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Road Constraints on Impala (Aepyceros melampus) Behavior

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Submission date: June 2014
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Dedication

Dear mama,

It has been three years since you left me and the pain is still as if it was today. Every day I miss you more and more. I believe that you watch me from above, high up in the sky and you are proud of me. You will always be in my heart and I dedicate my thesis to you mama.

Abstract

Protected areas play a key role in safeguarding and sustaining biological diversity. The development of infrastructure in protected areas facilitates management and tourism operations. However, infrastructure can affect wildlife populations through processes such as habitat loss, traffic mortality, resource inaccessibility, population subdivision and behavior change. The study of wildlife response to the existing road network in Serengeti National Park is a necessity to provide overview of whether or not there exists compatibility of infrastructure and wildlife conservation. In this study, I used 3,827 coordinates collected from four adult female impalas (*Aepyceros melampus*) fitted with satellite GPS collars and field observations recorded in Serengeti National Park, Tanzania to determine whether roads affect impala's behavior. Variables considered in the analyses included step length, habitat type, time (day or night), movement directionality (towards or away from road) and distance to road. Although impalas' response to road disturbances was different between locations and herds, the overall results suggest that there is a pattern of road avoidance. Impala movement was influenced by the road as there were longer step lengths close to than away from the road. However, contrary to expectations, impalas utilized habitats further away from the road during the night. Vigilance was higher close to than away from the road and could eventually lead to reduced feeding time close to road areas. Impala avoidance behavior due to road disturbances has repercussions on the energy budget. Avoidance behavior may cause functional habitat loss which could ultimately affect impala's population size. Roads and traffic is therefore of potential concern in conservation of impalas.

Acknowledgement

First and foremost, I would like to express my sincere gratitude to my supervisor, Prof. Eivin Røskaft for his guidance and invaluable insights. I am also very thankful to Dr. Craig Jackson and Dr. Frode Fossøy for their continued guidance throughout the thesis process. I would like to extend my appreciation to Serengeti, TAWIRI staff, especially Dr. Robert Fyumagwa for cooperation and assistance with field logistics and data collection.

My appreciation to the College of African Wildlife Management- Mweka for granting me a two years study leave to pursue my study. I am also thankful to the Norwegian State Educational Loan Fund (Lånekassen) for financial support. This thesis would have been impossible without the support of TAWIRI-IPBES project to purchase the GPS satellite collars.

I am also grateful to my family and friends for their support during my study period.

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Abbreviations

GPS	Global Positioning System
ID	Identification number of the collared impalas
IPBES	Inter-governmental Platform on Biodiversity and Ecosystem Services
IUCN	International Union for Conservation of Nature
MHz	Megahertz
SENAPA	Serengeti National Park
TANAPA	Tanzania National Parks
TAWIRI	Tanzania Wildlife Research Institute
UNEP	United Nations Environmental Programme
USA	United States of America
VHF	Very High Frequency

1 Introduction

Infrastructure such as roads usually leads to substantial environmental impacts even with low levels of traffic (UNEP 2001). The impacts occur at various spatial and temporal scales beyond direct physical footprints. In the United States, for instance, an estimated 15–20% of its landscape is ecologically impacted by roads (Forman and Alexander 1998). Infrastructure development represents a major driving factor of biodiversity loss (Benitez-Lopez et al. 2010). With biological diversity at stake, there has been a growing concern and interest to quantify ecological effects of roads and ultimately to avoid, minimize and compensate for their negative impacts on individuals, populations, communities and ecosystems (Forman et al. 2003, Coffin 2007, Balkenhol and Waits 2009, Fahrig and Rytwinski 2009). Roads and their associated vehicular traffic affect the persistence of wildlife populations through processes such as habitat loss, traffic mortality, resource inaccessibility, population subdivision and modification of behavior (Trombulak and Frissell 2000, Jaeger et al. 2005, Eigenbrod et al. 2009). The magnitude of road impacts varies considerably depending on road type and/or level of use, season, location, time of day, and species of organisms potentially affected (Forman and Alexander 1998, van Langevelde and Jaarsma 2004, Tremblay and St Clair 2009, Bennett et al. 2011). It is assumed that road width can influence permeability of roads to animal movement, though for some species, the more influential component of road width on road crossing decisions, is probably gap width relative to the surrounding habitat (St. Clair 2003). Habitat variables versus proximity to the road influences likelihood of disturbances as well. For example bird populations are likely to be more affected at short distances from the infrastructure whilst the effect on mammal populations extends over longer distances. This fact is justified by research findings showing a decline in species abundance of 28-36% (birds) and 25-38% (mammals) within 2.6km and 17km from the infrastructure respectively (Benitez-Lopez et al. 2010). Furthermore, scientific evidence suggests that when road networks and traffic volumes increase, road-effects on animal populations become more prevalent (Forman et al. 2003, Gagnon et al. 2007, Eigenbrod et al. 2008).

Of all the road impacts, road mortality is an evident and direct effect on wild animals which impair persistence of their populations (Bennett et al. 2011, Garriga et al. 2012). Probabilities of road mortality increase with the use of the road habitat, volume of traffic, and decreasing road sinuosity (Snow et al. 2012). Studies have shown that road mortality affects a taxonomically diverse range of species and their vulnerability is influenced by life history characteristics and behavior of the species (Drews 1995, Trombulak and Frissell 2000, van Langevelde and Jaarsma 2004, Gryz and Krauze 2008, Fahrig and Rytwinski 2009). Comparatively, amphibians and reptiles are most susceptible to road mortality, even at low traffic volumes due their physiological, ecological and behavior traits (Trombulak and Frissell 2000, Kimberly et al. 2008, Orlowski et al. 2008, Fahrig and Rytwinski 2009). Despite temporal variation most herpetofauna road mortality are spatially aggregated (Langen et al. 2009), leading to drastic abundance declines (Ashley and Robinson 1996, Forman and Alexander 1998, Glista et al. 2008, Gryz and Krauze 2008, Sillero 2008).

Road mortality may further lead to reduced survival rates and declining population growth rates. For example, with 3-8% road-kill of the population annually, Island foxes (*Urocyon littoralis*) living near roads suffered a lower annual survival rate (0.76) than those living further away from roads (0.97 annual survival rate) (Snow et al. 2012). Also, a study done in Australia on tammar wallabies (*Macropus eugenii*) showed that the impact of road mortality adjacent to a bushland population may result in its long-term decline, as the population may not be able to recover from the reduction in survival rates (Chambers and Bencini 2010). Moreover freshwater turtle populations in the proximity of roads have been found to have skewed sex ratios, as females are vulnerable to road-related mortality during their breeding season and signify eventual population declines as females are differentially eliminated (Steen et al. 2006, Gooley 2010).

During and after construction, roads causes direct and immediate loss of habitats (Chen and Chen 2009). This disrupts the physical conditions of parameters such as: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of run-off, and sedimentation on and adjacent to the road (Trombulak and Frissell 2000, Coffin 2007). Vegetation along the road experience considerably greater impacts at close ranges of <1km because of road dust (UNEP 2001). Moreover, roads and traffic are considered to be the vector for introduction of invasive species (Forman and Deblinger 2000, Trombulak and Frissell 2000). Depending on dispersal abilities invasive species may outcompete native plant species and lead to changes in vegetation composition (Kalwij et al. 2008). The series of continued impacts including pollution may further degrade habitat quality and render its unsuitability for some species temporary or permanently (Ndibalema et al. 2008). The other implication of road development is reduced landscape connectivity via habitat fragmentation

(Shepard et al. 2008). Considering different types of human expansion into animal habitats, roads have probably the strongest effect through habitat fragmentation (Neumann et al. 2013), which decrease the availability and quality of foraging habitats (Forman et al. 2003). Roads impose barriers and hinder movements of animals and thus create metapopulations with limited dispersal and recolonization possibilities (van Langevelde and Jaarsma 2004).

The presence of a road and traffic volume may modify animal's behavior either positively or negatively (Ashley and Robinson 1996, Forman and Alexander 1998, Trombulak and Frissell 2000, Jaeger et al. 2005). From a biodiversity point of view, behavioral responses of wildlife individuals toward roads may be more pervasive for population persistence by effectively reducing the functional connectivity of the landscape (Shepard et al. 2008, Bennett et al. 2011). Mechanisms responsible for behavioral changes include home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological states (Trombulak and Frissell 2000). Since behavior and habitat use patterns are different within and among wildlife species, the effects of road disturbances differ accordingly. Habitat use as 'where to be' and 'what to eat' at particular time is facilitated by individual movements. Individual movements are primarily a behavioral response governed by a set of decision making processes influenced by their surroundings and interactions (Severns 2008). Environmental cues such as adequate cover, predators, food resources, etc., dictate optimum decision making whereby one species may perceive road as a risk, while others do not (Bennett et al. 2011). On the other hand traffic volume, road width and road surface contribute to behavioral responses of wildlife and thus the barrier effect of roads (Forman and Alexander 1998, Fahrig and Rytwinski 2009). Traffic density in particular has been identified as a significant constraint on wildlife movements (Forman et al. 2003, Eigenbrod et al. 2008). Road traffic influences wildlife crossing probabilities on different spatial and temporal scales and thus determine their distribution and abundance on road verge (Clair and Forrest 2009).

Several studies have been conducted and documented the effects of roads on behavior of wildlife. For instance, traffic patterns caused a clear behavioral shift in grizzly bears (*Ursus arctos)* with increased use of areas near roads and movement across roads during the night when traffic was low. Grizzly bears selected areas near roads utilized by fewer than 20 vehicles per day but avoided roads receiving moderate traffic volume (20-100 vehicles per day) and strongly avoided high-use roads (>100 vehicles per day) at all times (Northrup et al.

2012). Moreover, bobcats (*Lynx rufus*) avoided areas less than or equal to 100m from roads as compared to areas with no roads (Lovallo and Anderson 1996). In north eastern Gabon, African forest elephants (*Loxodonta africana cyclotis)* preferred forests away from both roads and villages (Barnes et al. 1991). Furthermore, interference of communication among songbirds by traffic noise has been implicated as a possible cause for low abundances in populations adjacent to the roads (Reijnen et al. 1996, Rheindt 2003).

Road and traffic disturbances may distract feeding for some species while for few others it may enhance their feeding opportunities. Availability of carcass as a result of road kills persuades predators to forage along roadsides and increase their risk of vehicle collisions (Barrientos and Bolonio 2009, Benitez-Lopez et al. 2010). Some of the raptors such as black vultures (*Coragyps atratus*) and turkey vultures *(Cathartes aura)* established home ranges in areas with greater road densities (Fahrig and Rytwinski 2009).

Protected areas are usually established due to their ecological potential to conserve biodiversity and facilitate resilience of threatening processes (Roger et al. 2012). Nevertheless protected areas are not isolated compounds as they face many ubiquitous crossing-cutting threats, including infrastructure development which counteracts realization of its desired objectives. Abundance of road networks in protected areas is usually overlooked and is mostly unaccounted for conservation implications (Ament et al. 2008). To date most of the studies on impact of infrastructure on wildlife population have been done in Europe and North America. There is inadequate quantitative evidence of ecological impacts of roads in African ecosystem. For instance, at this particular juncture, there is urgent need for scientific evidence to support prognoses of the impacts of the highway construction which is planned to traverse Serengeti National Park (SENAPA) in northern Tanzania (Fyumagwa et al. 2013). Serengeti National Park is an area of national and international importance, a natural World Heritage Site and part of Serengeti-Ngorongoro Biosphere Reserve. Most importantly, Serengeti is at the heart of the broader Serengeti-Maasai Mara ecosystem which is defined by supporting world spectacular annual migration of vast herds of wildebeest, gazelles and zebras, followed by predators. As other protected areas, Serengeti National Park has various roads which support management and tourism operations and for public use. Depending on use, surface type and structure the SENAPA road network can be divided into three categories; main roads, minor roads and side roads with 0.28, 0.12 and 0.04 mean number of cars per minute respectively (Lunde 2013). Main roads include two-lane roads made of gravel, used frequently and allowing traffic to move at high speed, although the speed limit is 50km\hour as per SENAPA regulations. Minor roads include gravel roads as well but not regularly maintained and with relatively fewer vehicles in use. Side roads are less used as compared to the main and major roads and usually covered with grass.

The study of the response of wildlife to the existing gravel roads in Serengeti National Park is a necessity to provide overview of whether or not there exists compatibility of infrastructure and wildlife conservation. A previous study on impala (*Aepyceros melampus*) in Serengeti National Park revealed relatively higher faecal glucocorticoid metabolites, indicative of stress in impalas occurring along the main road as compared to other roads with less vehicles (Lunde 2013). Nonetheless, in order to understand full range of potential effects of infrastructure on wildlife, the behavioral response of individuals to roads needs to be addressed (Bennett et al. 2011). Hence, the focus of this follow up study was to examine if roads have any effects on impala behavior. Movements of individual impalas were monitored using GPS satellite data so as to better understand spatiotemporal dynamics which has ultimate consequence of individual behavior, physiological constraints and environmental impacts (Patterson et al. 2008). Specifically, the following hypotheses were tested; (1) Impala spend more time closer to the road during the night; (2) Impala movement pattern is influenced by the road; and (3) Impala are more vigilant when closer to the road. Information collected is intended to provide knowledge regarding ecological impacts and implications of transportation infrastructure to conservation practitioners and stakeholders to make decisions based on scientific knowledge.

2 Methodology

2.1 Study area

The study was conducted in Serengeti National Park (SENAPA), which was the first national park to be established in Tanzania aiming to ensure the survival and vigour of all species contained therein. It covers an area of 14,763km² being the country's second largest national park after Ruaha National Park (TANAPA 2012). SENAPA lies in the northern part of the country (Fig.1), bordered to the north by Kenya, where it is contiguous with Maasai Mara National Reserves. To the south-east of the park is Ngorongoro Conservation Area, to the south-west lies Maswa Game Reserve, to the western borders are Ikorongo and Grumeti Game Reserves, and to the north-east lies Loliondo Game Controlled Area (Kaltenborn et al. 2011). Serengeti National Park was inscribed as a World Heritage Site by UNESCO (1981) and together with Ngorongoro Conservation Area, became a UNESCO Biosphere Reserve (1981) due to its outstanding universal values. The exceptional resource values in SENAPA includes a large mammal migration cycle notably ungulates; rich flora and fauna; a natural self-regulating ecosystem; endless grassland savanna plains; large predator-prey population and interactions (TANAPA 2005). SENAPA is internationally renowned for the continuous migration of over 1.3 million wildebeest (*Connochaetes taurinus*), 0.6 million zebra (*Equus burchellii*) and Thompson's gazelles (*Gazella thomsonii*) (TANAPA 2005). Floristic diversity of Serengeti includes grassland plains, woodlands and matrix of grasslands and woodlands harboring other large populations of herbivores like buffalos (*Syncerus caffer*), giraffes (*Giraffa camelopardalis*), impalas and many others. The Serengeti also support one of the highest concentrations of predators in the world (TANAPA 2005). Furthermore Serengeti harbours some of the IUCN Red list species such as African elephants (*Loxodonta africana*), black rhinoceros (*Diceros bicornis)* and cheetah (*Acinonyx jubatus*). Also there are more than 500 species of birds that are perennially or seasonally present in the park and 5 species are endemic to Tanzania (TANAPA 2005).

2.2 Study species

In this study, impala was used as a model species to assess the impacts of roads and traffic on animal behavior. Impalas are medium sized, sexually dimorphic (male weigh 60-65kg, female weigh 40-45kg), gregarious African antelope. Impala prefer light woodland with little undergrowth and grassland of low to medium height. Impalas group size is related to food availability and dispersion, and thus varies seasonally, as do other features related to feeding behavior such as rate of movement and inter-individual distance (Setsaas et al. 2007). While depending on free water, soils with good drainage, firm footing, and no more than moderate slope, its special requirements produce an irregular and clumped distribution (Estes 2012). Impala are predominantly grazers while grasses are green and growing; browsing foliage, forbs, shoots, and seedpods at other times and when need be it also eats fallen dry leaves. Impala can also adapt to different habitats by being mainly grazer in one area and a browser in another. Impala's ability to utilize both monocotyledons and dicotyledons gives it varied, abundant, and reliable food supply enabling this antelope to lead a sedentary existence and reach high densities (Estes 2012).

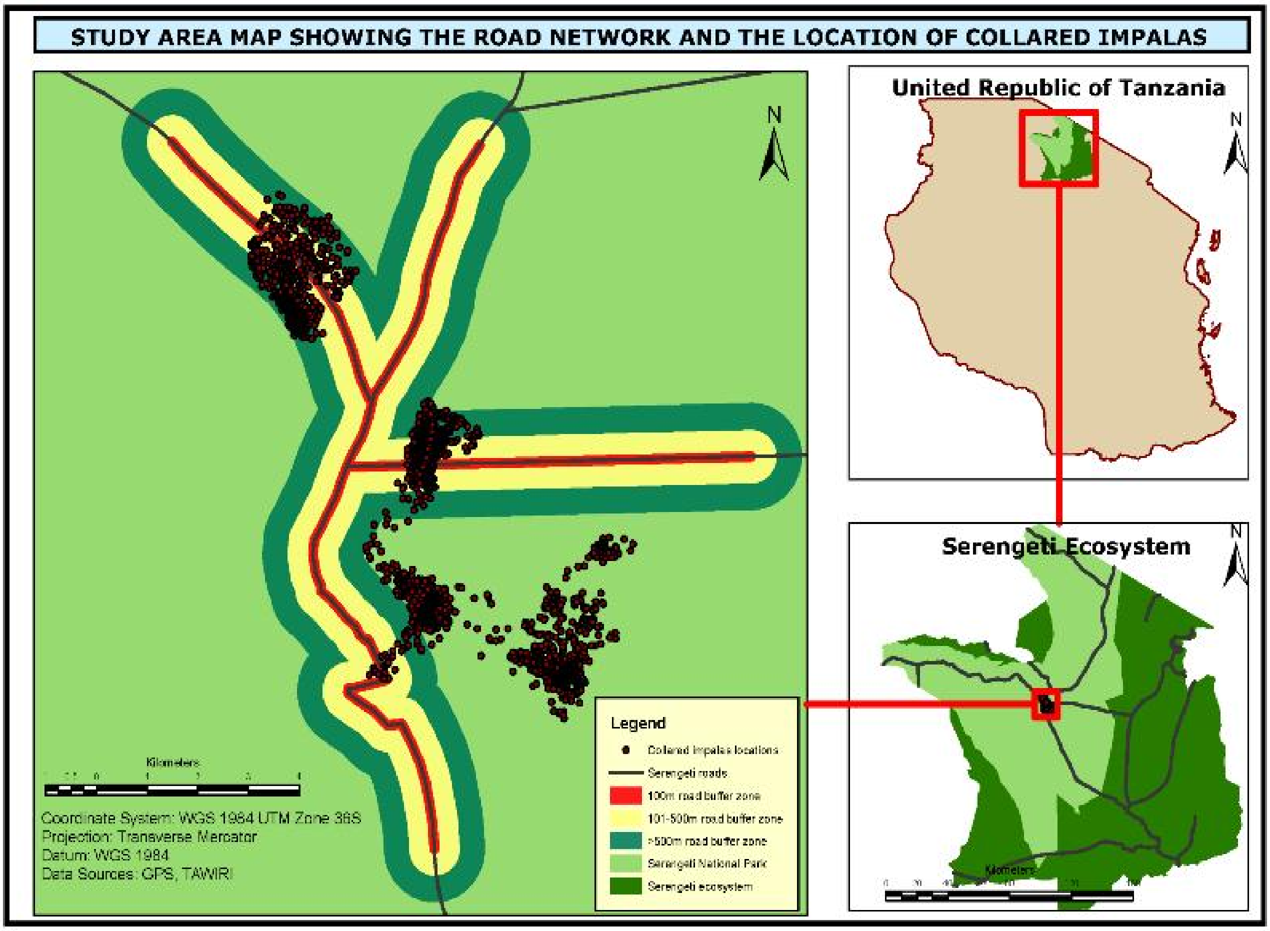

Figure 1. Map of the study area showing road networks and locations of the four satellite GPS collared impalas

2.3 Data collection

Between 7 June 2013 and 9 June 2013 four adult female impala were immobilized and then fitted with global positioning system (GPS) satellite collars (African Wildlife Tracking, Pretoria, South Africa). Adult female impalas collared were randomly selected from four different areas with different road types which vary in level of traffic volume. The focal areas with their respective impala GPS collar identification were around Serengeti Tanzania Wildlife Research Institute (TAWIRI) center (627), Seronera center (628), Nyarusiga (629) and Sero2 (630). The area around Serengeti TAWIRI center has side roads and therefore relatively less traffic. Seronera center is the park's headquarters and a retailing area, as a result is the busiest part of the park with continuous to and from traffic flow throughout the day. Nyarusiga area is adjoining to the major road which take relatively large number of vehicle including public buses to and from Arusha - Musoma regions. The other focal area is called Sero2 which is encircled by a river and road is on the outskirts.

Female impala were selected for this study so as to maximize and ensure adequate precision of data collected since movement rates of male impala is influenced by territorial behavior. Capture and handling procedures were approved and led by Tanzania Wildlife Research Institute (TAWIRI). During the process of fitting GPS satellite collars, blood, tissue samples and standard body measurements were taken. All the collared individuals were monitored intensively for two days continuously to ensure no effects of drug or collaring. The GPS collars were also equipped with Very High Frequency (VHF) transmitters (148MHz) that enabled tracking of the collared individual in the field using an antenna and receiver. GPS satellite collars were programmed to collect fine scale locations every 90 minutes. The GPS locations from all collars were uploaded via a satellite link to a server. Data were later retrieved by logging into the server.

Additional data were collected during field observations from 10 June 2013 to 10 August 2013 in order to supplement GPS satellite data. Field observations were randomly done on different collared individuals and/or the herd from dawn to dusk. Each day attempts were made to observe all four herds with collared impala so as to monitor their behavior in relation to the road. The latest coordinates were retrieved from the satellite server and there after uploaded to the GPS receiver. Within a range of 100m to 2km a VHF antenna and receiver were used to track the focal impala. Once encountered the GPS coordinates, time and distance to the road were recorded. Behavior of the collared female, as well as another randomly selected adult female and the adult male were simultaneously recorded for one hour in intervals of 10 minutes. Thus behavior of 3 individual impalas was recorded 6 times within one hour. Recorded behavior were foraging, resting, vigilant, sparring, travelling and for males' territory defending activities like chasing intruding males. Collected data were thereafter entered into a data sheet into Microsoft Excel 2007 for analysis.

2.4 Statistical analyses

A total of 3,827 GPS locations were retrieved from all four satellite collars. To determine whether impala use roads at varying degrees depending on the time of the day, time of the retrieved coordinates was categorized into day (07:00hrs-18:59hrs) and night (19:00hrs-06:59hrs). Using ArcGIS 10.1, all GPS locations were plotted on Serengeti digital thematic map provided by TAWIRI with various landscape features including road network, vegetation and habitat types. To investigate the influence of roads on impala movements, the shortest distance between each GPS location and closest road were calculated in ArcMap 10.1. All relevant combinations of set of explanatory variables to identify important determinants for impala behavior responses to roads were considered. Step length, the distance between consecutive GPS locations, was used as the response variable and I added habitat type, time (day or night), movement directionality (towards or away from road) and distance to road as predictor variables. To create normal distribution natural logarithm step length transformation was used. Mixed model with individual impala ID included as a random effect were used to control for differences between individuals (Bolker et al. 2009). Linear mixed models were performed in the statistical software R (R Core Team 2013) using the package lmerTest (Kuznetsova et al. 2013).

To test the effect of the road on impala behavior, recorded GPS locations during field observations and their associated attributes were plotted on the Serengeti map using ArcGIS 10.1. Using the SENAPA road network layer, nearest distance from the GPS locations to the road was calculated and 100m, 101-500m and >500m buffer zones centred on the road were created. For the cause of this study >500m road buffer zone was considered as control distance. I then used IBM SPSS version 21.0 for further analyses behavior aspects in relation to the distance from the road.

3 Results

3.1 Individual impala variations

Mean step length of the four GPS collared female impalas varied significantly, whereby ID 628 and ID 630 had relatively longer step lengths compared to ID 627 and ID 629 (F = 17.70, df = 3 and 3823, $p < 0.001$; Fig. 2). Furthermore, mean distance to nearest road for the four impalas differed significantly (F = 492.77, df = 3 and 3823, $p < 0.001$; Fig. 3).

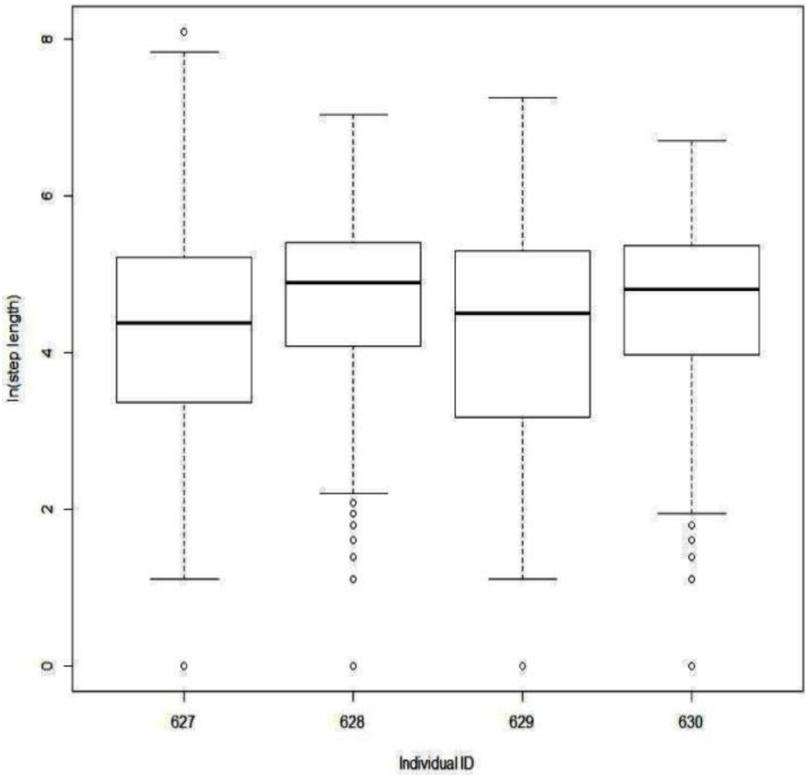

Figure 2. Mean step length for the four GPS collared female impalas

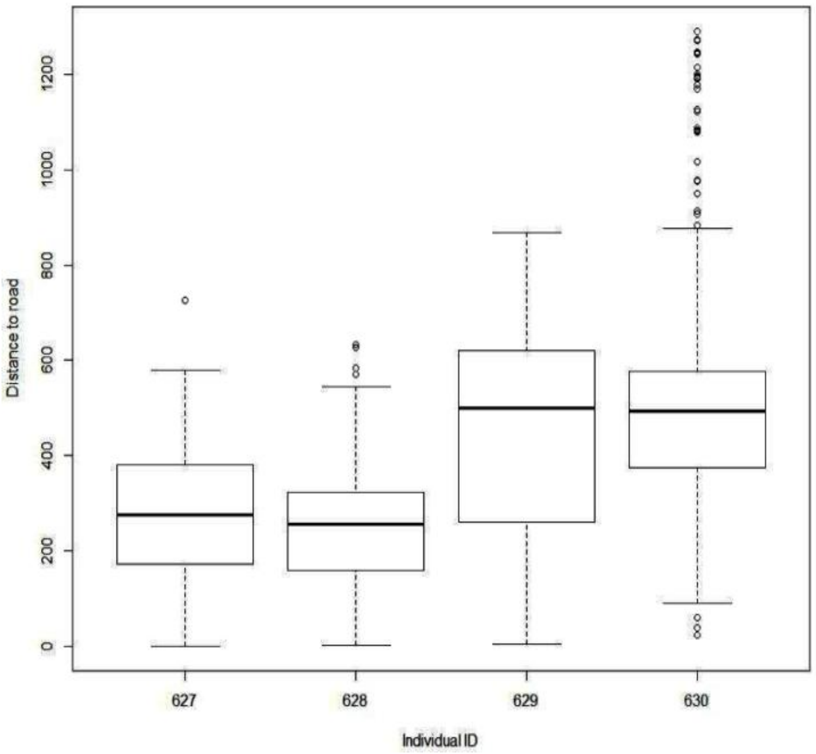

Figure 3. Mean distance to the nearest road for the four GPS collared female impalas

3.2 Step length

Mean step length during 90 minutes intervals was 155.0m (±SD= 183.7, n= 3827). Mean step length (m) varied significantly between the three different road buffer zones (F = 43.22, df = 2 and 3824, $p < 0.001$; Fig. 4). The mean step length of >500m road buffer zone which was the control distance from the road was the shortest (124.9m) whereas for the 100m and 101-500m road buffer zones the mean step length were 185.0m and 168.7m respectively, viz. mean step lengths decreased with increasing distance from the road.

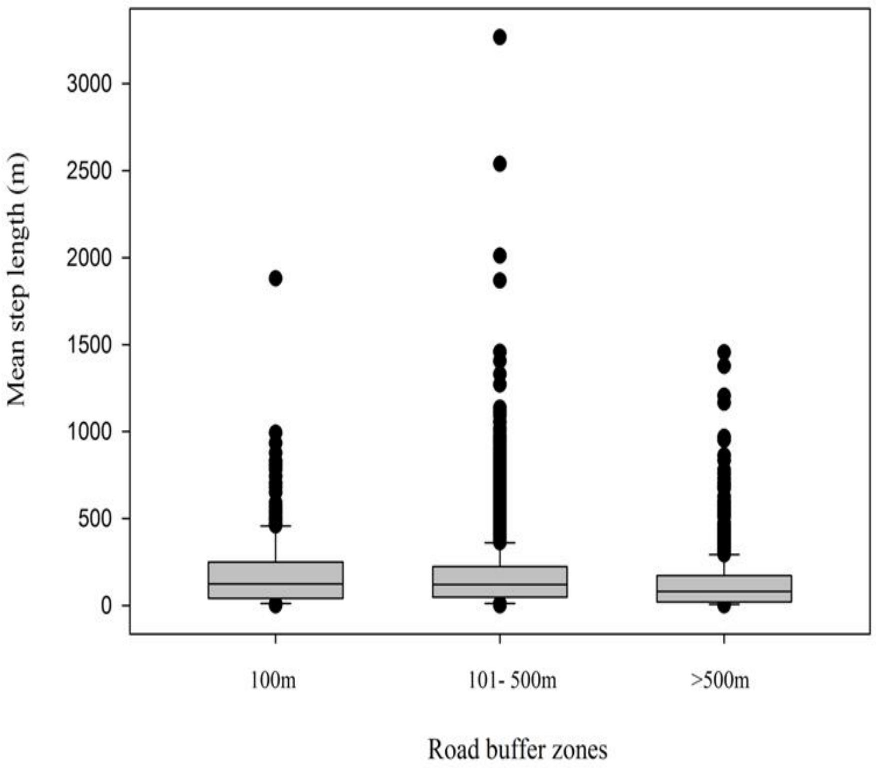

Figure 4. Mean step length at three different road buffer zones.

Table 1. Linear mixed model on impala step length in relation to movement directionality (towards or away from road), distance to the road, time of the day and habitat. Impala ID was included as a random factor to control for individual differences.

	Estimate	± SE	df	t	p
(Intercept)	5.19	0.103	5	50.5	< 0.001
Towards or away from road	-0.0610	0.0382	3820	-1.60	0.111
Distance to the road	-0.0004	0.0001	2920	-3.96	< 0.001
Night relative to day	-1.15	0.039	3820	-29.8	< 0.001
Shrubland relative to Grassland	-0.267	0.0688	3810	-3.88	<0.001

In a mixed model with natural log-transformed step length as a response variable and female identity as a random variable, day/night turned out to be the most important variable explaining step length variation (Table 1; Fig. 5). The second most important variable was distance to the road (Table 1; Fig. 4) and thirdly the habitat (Table 1; Fig. 6). However, step length in relation to movement directionality (towards or away from the road) was not statistically significant (Table 1).

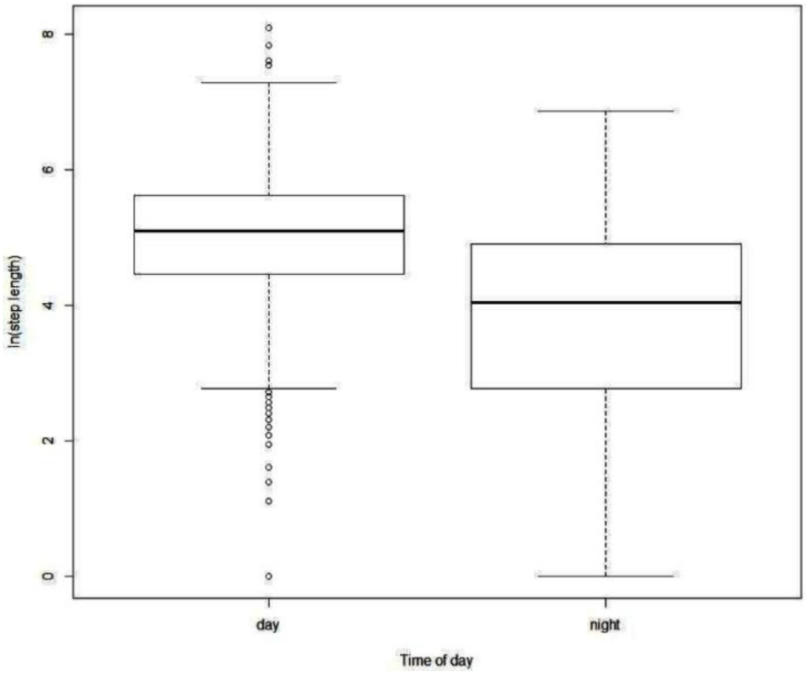

Figure 5. Mean step length (ln-transformed) in relation to time of the day

3.3 Impala distance to the road

Expected frequencies of random GPS locations within 100m, 101-500m and >500m road buffer zones were 10%, 40% and 50% respectively. However, the observed frequencies of GPS locations were 7.4%, 58,6% and 34% in those three areas respectively, which were statistically significant different from what was expected ($\chi^2 = 4575.6$, df = 4, $p < 0.001$). In another mixed model test, impala distance to the road was used as dependent variable with time of the day (day/ night) and habitat (grassland/ shrubland) as independent variables while controlling for female identity as a random factor (Table 2). Only time of the day turned out to be significant explaining the variation in mean distance to the road (Table 2; Fig.7). The mean distances of impalas from the road was not significant relative to the two habitats (shrubland/ grassland) (Table 2; Fig. 8).

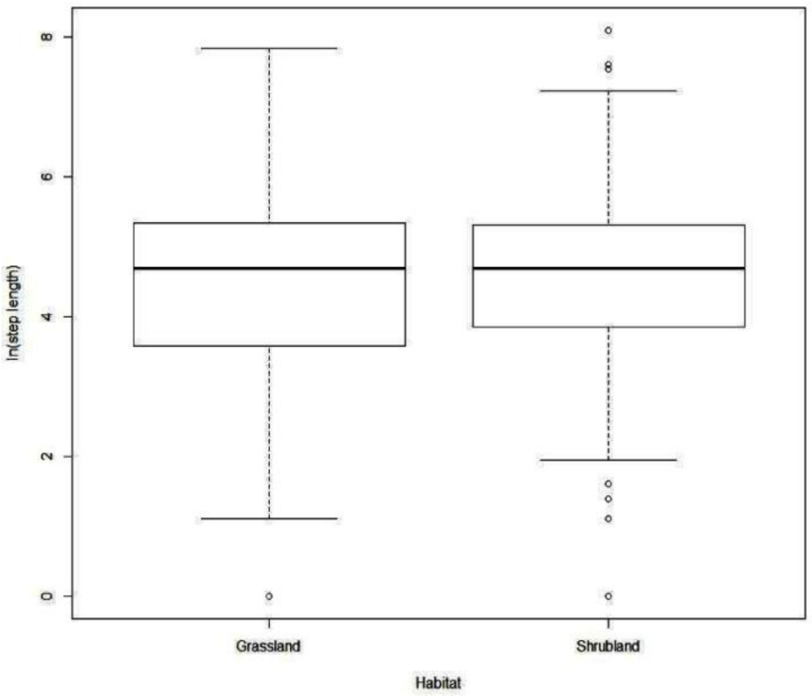

Figure 6. Mean step length (ln-transformed) in relation to habitats types (shrubland and grassland)

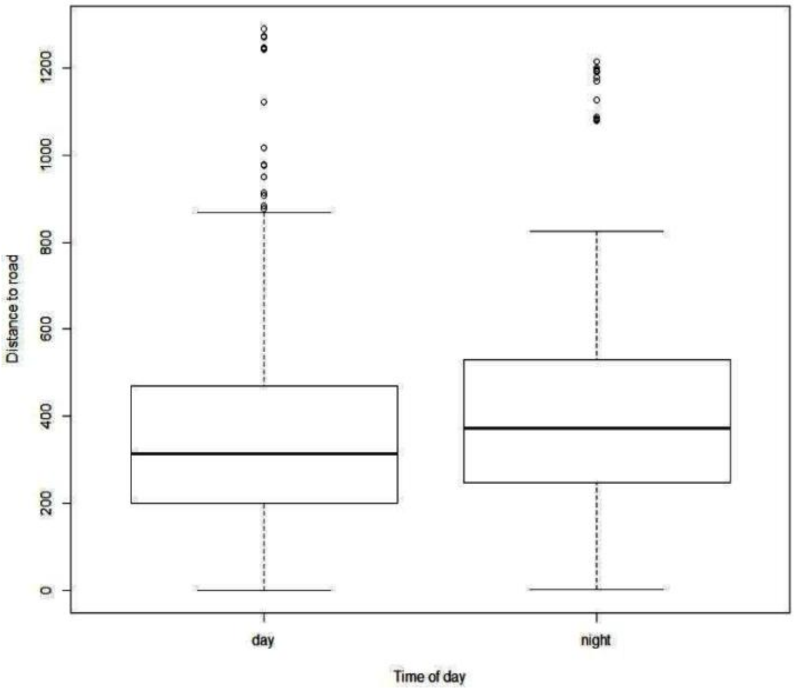

Figure 7. Mean distance to the nearest road (m) in relation to time of the day

Table 2. Linear mixed model on impala mean distance to the road in relation to habitat and time of the day. Impala ID was included as a random factor to control for individual differences

	Estimate	SE	df	t	p
(Intercept)	343.5	60.2	3	5.701	0.0106
Night time relative to day	43.9	5.45	3821	8.052	0.001
Shrubland relative to grassland	-5.4	9.82	3822	-0.547	0.5843

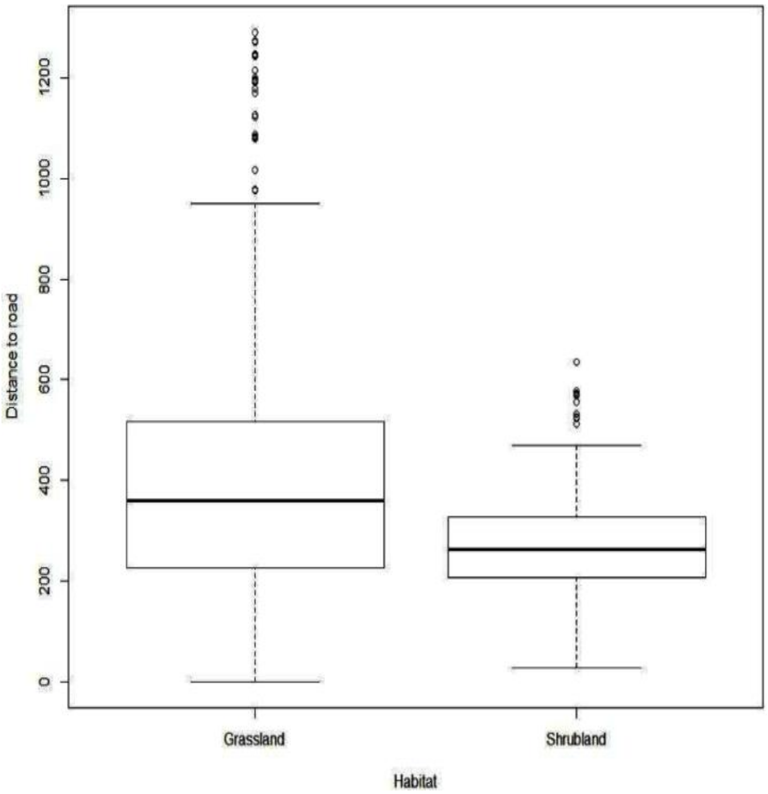

Figure 8. Mean distance to the nearest road (m) in relation to habitat types (shrubland/ grassland)

3.4 Behavior

Impala behavior differed significantly between the three different road buffer zones (χ^2= 30.6, df= 6, p < 0.001). Impalas spent more time being vigilant near roads and their feeding pattern varied considerably at different road buffer zones, whilst they rested and walked at a consistent pattern in different road buffer zones. The proportion of vigilance behavior was

35.9%, 26.8% and 16.1% within 100m, 101-500m and >500m road buffer zones respectively. In the same order feeding time increased as impalas moved away from the road (Fig. 9).

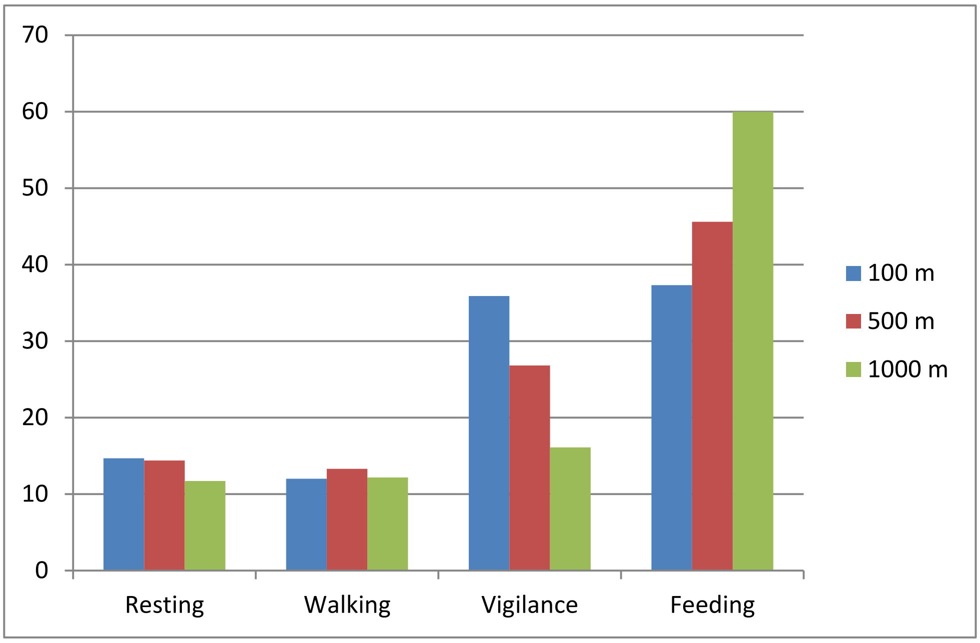

Figure 9. Frequencies of different behaviors within 100m, 101-500m and >500m road buffer zones

4 Discussion

4.1 Impala movement pattern in relation to road

During this study, I hypothesized that roads influence impalas' movement patterns and that impalas would tend to avoid areas in close proximity to the road. The findings suggest that there is a pattern of road avoidance. A greater proportion of impala locations were located in the 101-500m road buffer zone as compared to the 100m and >500m road buffer zones. Individual impala's GPS locations were found on both sides of roads indicating that at certain time during the study impalas crossed the road. Sightings during field observations confirmed that impalas crossed the road at certain times. Although impalas did cross roads and used habitat alongside roads, they spent less time at the area with the greatest disturbance which is indicative of avoidance behavior. This inference is in accordance with the widespread practice of interpreting reduced abundance of animals near the roads as evidence for a behavioral avoidance (Jiang et al. 2009). Furthermore, fewer GPS locations on the 100m road buffer zone might otherwise express effects of roads on animal abundance (Fahrig and Rytwinski 2009).

The animal response to functional connectivity depends on how an organism perceives and responds to the landscape structure within a hierarchy of spatial and temporal scales (Belisle 2005). The results of this study suggest that roads, as an example of anthropogenic landscape features, influence impala movement as all the four focal impalas had longer mean step lengths close to the road than at the control distance (>500m road buffer zone). Step lengths, a proxy for mean speed (Barraquand and Benhamou 2008), can be used to distinguish animal behaviors, with longer steps indicating increased travel and shorter steps corresponding to foraging or resting (Franke et al. 2004, Franke et al. 2006). Step lengths also can be an indicator of residency time because shorter steps increase the probability of remaining in a given habitat (Turchin 1998). It is assumed that within an area with optimal resources and less disturbance, an animal will often walk slower and with a constant step duration which lead to shorter steps (Barraquand and Benhamou 2008). For this particular study, step length provided insight on the movement pattern of the impalas in relation to road proximity.

Among the four collared impalas, impala with ID 628 at Seronera center maintained a relatively short distance from the road. Its mean step length was comparatively the longest and corresponds to reduced foraging and resting. The probable explanation for the longer step length is that impalas might be moving faster to counteract road and traffic disturbances.

Similar findings have been reported for other species, such as grizzly bear and elk, where step length increased near roads and was the longest near highly trafficked roads, indicating faster movement when near roads (Forester et al. 2007, Roever et al. 2010).

Moreover, each individual is an autonomous entity that is behaviorally and physiologically distinct from other entities, and that interactions among individuals and their environment is localized (Franke et al. 2004). Individuals in a population may vary in behavioral traits such as movement rates and their response to the disturbance of roads and associated traffic (Shepard et al. 2008). The focal impala with ID 629 confined at Nyarusiga area had shortest step length and maintained the longest distance from the road as compared to the other impalas studied. The herd at this particular area may have avoided the road and associated disturbances by being distant from the road. In line with the previous studies, reduced proximity to the road denote less road and traffic disturbances, which is the ideal habitat supporting shorter step lengths shown as a result of walking slowly. As it have been shown in elk (Rowland et al. 2000), this impala and the associated herd used habitat adjacent to roads less than similar habitats not affected by roads.

However, natural landscape features, in this case a river, which is linear and similar to roads appear to influence the step length of the collared impala with ID 630 at Sero2 area. Impalas' movement in that particular area is probably the function of predation risk rather than the road effects because it is most likely for predators to inhabit river areas in pursuit of their prey. Relatively longer impala step length at Sero2, suggest that they perceive this area as a "landscape of fear" (Fortin et al. 2005, Laundré et al. 2010, Ciuti et al. 2012a). Changes in movement pattern imply that impalas are possibly suspicious, cautiously and move relatively faster so as to minimize probability of encountering predators.

Despite being confined at the area with relatively less traffic use, impala with ID 627 around Serengeti TAWIRI center had more or less similar mean step length as the one at Nyarusiga area which has major road. This suggests that road and its associated traffic disturbances affect impalas regardless of the status of the road and traffic volume.

Model results seem to suggest a 'road effect' on impala behavior in respect to road proximity. The findings of this study ascertain consistent movement pattern of the impala's relative to distance from the road. The increased step length as impala approach the road suggests that impalas sense the threat of the road and associated traffic. Whereas when the distance from the road increase impalas step length decrease implying that the impalas perceive less risk at habitat further from the road. Fitness cost increases with large step length, and with time the increasing traffic volume disturbance might probably impair the wellbeing of the impala.

Impalas are primarily diurnal, of which under natural environment feeding, standing, and lying accounted for 18.6-19.2hours of a 24hours day for females (Estes 2012). The results of this study showed significant variation of the step length between different times of the day whereby impala step length was relatively longer during the day. Impalas' longer step length during the day would primarily attributed to their regular diurnal activity pattern. Alternative explanation might be the absolute variation of the traffic volume between day and night. Studies conducted to examine the impacts of roads on wildlife conform to the findings of this study. For instance, the results of the study done on moose showed that they moved faster near the roads and maintained relatively larger distances from the roads during the day time suggesting that moose did not perceive roads as neutral objects (Neumann et al. 2013). Similarly, Waller and Servheen (2005) documented that bear selection of roads was consistent throughout the day however, time of the day had a strong influence over the selection of forest structure and terrain variables.

In contrast to the tested hypothesis the studied impalas preferred areas far from the road during the night. A plausible explanation for this is that impalas acquired this as the strategy of minimizing predation risk, as during the night most of predators are more likely to be active and prefer relatively open areas (Fischhoff et al. 2007). Areas with relatively high vegetation cover provide concealment precluding impalas whilst minimizing the visibility of their potential predators. Areas adjacent to the road are mostly open and do not have cover thus increasing the likelihood of prey exposure to predators. The findings are contrary to related literature which documented that most animals utilizes road areas when traffic volume is rather low, which is the case during dusk and night. For instance elk in Oregon, USA shown consistent diurnal movement pattern relative to low traffic volume forest roads, moving closer at night and farther away during the day (Ager et al. 2003). Likewise moose spatiotemporal movement in relation to roads were influenced by variation in perceived human derived risk, of which moose moved closer to roads at night than at day (Eldegard et al. 2012).

On the other hand, movement directionality was not a significant predictor of impala movement in relation to the road. There was no significant variation of step length when the impala moved either towards or away from the road. This implies that movement of the focal impalas is function of the spatial dynamics relative to the road and not necessarily impala direction.

4.2 Impala behavior response to road and traffic

Animal response behavior results from a combination of proximate factors that may lead to risk aversion or tolerance to a given anthropogenic disturbance (Barten et al. 2001, Borkowski 2001, Stankowich 2008). Under normal undisturbed conditions, impala time expenditure during the day is as follows; feeding (66-72%), walking (10-16%), standing (11-15%) and grooming (6-7%) (Jarman and Jarman 1973). Impala demonstrated relatively high vigilance on 100m road buffer zone and there was vigilance increasing pattern with the decreased distance towards the road. However, the feeding pattern showed an inverse pattern, with the relatively high feeding routines on >500m road buffer zone and feeding trend decreased proportionally from >500m, 101-500m and 100m road buffer zones. Resources in 101-500m and 100mroad buffer zones are therefore not exploited to their full potential, reflecting effects of road disturbances. The results showed that impalas use proportionally more time being vigilant, other than feeding when they were at closer distance to the road. Vigilance inevitably involves trade-offs as it cannot occur concurrently with feeding (Gill et al. 1996). Therefore increased vigilance in impala may likely result to reduced fitness vigour. Nevertheless, there was neutral response of impala resting and walking on all three road buffer zones and given the low traffic volumes in the study areas it is unlikely that the disturbance was great enough to significantly affect fitness. Also Ciuti et al. (2012b) found evidence suggesting that elk reduced the time they devoted to feeding when they were closer to road, traffic volume of >1 vehicle every two hours caused elk to switch to a more vigilant mode of behavior with a subsequent loss in feeding time.

Despite the fact that impala found on the habitats near roads have elevated stress levels (Lunde 2013), the decision to leave or stay on the disturbed areas is context-dependent and has fitness consequences for the individual involved (Frid and Dill 2002). The impala herd near the road around Seronera center showed behavior suggesting a degree of tolerance towards road and traffic disturbances. At times during field observations, there were sightings of this impala herd feeding on the fallen seedpods from *Acacia* trees on the road verge. Probable cause of the tolerance tendency towards the road is either the benefits of foraging near the road outweigh the road disturbances or due to their inaccessibility of other habitats. Impala’s decision to stay on the disturbed environment may most likely result in increased energetic expenditure and continued stress. This is supported with the results on elk endurance of road and traffic disturbances at higher traffic volume when accessing high quality foraging areas (Gagnon et al. 2007).

4.3 Habitat analysis in relation to road

Animals tend to select habitat that minimize the ratio of mortality risk to net energy intake (Frid and Dill 2002, Fortin et al. 2005). Of the two habitat categories used for vegetation analysis, results showed that impalas preferred grassland over shrubland. Impalas like most other ungulates, preferred to forage in open habitat type, particularly open grassland with scattered trees (Fischhoff et al. 2007), where there is abundant and high nutritional quality so as to maximize opportunities to reproduce and increase their probability of survival. In relation to the roads and traffic disturbances, the results showed that habitat did not influence movement pattern and distance selection of the studied impalas.

4.4 Management implication

Behavioral states and changes in time spent for various activities due to effects of roads has repercussions on impala energy budget. If road disturbances lead to the reduced impalas' foraging time and\or increase energy expenditure by moving away from disturbances, then they may experience a net energy deficit attributable to disturbance avoidance.

Moreover, movement is a fundamental process underlying animal distribution (Turchin 1998) and it can shape the density of individuals and populations, govern community and ecosystem structure, and influence evolutionary processes and patterns of biodiversity (Liedvogel et al. 2013). Altered movement patterns may have nutritional and energetic cost due to reduced access to potential foraging and resting habitats.

Impala avoidance of habitats closer to the roads reflects the effect of road disturbances that may cause functional habitat loss and could ultimately affect population size. Roads and traffic is therefore of potential concern in conservation of impalas.

SENAPA management target to conduct full site specific environmental impact assessment according to Development-Action-Lease-Procedures and Pragmatic Environmental Assessment for the existing roads and prior to construction of new roads (TANAPA 2005). However, it is important to account for life history characteristics and behavior of the species at the focal sites during environmental impact assessment so as to avoid and minimize negative impacts of the road.

5 Conclusion and Recommendations

Conclusion

This study has shown that road disturbances affect impalas' behavior regardless of the status of the road and it’s traffic volume. In particular roads influenced impalas' movement patterns and the studied impala with associated herd’s response included; 1) Spending less time at habitats closer to the roads indicating impala avoidance behavior; 2) Tolerate the disturbance by remaining closer to the road but increased their step length as a strategy to escape from any danger resulting from the road and traffic. However, impalas' response to those disturbances was different between locations and herds.

The study further revealed that the ideal area was 101-500m from the road as most of GPS locations were confined on that road buffer zone. Impalas' response behavior towards the roads and traffic has fitness consequences as a result of increased vigilance behavior which compromise feeding time.

Recommendations

Roads are precursor for other human development activities which improve connectivity among humans whilst counteract connectivity of natural habitat and wildlife populations. At this crossroad, conservation practitioners should always prioritize protected areas of high habitat quality for effective ecosystem functioning. When and where need be, there should be synergetic infrastructure planning to balance human development and wildlife populations for persistence of healthy ecosystem. Furthermore, there should be continuous scrutiny for the control of road's negative effects to biological diversity.

Despite the financial constraint, wildlife telemetry and GIS has been important tools for conservation and management in monitoring wildlife resources. I recommend the continued use of those in future research to facilitate better understanding of roads ecological consequences and developing appropriate mitigation measures where necessary. Mitigation measure are costly and logistically challenging and therefore all pertinent factors such as biology of the target species, road characteristics or neighboring habitats and choice and design of particular mitigation measures should thoroughly be taken into account.

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