopotamus amphibius*), African buffalo (*Syncerus caffer*), giraffe (*Giraffa camelopardalis*), Burchell's zebra (*Equus quagga*), waterbuck (*Kobus ellipsiprymnus*), roan antelope (*Hippotragus equinus*), sable antelope (*Hippotragus niger*) and blue wildebeest (*Connochaetes taurinus*).

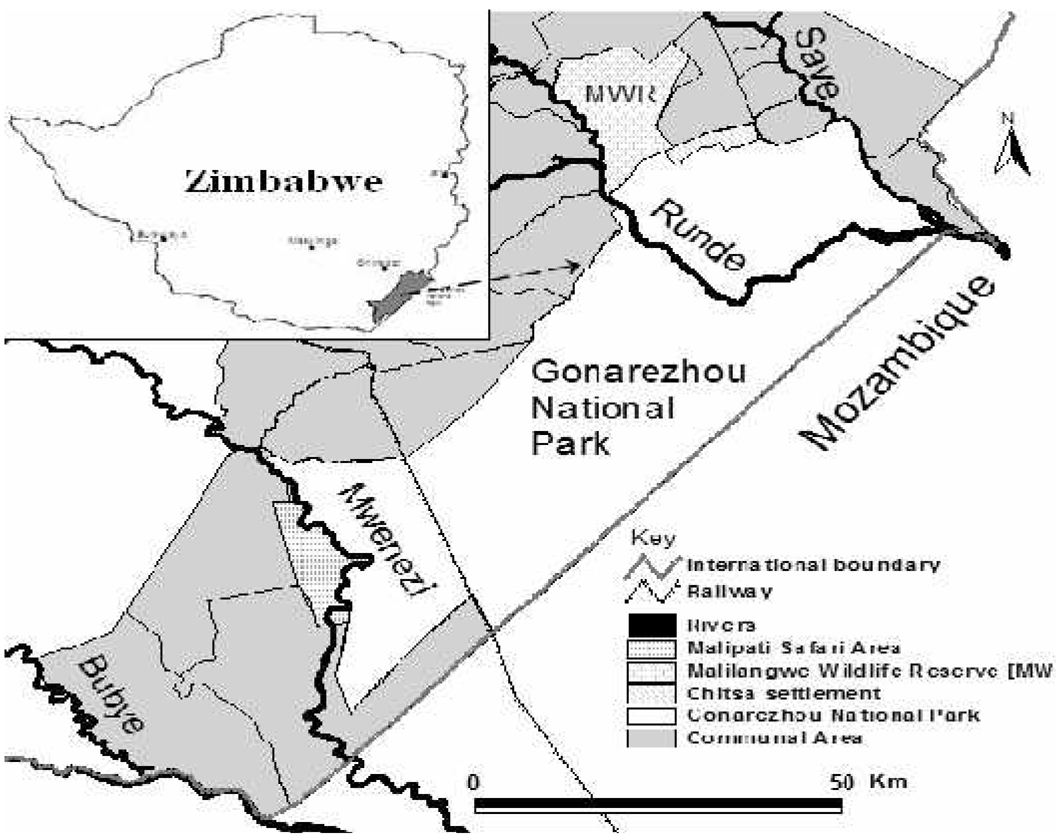

Figure 1: Location of study sites in Mabalauta section, southern Gonarezhou National Park (south of railway line) and Malipati Safari Area, southeastern Zimbabwe.

Sampling design and data collection: Data were collected through transect surveys on vehicles, along the selected stratifying road network across habitat types inhabited by common herbivores in southern Gonarezhou and Malipati. A total of 107.9 km long road transects in southern Gonarezhou and 39.4 km long road transect in

Malipati were covered. A vehicle was driven at a speed between 20 km/hr and 40 km/hr. In June 2013, data collection was carried out for four consecutive days in the morning between 6:30 a.m. and 10:00 a.m. and in the afternoon between 3:00 p.m. and 5:30 p.m. and this was conducted by three observers, one recorder and one driver.

Distance sampling procedures of estimating the absolute density of a population based on the observer to animal distance were used to collect data for animal densities as outlined by Buckland *et al.* (1993). Vigilance of animals, measured by flight behaviour was selected as the principle factor to measure the impact of sport hunting. The flight behaviour was ranked from 0-5 based on various animal behaviours being identified (Table 1).

Table 1. Wildlife Animal Vigilance rating used in this study

Vigilance Rating	Classification	Notes
0	Non-responsive	stops and stares
1	Vigilant	runs and stops < 10 metres away
2	Vigilant	runs and stops 10-50 metres away
3	Vigilant	runs and stops 51-100 metres away
4	Highly vigilant	runs and does not stop until it is out of sight (>100 m)
5	Extremely vigilant	short observation time and runs out of sight

At the beginning and end of each transect the vehicle odometer reading and times were recorded. At each sighting, the vehicle would be stopped and the following data were recorded: the vigilance of the animal, vehicle odometer reading, animal species, total number of animals at each individual sighting, herd composition, distance of the animal from the vehicle, estimated angle of sighting and habitat type in which the animal was sighted.

Data Analysis: First, Pearson's chi-square test was conducted in the R software (R Development Core Team, 2013) to compare the vigilance of kudu and impala in southern Gonarezhou and Malipati while a Kruskal-Wallis test was conducted in the Statistical Package for Social Sciences (SPSS) version 17.0 (SPSS Inc, Chicago, USA), to determine if the vigilance of impala and kudu varied depending on the group size and area. Second, animal densities were calculated by dividing the number of animals sighted for each species in each transect by the maximum sighting distance in transect length and the transect width (Hirst, 1969). The transect width was calculated by multiplying the sighting distance by the sine angle of the sighting position. The paired *t*-test was used in the SPSS software to compare the animal density of herbivores in southern Gonarezhou and Malipati, statistical significance was at $p < 0.05$.

RESULTS

Animal vigilance in southern Gonarezhou and Malipati: The vigilance of impala was found to be significantly dependent (Pearson Chi-square test, $\chi^2 = 61.69$, df = 5, $p < 0.001$) on the land use type area where the animals were observed. The impala were less vigilant in southern Gonarezhou than in Malipati (Fig. 2).

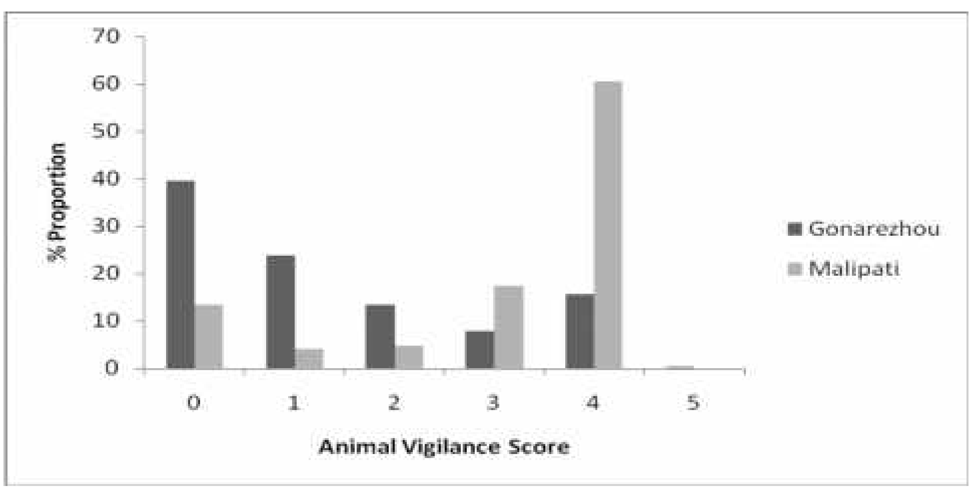

Figure 2: Percentage proportions of levels of vigilance of Impala in southern Gonarezhou National Park and Malipati Safari Area, Zimbabwe.

The vigilance of kudu was significantly (Pearson Chi-square test, $\chi^2 = 30.91$, df = 4, $p < 0.001$) dependent on the land use type where the animals were observed. The impala and kudu in Malipati were found to be more vigilant than those of southern Gonarezhou (Figure 3).

Animal group size in Gonarezhou and Malipati: The vigilance of impala was significantly non dependent (Kruskal-Wallis test, $\chi^2 = 1.93$, df = 5, $p = 0.859$) on their group size in both southern Gonarezhou and Malipati (Kruskal-Wallis test, $\chi^2 = 3.68$, df = 4, $p = 0.450$; Table 2).

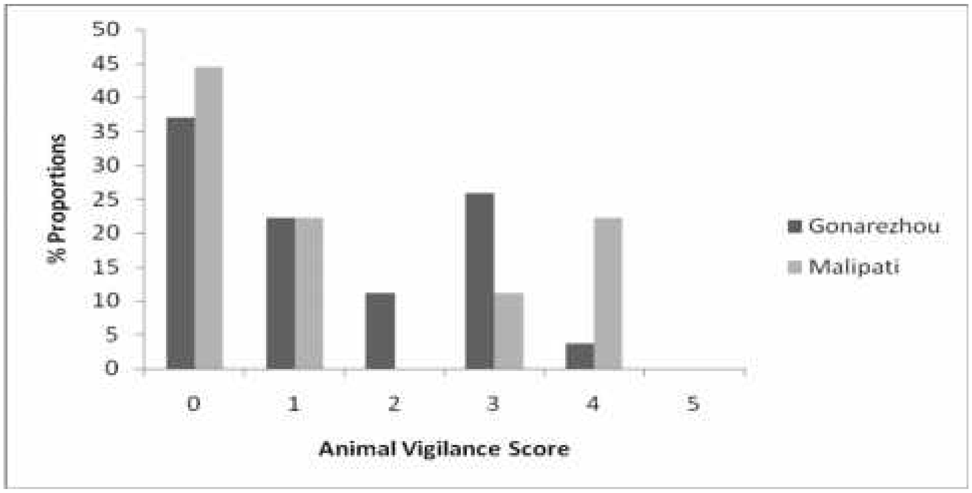

Figure 3: Percentage proportions of levels of vigilance of kudu in southern Gonarezhou National Park and Malipati Safari Area, Zimbabwe.

Table 2. Group size and vigilance behaviour of impala in southern Gonarezhou National Park and Malipati Safari Area, Zimbabwe

Study strata		**Southern Gonarezhou National Park**						**Malipati Safari Area**					
Vigilance score		0	1	2	3	4	5	0	1	2	3	4	5
Animal group size class	0-10	6	8	6	1	6	1	7	6	3	5	7	0
	11-20	2	2	1	0	2	0	1	1	0	1	0	0
	>20	1	0	0	0	0	0	2	0	0	0	1	0

Common large herbivore densities in southern Gonarezhou and Malipati: Densities of large herbivores including elephant, giraffe, impala, kudu and steenbok in southern Gonarezhou were found to be marginally higher than those of Malipati (Paired samples *t*-test, $t = 0.04$, df = 9, $p = 0.05$) (Table 3). The densities of nyala, warthog and waterbuck were relatively higher in Malipati as compared to Gonarezhou.

Table 3: Common large herbivore animal densities (km^{-2}) (± standard error) for southern Gonarezhou National Park and Malipati Safari Area, Zimbabwe

Common name	**Scientific name**	**Study area**	
		Southern Gonarezhou National Park	**Malipati Safari Area**
Common duiker	*Sylvicapra grimmia*	0.01 (0.02)	0.02 (0.01)
Elephant	*Loxodonta africana*	0.60 (0.01)	0.01 (0.01)
Giraffe	*Giraffa camelopardalis*	0.47 (0.14)	0.01 (0.03)
Impala	*Aepyceros melampus*	0.82 (0.43)	0.75 (0.24)
Kudu	*Tragelaphus strepsiceros*	1.29 (0.47)	0.75 (0.24)
Nyala	*Tragelaphus angasii*	0.03 (0.02)	0.29 (0.10)
Steenbok	*Raphicerus campestris*	0.30 (0.14)	0.06 (0.13)
Warthog	*Phacochoerus africanus*	0.25 (0.09)	0.73 (0.12)
Waterbuck	*Kobus ellipsiprymnus*	0.31 (0.03)	1.01 (0.01)
Zebra	*Equus quagga*	0.14 (0.01)	0.02 (0.01)

DISCUSSION

Vigilance of selected herbivore animals in southern Gonarezhou and Malipati: Wildlife managers could use flight initiation distance to identify habitats in which animal species are not impacted by humans (Rodgers and Smith, 1995; Fernandez-Juricic *et al*., 2005). Our study results revealed that there is a significant difference between the vigilance of selected herbivores in southern Gonarezhou and those found in Malipati. Given the uniform landscape and water availability of southern Gonarezhou and Malipati (Gandiwa *et al*. 2013c; Gandiwa, 2014), it is likely that there were other external factors that caused variation in animal vigilance across the study area. High levels of animal vigilance observed in Malipati may be explained by the higher hunting risk that the animals are subjected to in the area (Gandiwa *et al*., 2013a, 2014). The perceived risk of being hunted may have caused the herbivores in Malipati to increase their vigilance on interaction with humans. These results could, therefore, indicate that the hunting activities being carried out in Malipati have impacted on the behaviour of animals by increasing their vigilance as herbivores are known to make behavioural adjustments to hunting risk (Beinhaiem, 2008). Our study results are consistent with the findings elsewhere, of the similar characteristic of large herbivore populations in Hwange National Park, Gwaai Intensive Conservation area and Matetsi safari area in western Zimbabwe (Crosmary *et al*., 2012; Tarakini *et al*., 2014) and the Katavi National Park in Tanzania and its surrounding hunting areas (Caro, 2005).

Hunting of wildlife by humans is an activity that causes disturbance to wildlife species (Kilgo *et al*., 1998; Janis and Clark, 2002). Caro (2005) asserted that wildlife species which are subjected to hunting pressure by humans are significantly more wary of observers than species that are less exploited. In East Africa, elephants forage significantly faster along wildlife corridors than elsewhere in their range, which may suggest awareness of survival risk outside protected areas (Douglas-Hamilton *et al*., 2005). This may have a direct impact on herbivore populations as it may alter population dynamics by increasing mortality and distribution (Solberg *et al*., 1999, Creel and Christianson, 2008). It may also affect the reproductive output of populations as they divert their time to safety related behaviours rather than fitness enhancing activities such as foraging (Lima and Dill, 1990). It has been found that herbivores spend more time looking up when exposed to higher levels of predation (Lima, 1998). Stressed animals are more likely to be susceptible to diseases because high levels of corticoids cause immune suppression and because harassment is known to be energetically expensive (Lima and Dill, 1990).

Habituation makes animals allow potential predators such as humans closer if they exist in high densities (Crosmary *et al*., 2012). Our study results exhibits two forms of animal interactions with humans, consumptive and non-consumptive. The interaction of animals with humans in southern Gonarezhou is non-consumptive while in Malipati it is consumptive and often results in mortality. Caro (2005) suggested that there is a close association between behavioural wariness of an observer in a vehicle and relatively heavy exploitation. The extent to which an animal flees from or watches an observer could give an indicator of how much the population is suffering from human exploitation. This could give an indication of the hunting pressure within each habitat, i.e., southern Gonarezhou and Malipati. Our study results showed that the animals in southern Gonarezhou were more tolerant of humans while those in Malipati were less tolerant, most likely because of frequent lethal encounters with humans and thus a higher perceived risk of predation. The habituation of the animals in southern Gonarezhou could have also been as a result of frequent poaching activities within the park (Gandiwa *et al*., 2014). A school of thought suggests that animals may become habituated and less responsive to disturbance in parks as a result of frequent encounters with people (Ruxton and Beauchamp, 2008). However, the impacts of recreational activities such as hunting of wildlife are increasingly becoming a concern to natural resource managers (Knight and Gutzwiller, 1995) as animals experience direct risk of mortality and therefore habituation is unlikely in hunted populations (Crosmary *et al*., 2012).

All observations were carried out from the vehicles; hence, animals were fleeing from a vehicle. This observation may bring into question how ethical are the hunting activities carried out in the safari hunting area for the animals fleeing from a vehicle. It is expected that the animals would flee from an observer on foot, rather than from a moving vehicle (Caro, 2005) as the ethical hunting is done on foot. However, it is of importance to also note that animals are always wary of noises around them (Ruxton and Beauchamp, 2008). These results may also imply that the herbivores in southern Gonarezhou have become habituated to vehicles such that they are now less likely to flee from them. Across the world, there is an increase in the number of tourists seeking interactions with wildlife in their natural environments. Highly vigilant animals will have implications on management as there will have to be considerations on how to ensure that tourists get best possible viewing opportunities of wildlife (Gandiwa, 2011). The fact that the animals that were observed in this study were more vigilant in the safari hunting area than they were in the park suggests that parks are indeed refugia for animals that are being hunted in the surrounding areas. The results of this study further prove the assertion that animals show decreased flight responses in areas with high, non-lethal human activities while hunting increases flightiness

(Stankowich and Blumstein, 2005). Therefore, our study illustrates that behavioural studies of animals are indeed important to conservation biology (Gill *et al*., 2001) as knowledge of animal behaviour can contribute towards their conservation.

Effect of animal group size on vigilance: It is expected that there is a negative relationship between vigilance and group size (Fairbanks and Dobson, 2006) where an increase in group size results in the decrease of vigilance in herbivore species. However, our study results were contrary to those expectations and showed no significant difference in the vigilance of different impala herd sizes both in southern Gonarezhou and Malipati. Animals may not reduce their individual vigilance in response to predation owing to the possibility of being outrun by other members of the group and thus leaving them susceptible. Some studies have found an increase in vigilance with increasing group size in different taxa (Robinette and Ha, 2001; Favreau *et al*., 2010); these were in birds and kangaroos (*Micropus giganteus*), respectively. The Bertram's (1978) 'dilution of the predator effect' hypothesis suggests that the risk of an individual to be captured decreases with increasing group size, because the predator is progressively more likely to capture another individual simply by chance while Hamilton's (1971) 'selfish-herd effect' hypothesis proposes that having other individuals nearby decreases an individual's risk of capture when the predator chooses the closest prey. One of the many advantages of living in groups is that each member of a group spends less time to be vigilant and more time for feeding and other important behaviours (Pulliam, 1973). Thus, there is a general consensus among researchers that animal vigilance decreases with increasing animal group size. Our study results could have been affected by the few observations in some vigilance groups. Measuring the group size by observing the individuals that were vigilant per given time interval could have given results that are more indicative of the group size effect.

Animal densities of common large herbivores in southern Gonarezhou and Malipati: Animal densities of large herbivores are influenced by either anthropogenic or ecological factors (Gandiwa *et al*., 2013c; Gandiwa, 2014). Hunting may result in low densities of large mammals (Caro *et al*., 2004). Our study results indicated that there were higher densities of elephant, giraffe, impala, and kudu in southern Gonarezhou than in Malipati. Human activities and disturbances have been reported to influence herbivore distribution in southern African savanna (Gandiwa, 2014). For instance, large wild herbivores like elephants were reported to avoid areas with high human disturbance in southern African savanna ecosystems (Ogutu *et al.* 2010; Wallgren *et al.* 2009).

The uniform landscape and availability of surface water are some of the factors that may have led to the marginal differences in common large herbivore animal densities in southern Gonarezhou and Malipati (Ogutu and Owen-Smith, 2005). As wildlife animals are fugitive resources that move across varying land-use boundaries, it is not only important to conserve national parks but the areas contiguous to them as well (Gandiwa *et al*., 2011, 2013c). This will help maintain wildlife populations as they are protected in larger areas apart from single management units in the form of national parks. Van Aarde and Jackson (2007) proposed that clusters of protected areas be recognised as conservation units, defined by elephant movements as ecological units, rather than political units dictated by artificial boundaries. Defining wildlife populations through political boundaries has led to habitat fragmentation which has had detrimental effects on herbivore populations in Africa (Wittemyer *et al*., 2008; Balint and Mashinya, 2008; Estes *et al*., 2012). One of the strategies employed in conserving parks and the areas contiguous to them is through the creation of Transfrontier Parks. Gonarezhou and Malipati are part of the Greater Limpopo Transfrontier Conservation Area (GLTFCA). Part of the management objective of the GLTFCA is to maintain habitat connectivity. In this way, populations of herbivores can be better managed in an un-fragmented landscape as outlined by Gandiwa (2013).

Conclusions: The study results showed significant difference between the vigilance of impala and kudu in southern Gonarezhou and Malipati. We concluded that the perceived hunting risk is a possible factor that could have led to the high vigilance of impala and kudu in Malipati, while habituation and frequent non-lethal interactions with humans could have contributed to the low vigilance of herbivores as well as high densities of elephant, giraffe, impala and kudu in southern Gonarezhou. Our study also showed non-significant differences in the vigilance of impala herds as group size increased. Densities of common large herbivores were marginally different between Gonarezhou and Malipati. The uniformity of climate and vegetation are some of the factors that may have led to the marginal common large herbivore densities in southern Gonarezhou and Malipati. Further studies could be carried out on assessing the influence of varying vegetation cover/type on the vigilance, distribution and density of common large herbivores in the study area.

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