THE SPATIAL PATTERNS OF PRIMATE VEHICLE COLLISIONS IN DIANI, KENYA

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Abstract

Wildlife vehicle collisions are a serious global concern. Although there is a growing body of literature in relation to the issue, few studies have considered primate vehicle collisions. A long term dataset spanning 18 years was used to study the spatial collision patterns of four sympatric primates species; *Colobus angolensis palliatus* (colobus), *Cercopithecus mitis albogularis* (Sykes), *Chlorocebus pygerythrus hilgerti* (vervet), and *Papio cynocephalus ibeanus.* Statistically significant collision hotspots were identified using a modified kernel density estimation approach (KDE+). A total of 14 universal hotspots containing 579 (84 %) primate vehicle collisions were detected. The non-random distribution of primate vehicle collisions was further investigated using generalised linear models (GLMs) to assess the effect of five different variables on collision occurrence. The results of the model revealed that neither traffic volume nor primate abundance affected the frequency of collisions but did reveal an unevenly distributed risk across species. Baboons were the least vulnerable to vehicle collisions followed by vervets, colobus and finally Sykes. These results suggest that the small-bodied arboreal species could be disproportionately affected by road related mortality. Proximity to curves and large road intersections increased the risk of collisions possibly owing to shortened sight distances and reduced reaction times of both primates and vehicles along these road sections. Meanwhile speed bumps were found to be an effective means of mitigation reducing the local relative risk of collision. Using a combination of a clustering approach and modelling provides the best means of reliably identifying the factors influencing primate- vehicle collisions and thereby offers a robust basis upon which to form a mitigation strategy.

Introduction

1.1 Primates in Decline:

Non -human primates are one of the most diverse mammalian orders rivalled only by bats (*Chiroptera*) and rodents (*Rodentia*) (Estrada *et al.* 2017). As our closest living relatives, they provide invaluable insights into human evolution and behaviour providing, amongst other things, compelling evidence for the origins of tool use and cultures (Jolly 1985, Van Schaik *et al.* 1999). Their charismatic nature and close origin mean that we hold a unique affinity for our non-human counterparts (Hetman *et al.* 2018). Moreover, they contribute to numerous ecosystem services and processes, such as seed dispersal, that are essential to the persistence of tropical forests (Lambert and Garber 1998).

Alarmingly, a recent review reported that approximately 75% of all non-human primate populations are in decline and 65% are listed as either vulnerable (VU), endangered (EN) or critically endangered (CR) by the IUCN red list (Estrada *et al.* 2017). This high risk of extinction can be predominantly attributed to unsustainable human activity. Although threats vary depending on geographical region, the leading cause for decline is unequivocally habitat loss driven by an assortment of anthropogenic factors such as agriculture, logging and livestock (Estrada *et al.* 2017).

Other emerging challenges include poaching for bushmeat (Jones- Bowen and Pendry 1999), the exotic pet trade (Nijman *et al.* 2011), climate change (Graham *et al.* 2016) and the exposure to novel infectious diseases (Negrey *et al.* 2019). As a result, many populations are becoming increasingly confined to anthropogenically modified landscapes where they a face a variety of interacting pressures.

1.2 Roads as a threat:

Linear infrastructure such as power lines, railways and roads are ubiquitous features of human dominated landscapes (Laurance *et al*. 2009). The road network, in particular is proliferating at an unprecedented rate (Laurance and Balmford 2013, Alamgir *et al.* 2017). Indeed, it is predicted that in the next 30 years an additional 25 million kilometres of road will be constructed, with 90% of the expansion occurring in developing countries, many of which are in the tropics and characterised by exceptionally high primate densities (Laurance *et al.* 2013).

For example, the pan-African “development corridors” project plans to build in excess of 53,000 km of roads across the continent posing a serious threat to its 214 native primate species (Laurance *et al.* 2015, Estrada *et al.* 2017). Indeed, the expansion of the transport network is estimated to be a leading cause of habitat destruction for between 2-16% of all non-human primates globally (Estrada *et al.* 2017). Roads also act as an important source of chemical and light pollution as well as an acoustic nuisance resulting in a further reduction of suitable habitat (Van der Ree *et al.* 2011).

In addition to habitat loss and degradation, linear structures also represent a barrier to dispersal thereby reducing habitat connectivity and the ability of wildlife to move across the landscape (Shepard *et al.* 2008). This barrier effect is known to have far-reaching consequences; most notably, it has been reported to influence migratory patterns (Wilson *et al.* 2016), ranging behaviour (Rondinini and Doncaster 2002) and in some cases, even gene flow (Garcia – Gonzalez *et al*. 2012). The adverse effects of roads as barriers are most pronounced in small isolated populations where their persistence depends of the stability of a larger metapopulation. In such instances, micro populations become vulnerable to inbreeding depression and to stochastic events (Opdam *et al.* 1993).

However, although roads undoubtedly restrict the directional movement of wildlife, in most cases they constrain movement rather than limit it absolutely (Underhill and Angold 1999). The majority of species continue to cross roads intermittently in order to meet their ecological needs, for instance in response to resource availability (Underhill and Angold 1999). It is therefore inevitable that when fauna cross roads, individuals will occasionally fall foul of oncoming traffic. Indeed, wildlife vehicle collisions remain the most conspicuous consequence associated with linear infrastructure (Biggs *et al.* 2004).

1.3 Vehicle collisions

Traffic related mortality is one the leading causes of death amongst wildlife in heavily modified landscapes (Forman and Alexander 1998). Whilst road traffic collisions alone are unlikely to lead to the extinction of abundant species, they represent a considerable threat to the persistence of rare taxa particularly on a local scale (Land and Lotz 1996). In addition, because the vulnerability of individuals to roads can depend on both age and sex, road mortality can affect certain cohorts disproportionally and therefore result in structural population changes as well as diminished abundance (Aresco 2005). With the growth of the transport network substantial efforts have been made toward understanding the factors that contribute to roadkill.

Today, there is a consensus amongst road ecologists that wildlife vehicle collisions are rarely randomly distributed in space but rather, aggregated or clustered (e.g. Gomes *et al.* 2009). For instance, a study in North-eastern Spain found that over 70% of wildlife vehicle collisions took place in less than 8% of the total road network (Malo *et al.* 2009). Hotspot analysis is often adopted as the preferred means to identify road sections characterised by high roadkill densities (Litvaitis and Tash 2008). Hotspot approaches heavily rely on geographic information systems to inventory collision locations and subsequently apply appropriate geo-statistical methods.

Once fatality hotspots have been identified, understanding the environmental factors that determine clustering is the next logical step (Ramp *et al.* 2005). Many authors have attempted to use statistical models to study these factors (Litvaitis and Tash 2008). A wide variety of explanatory variables have been already been explored. Such variables tend to fall into two main categories; landscape or road related features. Examples of road related features include traffic volume (e.g. Joyce and Maloney 2001), road width (e.g. Clarke *et al.* 1998) and distance to the nearest curve (e.g. Lee *et al*. 2004). Landscape features include metrics such as road adjacent habitat type (e.g. Biggs *et al.* 2004) and topography (e.g. Malo *et al.* 2009).

Although some factors, such as speed, seem to have an almost universal effect, consistent predictors across different groups of taxa are hard to distinguish (Grilo *et al.* 2009). We know from the field of biogeography that a unique combination of factors is responsible for determining distribution of species (Barve *et al.* 2010). These factors are expressed across a geographic matrix that is itself dynamic. Likewise, the distributional determinants of collision hotspots appear to be highly species specific and may also depend on the local environmental context (Roger and Ramp 2009). Factors that act as key determinants for one species' collision patterns may have little or no explanatory power for another (Grilo *et al.* 2009, Teixeira *et al.* 2013). These differential responses to environmental factors stem from intrinsic interspecific differences. Differences may be behavioural and therefore determine a species ability to respond to the risks presented by roads (e.g. Lucas *et al*. 2019). Alternatively, they could be ecological, when for example a species' key resources are in proximity to roads thereby increasing their exposure to road-related risks (e.g. de Freitas *et al.* 2015). Accordingly, species that have a comparable ethology or occupy similar ecological niches should exhibit a high degree of overlap in their collision patterns.

By understanding the factors that determine the spatial distribution of wildlife vehicle collisions, studies can make recommendations to transport professionals (Barthelmess 2014). Guidance is given to improve existing road networks through the implementation and placement of mitigation structures such as fencing, over/underpasses, signage and speed bumps (Gunson *et al*. 2011). Moreover, they can also influence the design and routing of future transport infrastructure (Glista *et al*. 2009. Improving the performance of mitigation strategies is particularly important in the context of globalization where there is a marked increase in the flow of goods and persons across transport networks.

1.4 Primate vehicle collisions

Whilst an extensive suite of literature exists pertaining to road related mortality, most of it has been carried out in relation to large-bodied temperate species. Little is known about the spatio-temporal patterns of wildlife vehicle collisions of fauna restricted to the tropics. Currently, only a handful of studies exist that concern primate vehicle collisions (Hetman *et al.* 2019). For example, a scoping review conducted in 2009 identified 131 species in 30 species groups that were significantly affected by road infrastructure; however, none of those involved primates (Fahrig and Rytwinski 2009). Meanwhile, existing studies tend to be highly anecdotal, usually comprising of a case study involving a single individual (e.g. Dean and Milton 2003, Cibot *et al.* 2015).

The absence of solid quantitative data could suggest that primate vehicle collisions are a relatively rare phenomenon. However, a more recent study drawing on non-scientific resources collected 368 individual reports across 46 different primate species indicating that their occurrence is more common than expected (Hetman *et al.* 2019). The lack of robust scientific studies may be, at least in part, attributed to the order's restricted geographic range. Data from tropical and subtropical regions is frequently underrepresented across scientific literature (Martin *et al.* 2012). The paucity of knowledge surrounding primate vehicle collisions therefore does not necessarily reflect a lack of importance but rather an inherent reporting bias.

1.5 Responses to Roads

Primates are generally associated with superior levels of cognitive aBílity making them highly adaptable to environmental changes (Reader and Laland 2002). Many species exhibit behavioural plasticity in response to linear infrastructure. However, responses vary greatly from species to species owing to fundamental ecological differences. In some cases, for example chimpanzees *(Pan troglodytes verus),* a neutral response is observed, where movements appear unaffected by the presence of roads (Bryson- Morrison *et al.* 2017). Alternatively, other species may display an attraction to roads, choosing to forage or move in proximity to them. Indeed, baboons (*Papio* spp.) appear to have a marked affiliation for roads often choosing to travel along them despite the increased risk of collision (Strandburg-Peshkin *et al.* 2017). However, most arboreal primate species are repulsed by linear infrastructure and therefore alter their movement patterns to avoid them. Such avoidance behaviour and spatial displacement has been observed in both spider monkeys (*Atelles geoffroyi*) (Asensio *et al*. 2017) and golden lion tamarins (L*eontopithecus rosalia)*(Lucas *et al.* 2019).

1.6 Objectives of this study:

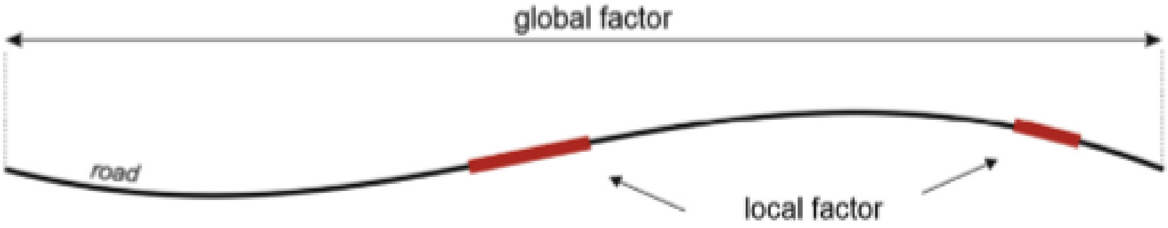
In Diani, road related mortality affects four sympatric primates: Angolan black-and-white colobus (*Colobus angolensis palliatus*), Sykes monkeys (*Cercopithecus mitis albogularis*), vervet monkeys (*Chlorocebus pygerythrus hilgerti*) and northern yellow baboons (*Papio cynocephalus ibeanus*). Although the annual road accident causalities vary from year to year, road related mortality has affected up to 5% of the local populations. The aim of this study was to describe the spatial patterns of primate vehicle collision through the identification of collision hotspots. The ultimate objectives being to 1) inform an effective evidence-based mitigation strategy and 2) produce a predictive model for primate vehicle collisions that can be applied to a wider ecological context. Based on the existing literature several preliminary hypotheses were determined.

1.7 Hypotheses

1.7.1 Non-random distribution

Firstly, I hypothesised that patterns of primate vehicle collisions would be non-randomly distributed in both space and time. Clustering would ultimately be determined by a combination of local and global factors. Global factor acting along the entire road stretch while local factors only influencing the concentration of collisions at certain points along the road (Figure 1) (Bíl *et al.* 2019). The global factors I choose to test were; species, traffic volume (using annual bed-nights as a proxy) and primate population size. While the local factors considered were the proximity to a curve/junctions and speedbumps.

Figure 1. Global factors act along the entire road, while local factors act at spatially distinct points along the road thereby causing the clustering of collisions



1.7.2 Global factors

1.7.2.1 Species

Previous studies have shown that not all taxa are equally affected by vehicle collisions (Teixeira *et al.* 2013). This is because certain characteristics predispose wildlife to higher or lower risk of collisions (van Langevelde and Jaarsma 2003). Indeed, nocturnal, small bodied and highly motile species tend to be disproportionately affected (Clevenger *et al.* 2003). Moreover, as reviewed in section 1.5, different primate species have been documented to respond to linear infrastructure in different ways which can either increase or reduced their exposure to road related risks. As a result, I wanted to test whether the relative risk of collision involvement was equal across the four species. Moreover, I wanted to ascertain the level of interspecific spatial similarity of the hotspot patterns to see if the spatial pattern of one species' collisions could be used to plan mitigation measures for the other species.

1.7.2.2 Traffic Volume

There is an intuitive relationship between traffic volume and collisions; increases in traffic volumes being directly related to a raised risk of accident. This relationship has been confirmed from observations in the field (e.g. Inbar and Mayer 1999, Joyce and Maloney 2001, Saeki and Macdonald 2003, Seiler 2003) as well as through modelling approaches (e.g. Poch and Mannering 1996, van Langevelde and Jaarsma 2003). Indeed, van Langevelde and

Jaarsma (2003), developed a model in for estimating the 'traversability' of roads and found traffic volume was the most influential parameter on the success of road-crossing. Traffic volume data is usually gathered using traffic sensors placed on along sections of road for a determined period, from which daily, monthly or annual traffic volumes can be extrapolated (e.g_Bisonette and Kassar 2008). However, no such data has been collected in Diani. Given the absence of exact traffic data, I chose to use hotel bed-nights as a proxy.

There is a direct association between tourism and land transport activities, as in most cases roads provide the main means of access to, and around tourist destinations (Saenz-de-Miera and Rosselló 2012). Previously, tourist arrivals have been shown to be a key determinant of traffic parameters including volume, flow, congestion and even human road-related mortality (Rosselló and Saenz-de-Miera 2011, Saenz-de-Miera and Rosselló 2012, Zdravko and Grzinic 2019). The aforementioned studies provide robust grounds to justify the use of bed-nights as a substitute for traffic volume.

1.7.2.3 Population size

It is widely acknowledged that roadkill occurrence is a density dependent phenomenon with many studies finding a significant positive correlation between abundance and roadkill (e.g. Seiler 2003, Guter *et al*. 2005,). In fact, various authors have used roadkill surveys to estimate population size in lieu of traditional capture- mark- recapture methods (Rolley and Lehamn 1992, Mallick *et al.* 1998, Baker *et al.* 2004). I therefore hypothesised that collision frequency would vary in relation to the respective population size of each species.

1.7.3 Local factors:

1.7.3.1 Curves and Junctions

Various studies have considered the impact of road geometry on collision occurrence and subsequently identified a positive spatial correlation between road sinuosity or intersections and road traffic accidents (Lee *et al.* 2004, Klöcker *et al.*2006) A greater number of incidents in the vicinity of curves and junctions is probably a result of the driver's and wildlife's shortened sight and subsequent reduced reaction time to avoid a collision (Lee *et al.* 2004, Klöcker *et al.*2006) . Moreover, drivers may be more hesitant to avoid oncoming wildlife as there is less opportunity to swerve and doing so could compromise their own safety or that of their passengers (Ramp *et al.* 2005). As a result, I predict that the density of primate vehicle collision should increase near such road features, namely curves and junctions.

1.7.3.2 Speedbumps

Much like traffic volume, traffic speed is known to have a significant effect on vehicle collisions (Seiler 2003, Danks and Porter 2010). In response to the hazard posed by speeding, road practitioners have produced a variety of traffic calming devices to ensure the compliance of drivers to speed limits (Huang and Cynecki 2000). Speed bumps are one of the most common and cost-effective means on controlling traffic speed by using vertical deflection to improve safety conditions. Although speedbumps have been shown to have side benefit of reducing wildlife vehicle accidents their primary intent is usually to reduce human-vehicle or vehicle-vehicle collisions (Huijser and Kociolek 2008 , Lav *et al.* 2018). As a result, their placement is usually determined by areas that are hazardous to vehicles or pedestrians, not necessarily animals. I wanted to investigate; firstly, whether speedbumps were an effective means of reducing primate vehicle collisions and secondly, whether prior to their instalment speedbump locations were disproportionately "risky".

2. Methods

2.1 Study site

Data was collected along a 10 km stretch of Diani beach road between Southern Palms Beach resort (−4.267569°, 39.595537°) and KFI Supermarket (-4.342196°, 39.563738°). The road runs parallel to the Indian Ocean, bisecting Diani forest, which is one of the last remaining patches of East African Coral Rag Forest and has been designated as a biodiversity hotspot (Myers *et al.* 2000, Katsis *et al.* 2018). The remnant forest is a mosaic of primary habitat interspersed with degraded patches dominated by human activities, namely tourism and agriculture (Dunham 2016). Despite its ecological significance, Diani forest does not benefit from any formal protection but is divided into numerous private lots. The road, which has played a pivotal role in this landscape's modification, is surfaced by tarmac and is 6 m wide with variable road verge widths between 0 and 3 m. The habitat adjacent to the road varies greatly reflecting the high degree of fragmentation and human disturbance. Existing mitigation includes over 30 canopy bridges ("colobridges"), 8 Speedbumps and speed signs. The designated speed limit is 50 Km/h for the entire stretch.

2.2 Study Species

2.2.1 Angolan black and white colobus *(Colobus angolensis palliatus)*

Angola colobus *(Colobus angolensis)* are long tailed, medium sized, sexually dimorphic (females: 7.1 kg, males: 8.9 kg) monkeys. The subspecies, *Colobus angolensis palliates*, is distributed across the now patchy coastal forests of Southern Kenya and Tanzania (De Jong and Butynski 2012). Whilst *Colobus angolensis* typically live in groups of 2 to 20 members throughout their pan-African range, the average group size in Diani is just 6 individuals (Anderson *et al*. 2007, Dunham 2013). Groups are usually composed of one or two adult males, multiple females and their immature offspring. They are highly arboreal spending over 90% of their time in the canopy or sub-canopy (Wijtten *et al.* 2012). Much of their reliance on forested habitats can be attributed to their diet which is roughly composed of 70% leafy matter (Dunham 2011). Colobines possess a complex multi-chambered stomach that harbour multiple symbiotic microbes. Their highly specialized digestive system enables them to convert primary plant compounds into readily digestible material. This digestive fermentation along with detoxification is energetically demanding and as a result colobus monkeys have adopted a relatively sedentary lifestyle (Dunham 2011, Dunham and Lambert 2016). The daily path length for groups in the area ranged between 330m to 600m, and their home range from 3.38 ha to 5.17 ha (Santarsieri unpublished).

2.2.2 Hilgert's vervet monkey *(Chlorocebus pygerythrus hilgerti)*

Vervets *(Chlorocesbus ssp.)* are matrilineal, medium sized (3.8- 5.6 kg) cercopithecines. They are widely distributed across East and Southern Africa where they mainly occupy open canopy forests (De Jong and Butynski 2012). *Chlorocebus pygerythrus hilgerti* form mixed sex groups of philopatric females and immigrant males (Teichroeb *et al.* 2015). Group size typically ranges from 12 to 24 individuals (Saj *et al.* 1999). Vervets are semiterrestrial, spending almost 50% of their time either on the ground or within 5m of the ground (Isbell and Young 1993). In unmodified habitats vervets predominately feed on fruits and invertebrates (Teichroeb *et al.* 2015). However, they exhibit a high degree of a dietary plasticity and will opportunistically exploit anthropogenic food sources in human dominated landscapes like Diani (Saj *et al.* 2001). Their home ranges can be anywhere between 5.2 ha and 24.9 ha and will sometimes overlap with neighbouring intra or interspecific groups and are far more mobile than the colobus with an average daily path length of 1000m (Isbell *et al.* 1990, Donaldson 2017).

2.2.3 Northern Yellow Baboon *(Papio cynocephalus ibeanus)*

The Northern yellow baboon is both the largest (15-20kg) and most terrestrial of the four study species (Altmann *et al.* 1993). Although yellow baboons are distributed across numerous different habitats in Central and East Africa, they are most frequently associated with moderately arid savannah dominated by grass with variable tree cover (Altmann 1974, Johnson *et al.* 2015). They form hierarchical multi-male groups that are composed on average of 51 individuals but can exceed 100 individuals (Post 1978). Unlike chimpanzees or orangutans, baboon groups do not exhibit fission-fusion dynamics; their structure and composition remain fixed (Johnson *et al.* 2015). They are described as “eclectic omnivores”, feeding on a wide variety of food types (Bentley – Conduit 2009). Much like the vervets, their dietary flexibility and terrestrial lifestyle predispose them to pest-like behaviours (Wahungu 1998). Their adaptability means that they readily vary their ranging patterns in relation to resource availability and other environmental conditions (Bronikowski and Altmann 1996). Baboon groups that rely solely on wild resources have an average daily path length of 5.5km while groups in proximity to human settlements with abundant anthropological food resources on average only travel 2-4 km a day (Altmann and Muruthi 1988). Likewise, their home range has been reported to vary from 518ha to 2409 ha depending on the ecological context (Altmann *et al.* 1993, Johnson *et al.* 2015).

2.2.4 Zanzibar Sykes Monkey *(Cercopithecus mitis albogularis)*

Like all the other study species *Cercopithecus mitis albogularis* are sexually dimorphic with males weighing 6kg and females 4 kg (Struhsaker and Leland 1979). Their geographical range encompasses forest fragments across coastal Kenya and Zanzibar. Although they form multi-female groups like colobus, their group sizes tend to be larger and range between 4 to 65 individuals (Foerester 2009). Sykes monkeys have a predominantly arboreal lifestyle spending most of their time in the canopy and subcanopy, occasionally feeding on the ground (Butynski 1990). However, in heavily fragmented landscapes such as Diani, where there is little continuous canopy, Sykes will travel either using man-made structures such as powerlines and walls or on the ground (Nowak *et al.* 2017, Bull unpublished). They have an omnivorous diet with a marked preference for fruit. Like vervets and baboons in Diani, Sykes are opportunistic foragers and will exhibit pest-like tendencies around humans (Amick unpublished). On average, their home ranges vary from 13.2 to 16 ha, although this can vary depending on how fragmented their territories become due to human disturbances (De Vos and Omar 1971, Struhsaker and Leland 1979).

2.3 Vehicle Collision Data

A total of 696 primate vehicle collisions were recorded from November 2000 to December 2018. Primate vehicle collision incidents are logged by a local NGO, Colobus Conservation that operates a 24-hour emergency response service in the Diani/Ukunda area. A dedicated team responds to call-outs from members of the local community. For every incident a report sheet is raised recording the date, location and species as well as the outcome. 64 reports had specific GPS coordinates, the remaining reports were georeferenced based on the description of the location given. The descriptions referred to recognizable landmarks such a resorts, shops or restaurants. A central GPS point was determined for these landmarks and assigned to the corresponding incidents. In cases where more specific details were provided about the location a separate GPS point was assigned. All the GPS points were collected using a hand-held GPS (Garmin eTrex 30x) and imported to ArcMAP 10.6 for analysis. Six primate vehicle collisions were omitted from the analysis as the information relating to location was absent.

2.4 Variables

2.4.1 Hotel bed-nights

Previous authors have described the relationship between traffic volume and tourist arrivals (e.g. Rosselló Saenz-de-Miera 2012) (see section 1.7.2.2). However, although tourist arrivals provide an insight into the magnitude of temporal immigration they do not account for its duration. Bed-nights are a measure of hotel occupancy that denote the number of guests and duration of their stay (Baron 1984). For example, two guests staying for a week is equal to 14 bed-nights. Annual bed-night data for Kwale County was provided by the Kenya National Bureau of Statistics (2018) from 2010-2018. For the missing years (2000-2009), I used the bed-night count for 2010.

2.4.2 Primate Population

Colobus Conservation carried out an annual census in October from 2004 to 2006 and 2010 to 2018 across Diani. The census area width was between 250–430 m and 400–600 m on the east and west sides of Diani's beach road, respectively. The same census method was adopted for the colobus, Sykes and vervets while an alternative approach was used to survey baboon population. Although different survey designs have been implemented both are presumed to have produced a total count (-/+ 10%) owing to their partial habituation to humans, the visibility conditions of the open habitat and relatively small survey area (Plumptre *et al.* 2013). For the missing years, I estimated the population based on the two closest years, assuming equal intervals of increase or decrease.

2.4.2.1 Colobus, vervet and Sykes counts

For the colobus, Sykes, and vervet counts, two-member teams visited plots on each side road, systematically beginning at the most northerly point of the study area (−4.267569°, 39.595537°). A minimum of four teams carried out east-to-west line transects. Vegetation type and anthropogenic structures (e.g. houses, fences, and walls) determined the choice of transect width. When an individual or a group of monkeys was encountered, the census team moved off the transect to record the GPS coordinates as well as the number of individuals. Once the data was recorded the team resumed their trajectory along transect. The teams walked at a pace of approximately 1–1.5 km/h. A team leader was positioned on the roadside and coordinated the two census teams on either side of the road to ensure they were moving southwards in parallel. The team leader reviewed data in the field and deleted double counts to avoid pseudo replication. The census was completed over the course of three consecutive days. Transects began at 07:00 and ended at 18:00 with a midday break occurring from 12:30 to 14:00 to ensure surveying took place when the animals were most active.

2.4.2.2 Baboon counts

Unlike the methods outlined above the baboon survey followed a non-linear pattern. Teams of two visited all groups in the Census area across a one-week period. The team positioned themselves ahead of the group and waited for all baboons to cross a stationary linear object such as a fence, road or wall. Researchers were no closer than 5m from the focal group and no further than 15 m. As the group crossed the chosen linear structure, one researcher called to a recording individual. The teams conducted the counts for each group three to six times. The mode of these repeated counts was used to determine total counts.

2.4.3 Speedbumps

Eight speedbumps have been installed along Diani beach road at unequal intervals. Their locations were geo-referenced using hand-held GPS (Garmin eTrex 30x) and imported into ArcMap 10.6. Speedbump locations were selected by Kwale district’s Rural Roads Authority (KRA) based on a combination of community requests and road traffic accident records (verbal communication). In 2014, the whole road was resurfaced, and 6 speedbumps were installed. The final two speedbumps were installed in 2018 and therefore omitted from the analysis as they fell outside the study period.

2.4.4 Curves and intersections

Diani beach road is almost entirely linear apart from a single section of the road that has an S-shaped curve. The two points of inflection for the curve were identified using the “curves and lines” add-on in ArcMAP 10.6, their coordinates were (-4.315677, 39.573708) and (-4.320871, 39.573032). Although there are several intersections along Diani beach road, most of them are small dirt roads that do not experience high traffic volumes. As a result, I chose to focus on the main T junction located at -4.290504, 39.585931. This junction is of significance because it connects Diani to Ukunda, which is the largest urban settlement in Kwale district and is where most of Diani’s workforce reside (NEMA 2017). Moreover, the fastest route from Diani to Moi international airport or Mombasa (Kenya’s second largest city) requires vehicle to transit through this junction.

2.5 Analysis

2.5.1 KDE+ Hotspot identification

KDE+ method developed by Bíl *et al.* (2013) was implemented to visualise collision hotspots. This nonparametric approach builds on the traditional Kernel Density Estimate (KDE) method (Chung *et al.* 2011), which estimates the probability density function of the underlying data by using a symmetrical kernel function of a predefined bandwidth, thereby identifying hotspots through an additive process. However, one of the inherent weakness of applying a conventional KDE is that it fails to provide a measure of statistical significance of hotspots (Bíl *et al.* 2013, Bíl *et al.* 2016). KDE+ selects and ranks significant clusters according to strength by objectively determining a threshold through repeated random simulations (Monte Carlo method). Hotspot strength is mainly determined by the number of incidents within the cluster and its length (Bíl *et al.* 2016).

The KDEplus 3.0 ArcMAP toolbox was downloaded and the analysis performed for the whole dataset (Fig. 2) and subsequently repeated for 4-year time brackets. The same approach was used to identify species specific hotspots (Fig. 3). A 100m bandwidth was selected and 800 simulations were used to map the hotspot patterns based on the recommendations made by Bíl *et al.* (2016). In addition to the hotspot maps, the location, length, density, rank and strength of each cluster was recorded.

2.5.2 Hotspot overlap:

Once the KDE+ analysis was performed across the four species and three time brackets, I tested for the similarity between the different hotspot distribution. The hotspots underwent linear referencing and strength (calculated by KDE+) were plotted in R 3.5.3 (Fig. 4 & 5). I then performed pairwise correlation testing using Pearson's correlation which was ultimately used as a means of comparing the resemblance between different hotspot patterns**.**

2.5.3 Model approach

Generalized linear models (GLMs) were implemented to test for correlations between collision occurrences and the explanatory variables using R (version 3.5.3). Both a Poisson and a quasi-Poisson distribution, the latter to correct for the slight over-dispersion in the data. For the global factors (species, annual bed-nights and population count), the model tested their power in determining the collision frequency across the entire length of Diani beach road. Whereas, for the local factors (curves and speedbumps), their power in explaining the higher frequency of collision in certain locations relative to others was measured. To do so, I tested the number of collisions in relation to their proximity to both speedbumps, curves and junctions. As collision locations were only approximations (section 2.3), I chose to divide the road into 100 equal sections. I subsequently measured the distance between each road section and the nearest speedbump and curve or intersection using the 'near' tool in GIS. Meanwhile, the number of collisions in each road section were counted using the 'spatial join' tool. I selected the models with the best fit based on Akaike Information Criteria (AIC) and by systematically removing the variables that did not have a significant effect. As the speedbumps were only installed in 2014, I also tested the explanatory power of the interaction between distance to speedbumps and collisions occurring from 2015 onwards.

3.Results

3.1Universal Hotspots

The KDE+ method identified 14 significant universal hotspots containing 579 (84 %) primate vehicle collisions (Fig. 2). The remaining 111 collisions (16 %) did not fall within clusters. The hotspots account for 38% (3896m) of the total road length. This outcome suggests that almost all primate vehicle collision could be prevented by concentrating mitigation across only percent 38% of total study area. The strongest hotspot (labelled 1 on fig.2) included 56 incidents and was 174m long.

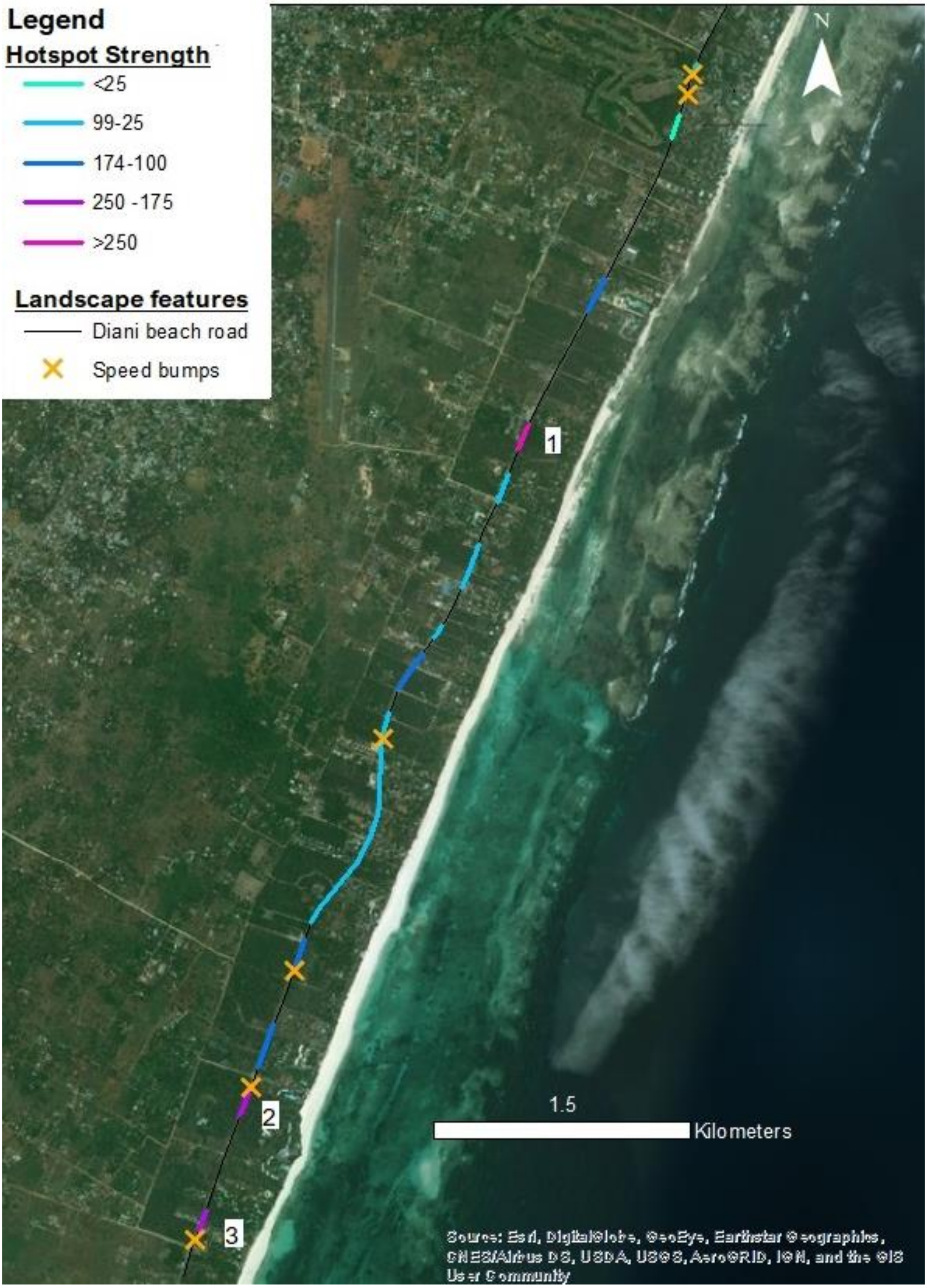


***Figure 2.** Universal collision hotspots calculated with KDE+. The hotspots were colour coded according to Strength*Density^2. Labelled are the three highest ranking hotspots.*

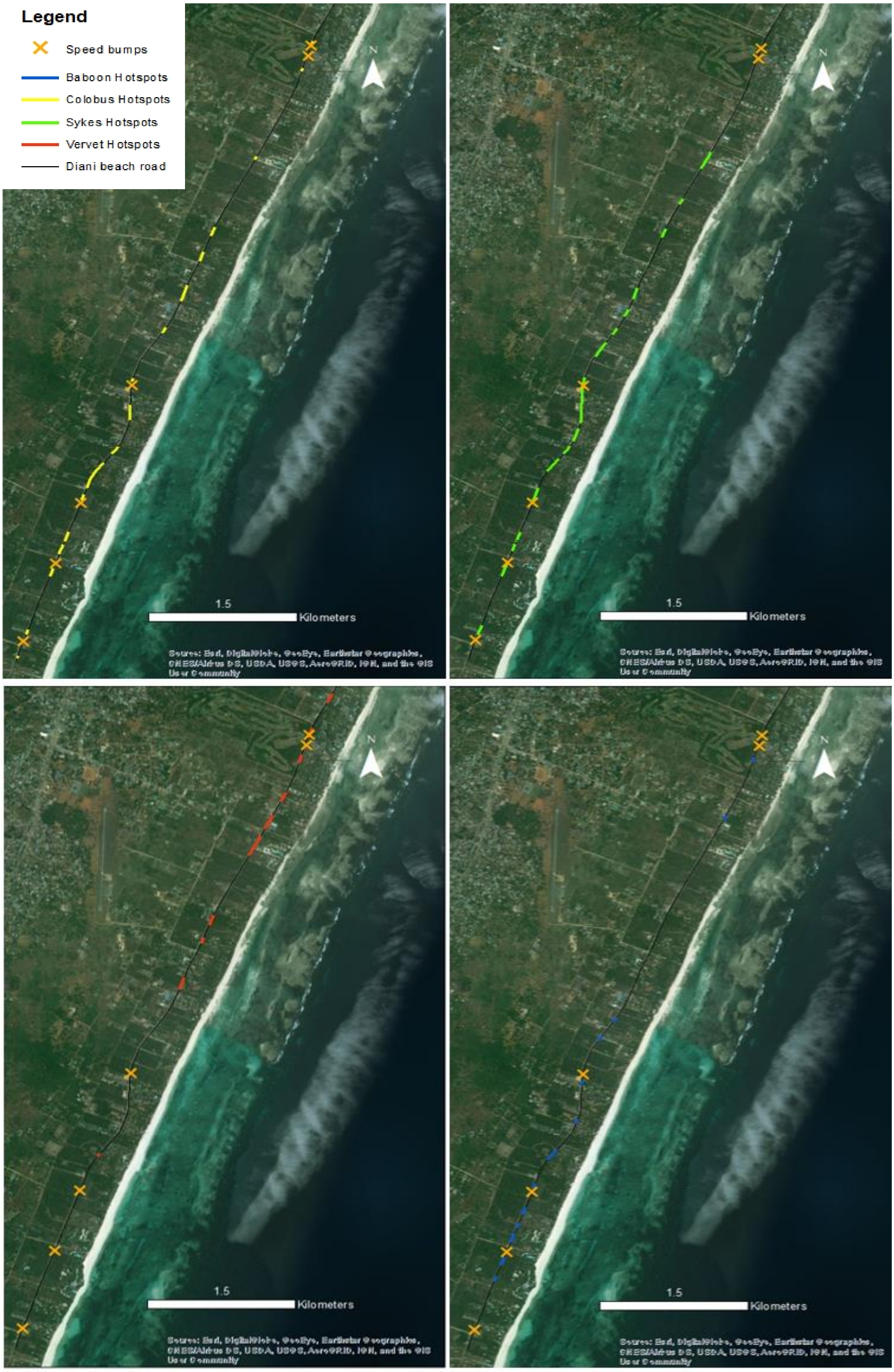


Figure 3. Baboon (blue), colobus (yellow) , Sykes (green) and vervet (red) road-kill hotspots calculated with KDE+

3.2 Species specific Hotspots

A total of 56 species specific hotspots were identified (Figure 3, Table 1). Between 74-84% of incidents were fell within the hotspots demonstrating that primate vehicles collisions were also highly aggregated at even a species level.

Table 1. Summary table of species specific KDE+ analysis

Species	**Number of Clusters**	**Number of points in cluster**	**% of points in cluster**	**Total length of clusters**	**% of road which cluster**
Baboon	13	32	74.4	1065	10.4
Colobus	17	135	81.3	1947	19
Sykes	16	317	84.1	2789	27.2
Vervet	10	86	82.7	1409	13.8

3.3 Hotspot patterns over time

A significant relationship was found between the spatial distribution of hotspots for all three time brackets (Table 2), although the strength of the relationship varied considerably. The strongest correlation was found between 2006-20011 and 2012-2017 (Pearson's coefficient = 0.66) suggesting the highest degree of spatial fidelity between these two periods. Four hotspots have remained stable over the course of the entire study period starting at approximately 3200m, 4500m, 8700m and 9100m (Figure 4).

Table 2. Summary table of Pearson's correlations between hotspot distribution pattern over time

TIME BRACKET 1	**TIME BRACKET 2**	**PEARSON'S CORRELATION COEFFICIENT**	**P-VALUE**
2000-2005	*2006-2011*	0.29	<0.001
2000-2005	*2012-2017*	0.28	<0.001
2006-2011	*2012-2017*	0.66	<0.001

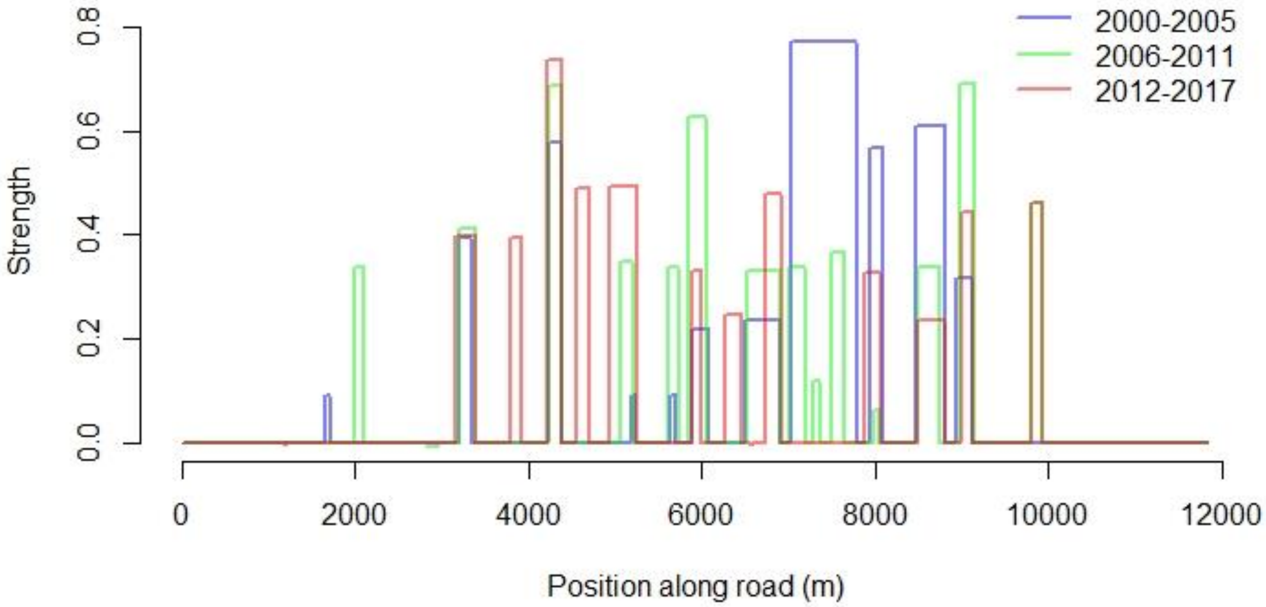


Figure 4. Graph illustrating the evolution of the hotspot distribution over time

3.4 Interspecific hotspot similarities

A degree of overlap was found between all hotspot patterns apart from the baboon and vervets, where no significant correlation was found ($p > 0.05$). Interesting, both the strongest hotspot for the baboons and colobus as well as for the Sykes and vervet overlapped demonstrating that the most high-risk areas were universal. The highest degree of similarity was between Sykes and vervet (Pearson's coefficient = 0.45) and the Sykes and colobus (Pearson's coefficient =0.44) hotspot patterns. Overall the baboon hotspot distribution was the most dissimilar to all other species (table 2).

Table 2. Summary table of Pearson's correlations between species hotspot distribution patterns

Species 1	**Species 2**	**Pearson's correlation coefficient**	**P-value**
Baboon	*Colobus*	0.28	<0.001
Baboon	*Sykes*	0.27	<0.001
Baboon	*Vervet*	-0.03	>0.05
Colobus	*Sykes*	0.44	<0.001
Colobus	*Vervet*	0.30	<0.001
Sykes	*Vervet*	0.45	<0.001

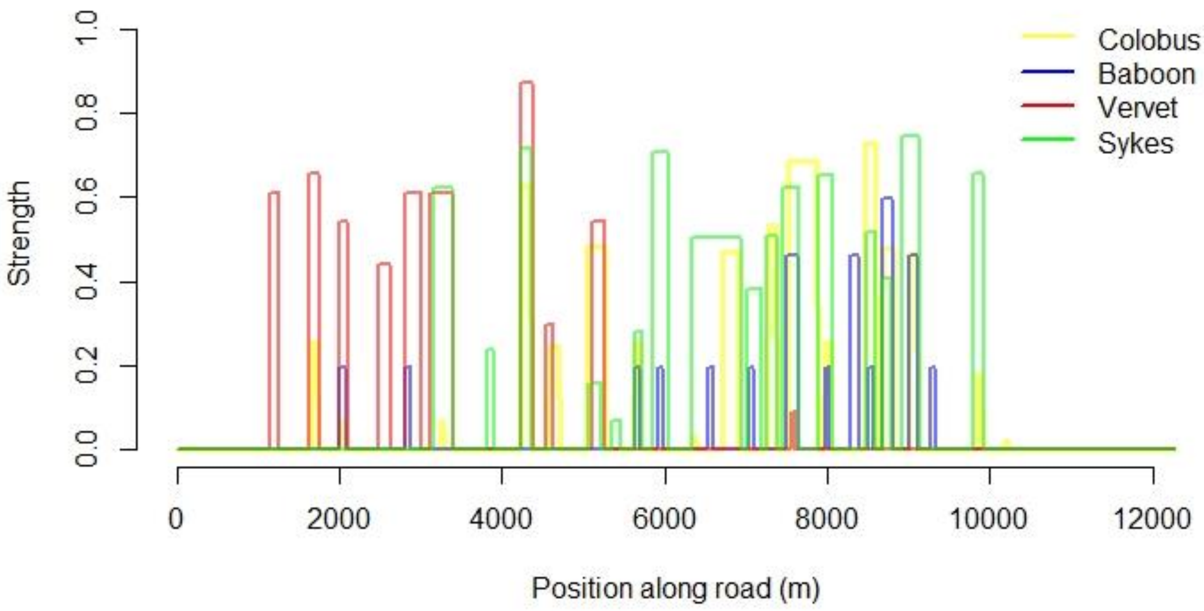


Figure 5. Graph illustrating the extent of interspecific hotspot similarity.

3.5 Model

Model selection indicated that species was a key determinant of collision frequency (p<0.001) (Table 5). Meanwhile, the other two global factors; population size (t=0.09, p= 0.37) and bed-nights(t=-0.40, p=0.69) did not have a significant effect on collision frequency and were therefore excluded from the final model. The distance to curve (t= -3.70, p<0.001) and distance to speedbump* Post 2014(t=2.41, p<0.05) were also significant determinants of collision locations (see Table 1). Interestingly, the results indicate that speedbump locations were positively correlated to higher collision frequencies prior to 2015 when interventions were installed (estimate =3.636e-04, p <0.001).

Model	Species	Bed-nights	Primate Population	Distance to curve	Distance to speedbump	Post 2014	Speedbump x2014	AIC	ΔAICc
1	+	+	+	+	+	+	+	6916	2992
2	+			+	+	+	+	4986	362
3	+			+			+	4640	16
4	+			+	+		+	4624	0
5	+				+		+	4644	20
6	+							4660	36
7				+				4986	62

Table 4. Akaike's Information Criterion (AIC) and ΔAICc Top 7 Candidate models based on AIC for primate vehicle collision frequency fitted to a Poisson distribution. For each model '+' shows whether the specific parameter is included into the model

This suggests that although speedbumps are designed to reduce pedestrian or vehicle crashes, they were also placed in areas prone to higher rates of primate vehicle collisions. The most parsimonious model (AIC =4624) included species, proximity to curves, proximity to speedbump* post 2014, all other variables were omitted.

Table 5. Parameter estimates and test statistics from for all the variables tested using a quasi-Poisson distribution

Parameter	Estimate	SE	T-Value	Lower 95% CI	Upper 95% CI	Significance
Species						
Colobus	1.346e+00	2.866e-01	6.21	2.56	5.82	P<0.001
Sykes	2.148e+00	3.138e-01	6.84	5.96	12.90	P<0.001
Vervet	8.811e-01	2.233e-01	3.95	1.57	3.98	P<0.001
Bed-nights	-1.001e-07	2.515e-07	-0.40	1	1	P=0.69
Population	4.296e-05	4.562e-04	0.09	1	1	P=0.37
Year > 2014	-1.697e-01	1.874e-01	-0.91	0.58	1.22	P<0.001
Proximity to curve	-2.378e-04	6.426e-05	-3.70	1	1	P<0.001
Proximity to Speed bump	-3.636e-04	1.023e-04	-3.56	1	1	P<0.001
Year>2014*Speed bump	4.762e-04	1.973e-04	2.41	1	1	P<0.05

4.Discussion

Using the KDE+ method, primate vehicle collision hotspots were identified. The results of the hotspot analysis support the hypothesis that primate vehicle collisions tend to be clustered, with a large majority of all incidents located within hotspots. Although the distribution of clusters evolved over time, a strong correlation (Pearson's coefficient =0.66) was found between the 2006-11 and 2012-2017 distributions, suggesting hotspot locations have remained more or less fixed over the last 10 years. I believe that changes in hotspot positions from 2006-2011 can be attributed to the rapid landscape modifications during this period which was predominantly precipitated by a boom in tourism across Kenya from 2003(Mwanguni *et al*. 2017). These anthropogenic habitat changes altered the distributions of primates in Diani and consequently their road-crossing routes. In late 2013 the tourist industry hits a dip, from there onwards tourist arrival patterns fluctuate and investment wanes (Mwanguni *et al*. 2017). As result, fewer big structural changes took place between 2012-2017 and the distributions of primate groups stabilise as do their hotspot patterns. These temporal patterns demonstrate that a combination a of permanent (e.g. speed bumps) and semi-permanent (e.g. 'colobridges', see section 2.1) mitigation would produce the best collision prevention strategy, using semi-permanent structures to tackle dynamic hotspots and permanent interventions for established ones.

As predicted, hotspots exhibited species specificity, with each species producing a unique hotspot distribution pattern. However, whilst no two species collision patterns were the same, most were at least loosely correlated, demonstrating that some road sections were universally hazardous. Interestingly, my results seem to reflect previous work on the sympatric associations of these four primates in Diani. Moreno- Black and Maples (1977) reported frequent colobus- Sykes and Sykes-vervet associations in Diani, noting predominantly passive or neutral interactions between the two. Consequently, the resemblance in their collision patterns could merely be the product of similar spatial occupancy. Likewise, the same study did not observe a single association between baboons and vervets over the course of the 6-month study period, mirroring the lack of correlation between their hotspot patterns. Ultimately, the low level of likeness between baboon hotspots and the other species illustrates their ecological differences.

Indeed, my model demonstrated that baboons were at a significantly lower risk of collision than the other species. This finding can be attributed to numerous factors. Firstly, baboons have been observed to exhibit social vigilance in relation to roads, demonstrating an increased ability to perceive and avoid traffic related risks (Hall 1960, Amick unpublished). Part of the reason they possess a heightened awareness to linear infrastructure is because they are adapted to terrestrial movement and by extension, the evasion of ground predation (Cowlishaw 1994, Amick unpublished). In addition, being large-bodied renders them more conspicuous to drivers and therefore easier to avoid. Not to mention, their size provides an additional incentive for vehicles to avoid them as they could incur significant damage upon collision.

The colobus and Sykes were the two most vulnerable species to traffic related mortality. Again, this can be ,in part, attributed to their body size, as smaller objects are generally harder to detect from a moving vehicle (Barthemless and Brooks 2010). Moreover, these results are consistent with those of Amick (unpublished), demonstrating the two species have strikingly similar road-crossing behaviour. Both species exhibited low levels of traffic vigilance and were seldom observed to abort crossing attempts, even under risky circumstances (i.e. when a vehicle is approaching). The higher risk of collision in Sykes (exp(estimate) = 8.77) than in colobus (exp(estimate) = 3.86), is likely a product of their larger home ranges (see section 2.2.4) resulting in more frequent road encounters and therefore a greater exposure to road related risks.

Contrary to my predictions neither of the other two global factors (traffic volume and population size) had a significant effect on the frequency of primate vehicle collisions and were therefore excluded from the final model. Although an apparent the relationship exists between traffic volume and collisions, it should be acknowledged that increases in volume can affect other traffic parameters such a flow and speed (Davis 1998). An increase in the number of vehicles on the road often results in a reduction in speed owing to congestion (Davis 1998). Speed is another factor that has been closely linked traffic accidents (Seiler 2005, Danks and Porter 2010). So, whilst tourist arrivals may increase vehicle volume, the simultaneous decreases in traffic speed could explain why there was no appreciable difference primate vehicle collision frequency.

Furthermore, although tourist numbers may broadly determine traffic volume, bed-nights fail to capture the how the composition of the vehicle fleet has evolved over time. Owing to the privatized nature of the public transport sector in Kenya, vehicle sizes and passenger capacities vary greatly (Ogot *et al.* 2018). For example, matatus, public minibuses that carry between 10-14 passengers, were once ubiquitous up and down the coast. However, from January 2011, a directive was issued by the government phasing out 14 seaters; this combined with heighten securities threats in relation to terrorism warnings, prompted a marked shift towards smaller capacity operators (e.g. tuk-tuks and motorbikes) Ommeh *et al*. 2015). Although the demand remained fixed, as the number of passengers stayed the same, there was still a net increase in vehicle volume owing to changes in the average vehicle size (Ogot *et al.* 2018). It is therefore plausible, that hotel bed-nights are not an appropriate proxy for vehicle volume as they cannot reflect the structural changes in transport sector.

Likewise, primate abundance did not have significant impact on the occurrence of primate vehicle collisions. Caution should be taken interpreting this result as population sizes did not vary significantly throughout the study period. Moreover, a limitation of this study was that it failed to consider relative abundance or distribution of individuals across the study site which could have provided a more complete picture of how local primate densities affect collision patterns.

In accordance with my predictions, proximity to curves and junctions were positively correlated to high local collision densities. This was an expected result given that many of collision hotspots highlighted by the KDE+ were in the vicinity of these road features (Figure 2/3). As previously stated, intersections and sinuous road sections provide the drivers and primates with a much shorter response time to avoid collision and therefore represent particularly hazardous road sections (section 1.7.3.1). Furthermore, when considering the universal hotspot distribution, the high-risk zone extends for some distance after leaving the actual points of inflection. The extended influence of the curve can be explained by the tendency of vehicles to accelerate after a curve thereby creating a short stretch of road predisposed to speeding and hazardous driving.

Local collision frequencies decreased with proximity to speed bumps thereby confirming that they are an effective means of mitigation. The results of the GLM also demonstrated that prior to the installation of the speed bumps, their locations were positively correlated with collision occurrence. As speed bumps were installed in relation to human traffic accident reports, this shows that the incidence of primate vehicle collisions and human vehicle collisions are closely interconnected. This finding is significant because it provides an additional impetus to persuade decision makers a governmental level to install speed bumps at primate hotspot location, as they will most likely provide concurrent benefit to human road safety. Moreover, this finding also supports the hypothesis that speed is an important determinant in vehicle collisions along Diani beach road.

5. Implications for mitigation

The adoption of hot-spots analysis enables practitioners to focus their limited resources in micro-places where collisions are concentrated. the KDE+ method is a particularly advantageous hotspot approach as not only does it provide a method of visualising high-risk areas but also a means of comparing relative risk along the road. Consequently, KDE+ results can be used to systematically prioritise locations for the placement of interventions in Diani based on an objectively determined strength parameter. Combined with the results of the GLM, I have come up with a set of specific recommendations for the deployment of mitigation along Diani beach road to reduce the occurrence of primate vehicle collisions.

An obvious starting point is the placement of mitigation, such as speedbumps, in areas with the highest universal relative risk. Figure 2 indicates the 3 strongest universal hotspots; these three hotspots are comprised of 20 % of the collisions and just 5% of the total road length. B installing speed bumps along these sections of road a significant reduction in collisions is to be expected. Moreover, the temporal analysis revealed that the strongest universal hotspot has remained fixed over the entire study period and is, in fact, increasing in strength suggesting this location is the best candidate for permanent mitigation.

Another area that needs to be taken into consideration for a multi-species approach is accidents along the curve. The model results found a strong correlation between the proximity to a curve and collisions occurrence. Moreover, although the hotspot along the curve was not one the strongest according to the KDE+ analysis it was still identified as significant and was comprised of the largest number of collisions (n=175). The main reason for which this hotspot did not rank as strongly is that the collisions were spread across the entire curve rather than being concentrated at a single position.

Previous research has demonstrated that area of influence for speed bumps is limited to ~130 m on roads with a speed limit of 50km/h (Ziolkowski 2014). This makes them an appropriate intervention for tackling the smaller hotspots (<200m) but not as effective for dealing with larger road sections such the curve which is 1495m long. As a result, an alternative means of mitigation is needed to manage collisions along the curve. The use of fencing in conjunction with overpasses has been used effectively to reduce wildlife vehicle collisions where the relative risk is spread across a large area. In some cases, the number of local collisions was reduced by at least 80% (Clevenger *et al*. 2001). However, this approach has only been successful in relation to large ungulates such as deer and elk. Give the climbing ability of primates, the design and implementation of fencing and over passes would need considerable investigation to ensure the right results were obtained.

6. Conclusions

This study confirms that primate vehicle collisions are not evenly distributed in space but are aggregated into collision hotspots. The KDE+ method was used to visualise and rank high-risk road sections thereby providing a basis upon which mitigation resources can be allocated. Although the hotspot patterns did change over time the most significant hotspots remained fixed, suggesting that complimentary permanent and semi-permanent interventions would produce the best results. The hotspot clustering exhibited species specific patterns, probably owing to intrinsic biological differences. However, further analysis of the revealed some areas of overlap indicating universally hazardous zones that should therefore be prioritised for mitigation.

To gain a better understanding of variables responsible for creating the distribution of collisions a generalized linear model was used. The results of the model demonstrated that neither vehicle volume (using bed-nights as a proxy) nor primate abundance were powerful explanatory factors for the frequency of collisions. However, the GLM did reveal that species were unequally affected by road related mortality. Sykes and Colobus were found to be particularly vulnerable, possibly owing to their lack of traffic vigilance stemming from their maladaptation to gauging terrestrial threats. Meanwhile the proximity to curves, intersections or speedbumps were found to be significant local factors demonstrating the road features and geometry are important determinants of primate vehicle collisions.

To the best of my knowledge, this is the first study to examine primate vehicle collision patterns and evaluate the combination of global and local factors responsible for producing them. While a variety of other variables, such as habitat type, speed and topography still need to be investigated, this project represents an initial understanding of an under researched area of primate conservation.

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