Impact, evaluation, and mitigation of linear infrastructure development on primates in Diani, Kenya

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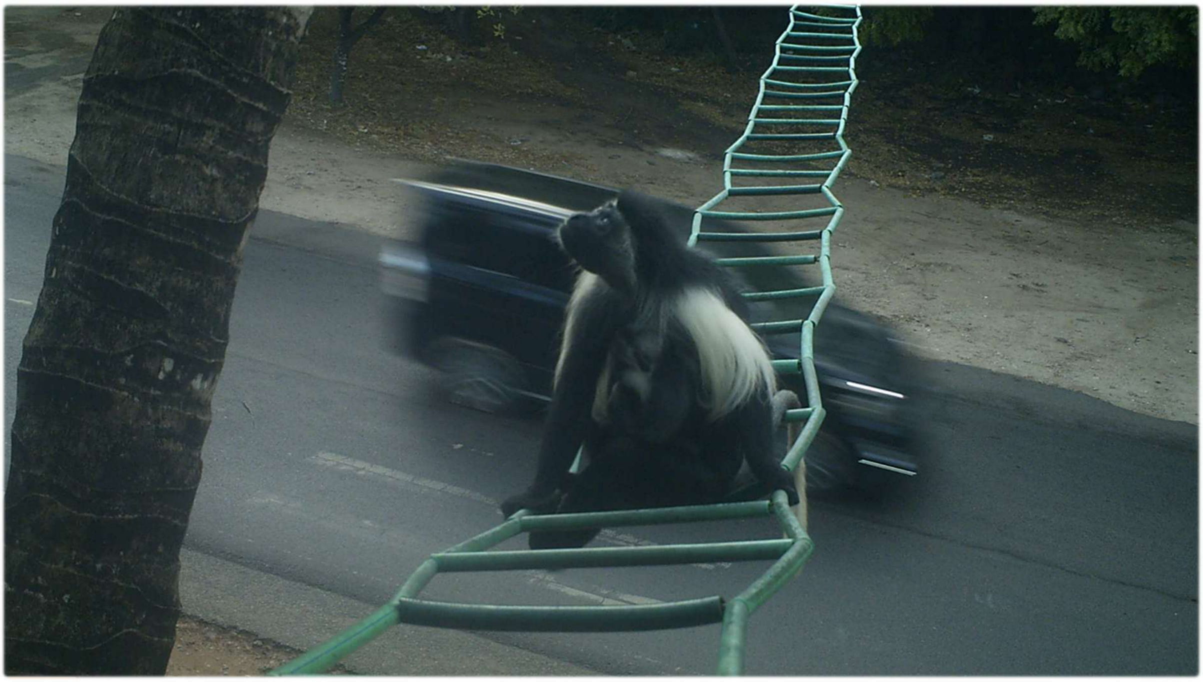

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As I conclude more than twenty years of research, I am reminded that this achievement is not just my own, but a reflection of the collective effort and support of all those who have walked alongside me.

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Author's declaration

Pamela May Karen Cunneyworth (P.M.K.C.) wrote chapters 1–5 & 7, and Appendix II, with significant input into Chapter 6, as described below. Chapters 2, 5 & 6 were published in the International Journal of Primatology, Chapter 3 was published in the Special Issue on Canopy Bridges, Folia Primatologica, and Chapter 4 was published in the American Journal of Primatology. P.M.K.C. conceived all analytical chapters. For Chapters 2–6, P.M.K.C. developed data collection and data curation methods resulting from the animal welfare response team, primate census, and canopy bridge surveys. P.M.K.C. also collected aspects of each dataset. Chapters 2–6 include collaborations with researchers outside of the supervisory team. Co-authors are listed for the relevant chapters below. Chapters 1 & 7, and Appendix II include editorial reviews made by PhD supervisors Dr. J.E. Bicknell and Dr. T. Humle.

Chapter 2. P.M.K.C. performed the analyses and wrote the publication. Joshua Duke wrote the first draft as a BSc (Hons) thesis, Zoology, Anglia Ruskin University with P.M.K.C. as a supervisor for the thesis and provided editorial feedback on the final draft for publication.

Chapter 3. P.M.K.C. performed the data analyses and wrote the publication with Andrea Donaldson and Fredrick Onyancha providing editorial feedback. Each author was responsible for organising and training the data collection teams for one of the three surveys.

Chapter 4. P.M.K.C., Richard Andrášik and Michal Bíl performed the data analyses jointly. P.M.K.C. wrote the article for publication with R.A. and M.B. providing editorial feedback.

Chapter 5. P.M.K.C. performed the data analyses and wrote the publication. Alice May Slade wrote the first draft as a MSc thesis, School of Veterinary Sciences, University of Bristol with P.M.K.C. as a supervisor for the thesis. A.M.S. provided editorial feedback on the final draft for publication.

Chapter 6. Lydia Katsis performed the data analyses and wrote the first draft as a MSc thesis, School of Veterinary Sciences, University of Bristol with P.M.K.C. as a supervisor for the thesis. As noted above, P.M.K.C. conceptualised the project, developed the methodologies for data collection and curated the various datasets used for analysis. P.M.K.C. also provided direction for the writing and editorial feedback on the final draft for the publication.

Abstract

Roads and electrical infrastructure are essential for achieving the United Nations Sustainable Development Goals. Twenty-five million kilometres of new roads are expected to be built globally by 2050, and governments are targeting universal access to electricity. However, linear infrastructure is known to have devasting impacts on wildlife including a wide range of non-human primates. Yet, the effects and the complex interactions between these various impacts are often overlooked, particularly in urban environments. This thesis examines the effects of roads and power lines on six primate species in Diani, a town in southeastern Kenya where development is interspersed with forest patches of a Global Biodiversity Hotspot. The research draws on 25 years of data on primate populations and cases of injury and death, collected by Colobus Conservation, a local conservation organisation. The data show that colobus monkeys suffer significant losses, with approximately 8% of the population affected annually due to vehicle collisions and electrocutions. Sykes' monkeys, vervets, and baboons experience sustainable losses (3.3%, 2.0%, and 1.8%, respectively), but these still represent over 1,000 individuals reported injured or killed since the organisation's inception in 1997. The impact on two species of galagos remains uncertain. This study highlights key ecological factors that influence species' vulnerability to roads and power lines, with arboreal species at higher risk on roads than more terrestrial species and larger individuals of arboreal species are at higher risk on power lines. The efficacy of canopy bridges in mitigating the road barrier effect and primate-vehicle collisions was assessed and shown to be successful and cost-effective overall. In addition, this research highlights that a commonly used approach to quantify the number of wildlife-vehicle collisions and electrocutions–carcass surveys–underestimate the true scale, because injured individuals who survive the initial impact make up a significant proportion of total collisions. This thesis found that correction factors of 1.5 for vehicle collisions and 2.15 for electrocutions are needed to improve carcass survey estimates. Regarding power lines, Diani's growth has not led to an increase in electrocution cases, indicating that the mitigation strategies of trimming vegetation near power lines and insulating cables are effective. Overall, this thesis calls for the protection of wildlife to be explicitly considered in road and electricity infrastructure planning by using the findings of this and previous research.

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Chapter 1. Introduction

1.1 Biodiversity in crisis

The decline of global biodiversity over the past few centuries and particularly in recent decades, is regarded as Earth's sixth mass extinction event (Ceballos et al., 2017). This event reflects humanity's global impact on the Earth, leading to the term "Anthropocene" to represent the current geological epoch (Crutzen & Stoermer, 2021). It is characterised by widespread records of species' range contractions, with 30% of described species at risk of extinction (IUCN Red List of Threatened Species, 2024). The current extinction rate is considered at least 1,000 times higher than the natural background rate (Pimm et al., 2014), and the situation is worsened by mass mortality events across a broad range of animal taxa. Between 1940 and 2010, at least 727 such events have affected 2407 populations (Fey et al., 2015). But because population losses can remove entire trophic levels, examples of cascading effects causing ecosystem disruption and decline are increasingly reported (Tye et al., 2024). Even species listed as Least Concern on the IUCN Red List of Threatened Species (hereafter referred to as the IUCN Red List) are experiencing significant population losses (Ceballos et al., 2017), and in just the 50 years between 1970 and 2018, there has been a staggering 69% decline of the relative abundance of monitored species globally (WWF, 2022).

Declines are observed across taxa (Pimm et al., 2014), with losses in forest-dependent species primarily driven by tree-cover reduction of almost 30 million hectares annually (Garcia et al., 2020). While protected areas contribute to biodiversity conservation, it is unlikely that they can mitigate these losses (Pimm et al., 2014; Strier & Ives, 2024) in the face of ongoing 'biological annihilation' (Ceballos et al., 2017, p. 1). Given these dire warnings, in 2010, the Parties for the Convention on Biological Diversity (CBD) agreed to the Aichi Targets to safeguard biodiversity but none of those targets were achieved in full by their 2020 deadline (Vaughan, 2020). However, in July 2022, the United Nations (UN) General Assembly adopted a landmark resolution, recognising the human right to a clean, healthy, and sustainable environment (United Nations General Assembly, 2022) and later that year, the CBD introduced the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022), which notably, aims to protect at least 30% of the world's land, inland water areas, and marine and coastal areas by 2030.

1.2 Linear infrastructure as the foundation to social and economic growth

Linear infrastructure are developments that extend along continuous, often long routes across landscapes. These types of developments are diverse including roads, power generation and distribution infrastructure, railways, pipelines, telecommunication lines, canals, high-speed rail networks, and shipping lanes. They play a major role in human development. In pursuit of the UN Sustainable Development Goals (SDGs), priority is placed on two types of linear infrastructure–road (SDG 9A) and power generation and distribution (SDG 7). SDG 9A emphasises the importance of ‘Industry, Innovation, and Infrastructure’ in fostering economic growth (United Nations, 2015b). The World Bank's substantial investment in road infrastructure surpasses funding allocated to education, health, and social services combined (Berg et al., 2015). This investment has resulted in the construction of approximately 260,000 km of roads globally between 2002 and 2015 (Berg et al., 2015) with a staggering additional 25 million km expected by 2050 (International Energy Agency, 2013; Laurance et al., 2014). For power generation and distribution, SDG 7 specifically addresses energy issues with that goal titled 'Access to Affordable, Reliable, Sustainable, and Modern Energy for All' (United Nations, 2015a). This goal highlights the critical role of electrical infrastructure for addressing poverty, improving human health, and promoting economic growth.

The social and economic implications of linear infrastructure have been recognised for over a century (Estevadeordal et al., 2003; Tuttle et al., 2016). However, as early as the 1930s, warnings started to emerge that road infrastructure was detrimental to wildlife (Simmons, 1938), and in the 1970s, similar warnings arose regarding power lines (Schreiber & Graves, 1977). While significant gaps exist in our knowledge on how linear infrastructure affects biodiversity and ecosystems, there is sufficient scientific evidence demonstrating that these types of developments pose a much more substantial threat to wildlife than the early authors foresaw.

1.3 Assessing wildlife risk from linear infrastructure, with a focus on primates

Linear infrastructure is now recognised as one of top ten threats to global biodiversity (Maxwell et al., 2016) with a variety of impacts on wildlife, of which most are considered negative (Fahrig & Rytwinski, 2009; Galea & Humle, 2022). For example, the most obvious impact of roads and power distribution infrastructure are wildlife deaths resulting from vehicle collisions and electrocutions[1], respectively. Other important but less obvious impacts include the barrier effect where the presence of roads and power lines act to restrict to varying degrees, the movement of animals (Jaeger et al., 2005; Jaeger & Fahrig, 2004). However, at the landscape level, the presence of these types of linear infrastructure can result in significant habitat loss and fragmentation (Botting et al., 2023; Dániel-Ferreira et al., 2020; Estrada et al., 2017; Hewavithana et al., 2023; Mullu, 2016), contributing to destabilising ecosystem integrity (Trombulak & Frissell, 2000).

To understand the risks of linear infrastructure to wildlife, some studies have aimed to assess taxon or species-specific responses (Caceres, 2011; Dwyer et al., 2014; González-Suárez et al., 2018). One approach to do so is to identify the road-effect zone by determining the distance away from roads over which species' density decreases (Forman et al., 1997; Forman & Alexander, 1998; Forman & Deblinger, 2000). Species attributes that contribute to the road-effect zone include species' body size, diet, attraction to roads, and their ability to avoid vehicles if they cross roads (Benítez-López et al., 2010; Bennett et al., 2017; de Jonge et al., 2022; Fahrig & Rytwinski, 2009). Given these attributes, the authors conclude that for roads, amphibians, reptiles, some birds, and large mammals are likely to

[1] Electric shock denotes contact with an electrical current which can lead to non-fatal injuries while electrocution is death caused by the electric shock. In this thesis, the term electrocution is used as the collective term for both electric shock and electrocution cases, except where the distinction is made explicitly.

be negatively impacted, while small mammals and vultures are likely to be positively affected or unaffected.

Similarly, the morphological, behavioural, and ecological attributes associated with electrocutions of birds are relatively well-documented (APLIC, 2006). Bird electrocution risks are linked to species range relative to power line density and wing length (Biasotto et al., 2022). Larger birds, like eagles and vultures, are at greater risk due to their wingspans bridging power cables and hardware when perched on poles, causing short-circuits (Montijo, 2023). In addition, some species have specific behaviours that place them at risk of electrocution. For example, the unusual behaviour of parrots (order: Psittaciformes) pecking on pole hardware heightens their vulnerability to electrocution (Biasotto et al., 2022).

The road-effect zone varies across taxa. Bird densities decrease up to 1 km from roads, while for mammals, the decline can extend to 5 km (Benítez-López et al., 2010). However, some species, like chimpanzees, are affected up to 15 km from roads (Andrasi et al., 2021). Despite 218 primate species recognised as being impacted by linear infrastructure (Galea & Humle, 2022), research has largely overlooked this taxon. For them, a landscape perspective is considered more suitable than focusing on species' attributes to understand the impact from habitat complexity, fragmentation, and loss (Arroyo-Rodríguez & Fahrig, 2014; Ascensão et al., 2022). With that approach, those species listed on the IUCN Red List as Critically Endangered, Endangered, or Vulnerable are thought to be more affected by infrastructure than those species listed as Least Concern, Data Deficient, or Not Evaluated (Ascensão et al., 2022; Estrada et al., 2020; Fernández et al., 2022; Galea & Humle, 2022). While these approaches are important and provide overarching guidance for protecting primates across regions, there are limited studies on how linear infrastructure impacts primate populations

(Beamish, 2009; Ram et al., 2015). This hinders our ability to predict future trends, and importantly, to make informed conservation decisions at the local level.

1.4 Mitigation measures, their effectiveness and financial feasibility

To address the environmental impacts of development projects, including linear infrastructure, the Mitigation Hierarchy was developed as a framework aimed at avoiding and reducing project impacts, restoring habitats and species, and, as a last resort, offsetting residual impacts (Bennett, 2017). In response to the road and power distribution infrastructure priorities embedded within SDGs 9 and 7, most projects impacts are unavoidable, as development goals are prioritised over biodiversity concerns (Elder & Olsen, 2019). Consequently, minimising impacts on wildlife—the second step in the Mitigation Hierarchy—has led to the creation of diverse mitigation measures (Janss & Ferrer, 2001; Smith et al., 2015). This diversity is illustrated by, for example, fencing designed to direct migrating elephants to large road underpasses (Weeks, 2015), while insulator pins on power poles provide safe perching and nesting for birds of prey (Martín et al., 2022).

Primate species present some unique challenges to mitigating the impacts from roads and power lines due to their excellent climbing skills, complex social groupings, and their high cognitive abilities, making fencing and traditional wildlife over and underpasses often ineffective to mitigate risks. Consequently, a mix of traditional and alternative mitigation measures have arisen. For primates, road mitigation measures include speed limit enforcement, road signs, speed bumps, overpasses, and canopy bridges, although their effectiveness remains generally understudied. Anecdotal evidence suggests speed limits are effective in central Africa (Laurance et al., 2006), but a study in Tanzania found that drivers often fail to adjust their speed to avoid primate collisions (Kioko et al., 2015). While road signs for primates exist in many range countries (Wikimedia, 2024), their effectiveness in reducing collisions remains unstudied. Although these signs may raise awareness of primates in the area, standard warning signs alone appear to be ineffective at reducing wildlife-vehicle collisions (Huijser et al., 2015). In contrast, speed bumps have reduced collisions with red colobus monkeys (*Piliocolobus kirkii*) in Zanzibar, Tanzania (Olgun et al., 2021). A vegetated viaduct overpass has recently been built in Brazil, the first specifically for a primate, the tamarin monkey (*Saguinus ursulus*) (Jornal Nacional, 2022). It is, however, too early to assess the overpass effectiveness as the trees have not yet matured enough to create an overlapping canopy for this arboreal species to cross the 4-lane highway.

Power line mitigation measures to prevent primate electrocutions include vegetation management, cable marker balls (Lindshield, 2016), post shields (Dittus, 2020), cable insulation (Aggimarangsee et al., 2022; Lokschin et al., 2007), and canopy bridges (Lindshield, 2016; Lokschin et al., 2007; Maria et al., 2022). Three of the mitigations have been assessed for their effectiveness (cable insulation: Aggimarangsee et al., 2022, Lokschin et al. 2007; Post shields: Dittus, 2020; canopy bridge: Maria et al., 2022), showing significant reductions in electrocutions after their installation.

The more commonly used mitigation measure to reduce the impact of roads and power lines for primates are canopy bridges, which feature a diverse range of designs (Figure 1.1) accommodating morphological, behavioural, and ecological attributes of a target species. There are single and double-stranded bridges, ladder bridges, and net bridges, and even bridges with a third line for species with prehensile tails, among other designs (Birot et al., 2020). The few studies that have tested canopy bridge design effectiveness demonstrate that species have design preferences (Garcia et al., 2022; Linden et al., 2020; Narváez-Rivera & Lindshield, 2022; Yap et al., 2022). This is reflected in research outcomes where canopy bridges used by multiple primate species show variations in crossing frequencies across species (Mass et al., 2011; Narváez-Rivera & Lindshield, 2022; Ow et al., 2022). Given these design preferences, it is an important consideration that the bridge design chosen for a target species is unlikely to mitigate the impacts equally for all species that use the bridge.

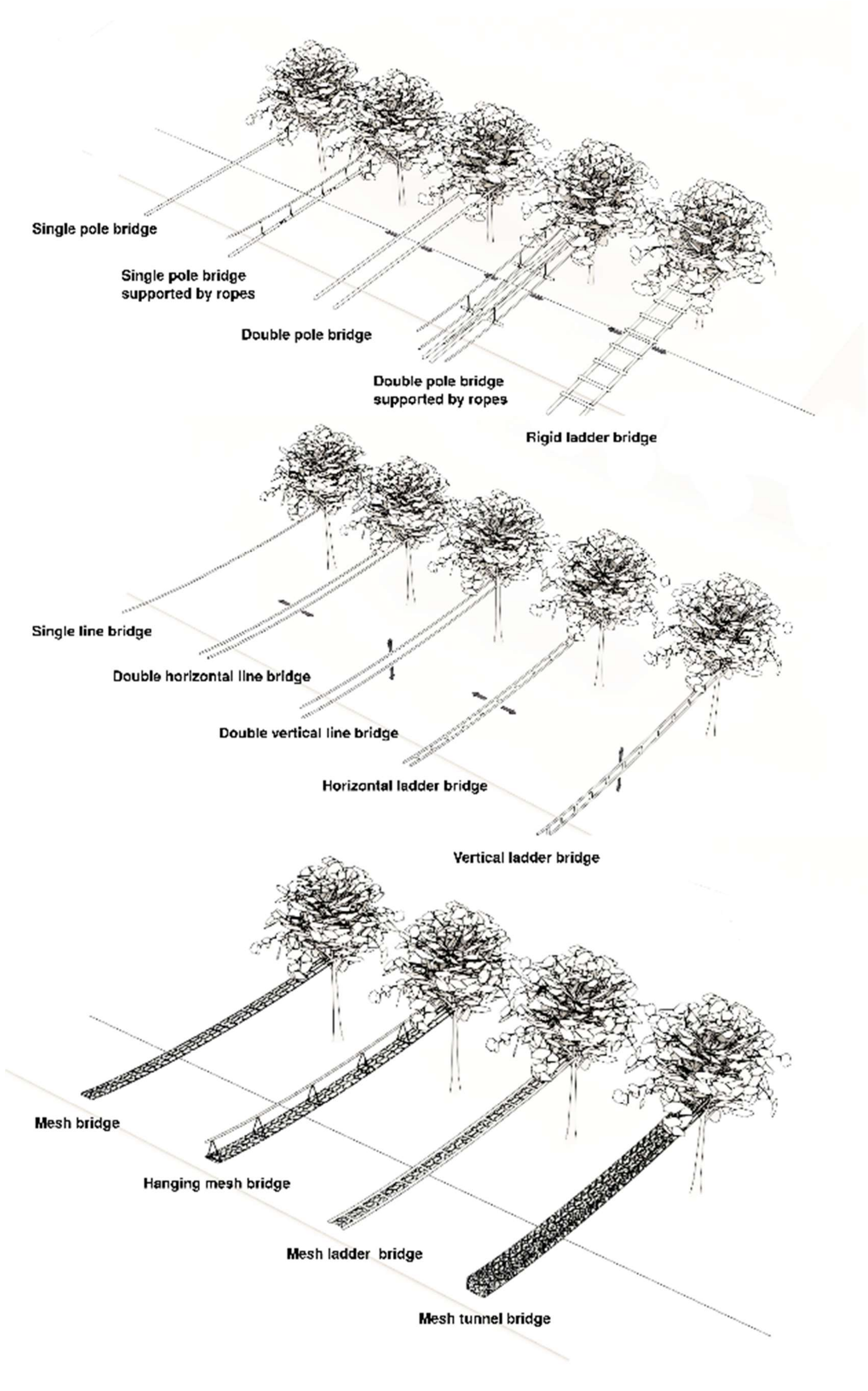

Figure 1.1 Canopy bridge designs (Fan et al., 2025).

Developing monitoring strategies for determining mitigation effectiveness is essential (van der Ree et al., 2015). Van der Grift & van der Ree (2015) reviewed methodologies to do so. While the review includes approaches for a broad taxonomic range of wildlife from large mammals to invertebrates, the authors did not include those best suited to primates. This may be because published research exploring monitoring of canopy bridge use by primates has only emerged in recent years. These methodologies include camera traps (Fan & Lindshield, 2022; Monticelli et al., 2022; Moore et al., 2021; Yap et al., 2022), sand track beds (sand placed at bridge ends to document footprints used for species identification) (Franceschi et al., 2022), and direct observations (Laidlaw et al., 2021; Narváez-Rivera & Lindshield, 2022) including those reported by citizen scientists (Raño et al., 2022; Teixeira et al., 2022).

Five studies have conducted before and after analyses to assess whether canopy bridge installation reduced primate-vehicle collisions. Four of these found a substantial reduction in collision number after bridge installation in a range of primate species (Bangladesh: Maria et al., 2022; Brazil: Monticelli et al., 2022; Costa Rica: Rojas & Gregory, 2022; Malaysia: Yap et al., 2022). A fifth study used the spatial cluster analysis, 2D Ripley's *K* statistic, to analyse the road distribution pattern of vehicle collisions with tufted-eared marmosets (*Callithrix geoffroyi*). That study indicated that the canopy bridge did not reduce collisions because the collision hotspot remained in the same location before and after canopy bridge installation (Brazil: Franceschi et al., 2022). However, these studies tested either the temporal or spatial aspect of the dataset, rather than combining both into a spatiotemporal analysis to identify the primate-vehicle collision patterns. Similarly, in the single study evaluating the effectiveness of canopy bridges in reducing electrocutions (Maria et al., 2022), the same methodological issue occurs, where in this case, only a temporal analysis was conducted.

Given study design challenges associated with evaluating the effectiveness of canopy bridges, conclusions that canopy bridges are effective at reducing primate-vehicle collisions and electrocutions are potentially premature. Furthermore, how bridges impact the road barrier effect based on before and after studies of road crossings (ground vs bridge), and additional factors, such as how vehicle volume (Bíl et al., 2020; Kruuse et al., 2016) affects primate bridge use, need to be incorporated. Only one study has addressed the impact of vehicle volume on canopy bridge use by six species of lemurs (Mass et al., 2011), finding no effect on bridge crossing frequency (Mass et al., 2011). However, the low vehicle volume in that remote forest (<15 vehicles/day) limits the scope of its conclusions to other contexts with greater levels of vehicle traffic.

As the Mitigation Hierarchy is employed to reduce the impacts from linear infrastructure, questions on the financial feasibility of primate infrastructure mitigation measures comes into play. Mitigation measures for roads and power lines vary widely in size and construction methods and, therefore, cost. A cost-benefit formula is sometimes employed as a decision-making tool to determine if a mitigation is to be installed (large ungulates: Huijser et al., 2009, capybara: Huijser et al., 2013, lowland tapirs and giant anteaters: Ascensão et al., 2021). The formula calculates the number of collisions per km per year that a specific mitigation type needs to prevent to render the mitigation economically viable. For those studies, the results indicate that the financial viability for mitigations exists primarily at a few specific road locations where collision hotspots occur. The cost-benefit analysis, however, is strictly a monetary calculation, overlooking non-financial economic and societal costs and benefits as well as those that are difficult or costly to measure. Furthermore, they also overlook road sections with few collisions, which may still be important for mitigation efforts. For instance, these locations may have experienced population declines due to previous high collision rates or where the road barrier effect is significant. As a result, these road sections are missed opportunities for mitigation strategies that could promote resource use and genetic flow across the road (Ascensão et al., 2019; Bouchard et al., 2009; Eberhardt et al., 2013).

To date, no financial analyses have been attempted for primate canopy bridges. The information provided in the literature is limited to bridge capital expenses (Mass et al., 2011; Nekaris et al., 2020), although in a few cases, installation costs are also included (Chan et al., 2020; Garcia et al., 2022;

Teixeira et al., 2013). Bridge maintenance and replacement costs remain unreported. Because of these omissions, the literature underestimates the of direct project costs and provides no information on the costs compared to bridge effectiveness in facilitating crossings.

1.5 Urbanisation, biodiversity threats and conservation opportunities

While urbanisation is a significant driver of biodiversity decline (Maxwell et al., 2016), it is also actively promoted by the global economy (Chen et al., 2014) because of the job opportunities and better access to education and healthcare that it tends to create (Jedwab et al., 2017; Lee, 1966). As a result of the rural-to-urban migration and population growth from surplus urban births, urban sprawl continues to convert natural and rural lands into a matrix of developed land uses (Lerch, 2017; Mcdonald et al., 2009; Smiraglia et al., 2021). In 1800, only 2% of the world's population lived in urban centres, but by 1900 that increased to 15% and represented 250 million people. A half century later, the percentage doubled and 2007 marked the year that urban populations exceeded rural populations (Ritchie et al., 2024). It is expected that five billion people, almost 70% of the global population, will be living in urban areas by 2030 (Ritchie, 2018; United Nations, 2019). This transformation has a clear and ongoing trend because 80% of global economic activity is generated in cities (Global Monitoring Report 2013).

Urbanisation–urban lands, built-up areas, and surfaces impervious to life–covers 5 million km^2 globally, which is 4% of the world's total land area (excluding Greenland and Antarctica) (Liu et al., 2014). From 1990 to 2014, urban sprawl surged by 95% with nearly 4% growth annually (Behnisch et al., 2022). While this may appear at first glance to be negligible, urban lands have a disproportionate negative impact on the environment (Bai et al., 2017). These impacts are expected to continue growing as cumulative biophysical changes lead to further alterations to the local and global ecological processes (Liu et al., 2014).

Despite the on-going surge of urbanisation, these environments can support some species providing opportunities for developing wildlife conservation actions. This is because of the network of green spaces that various forms of urbanisation create (Barrico & Castro, 2016; Tate et al., 2024) and the resources that such development may provide, such as wildlife feeders, access to food waste, and irrigation (Murthy et al., 2016). In this context, road verges have emerged as valuable in promoting urban ecology by providing wildlife habitats and corridors (Aronson et al., 2017; Filazzola et al., 2019; Kütt et al., 2016; Ligtermoet et al., 2022; O'Sullivan et al., 2017; Phillips et al., 2020). However, in many areas, road verges also accommodate power lines that require vegetation management to maintain the safety and functionality of the infrastructure (Omollo, 2022; The Kenya Roads Regulations, 2023). This requirement diminishes the conservation value of road verges. The complex nature of roads and power lines, separately and together, create conservation challenges. Incorporating biodiversity-friendly mitigation measures for these types of linear infrastructure into planning and design aligns with Sustainable Development Goal 11 to make cities and human settlements inclusive, safe, resilient, and sustainable (United Nations, 2015c). Certainly, trophic level maintenance and ecosystem function could be preserved with deliberate planning (Arenas et al., 2017; O'Sullivan et al., 2017; Phillips et al., 2020; Vakhlamova et al., 2016).

Considering the extent that urbanisation negatively impacts biodiversity and ecosystems, corresponding with the dramatic changes of the biophysical environment at the local and global levels, in 2007, at the Convention on Biological Diversity, the Executive Secretary, Ahmed Djoghlaf, poignantly stated that 'the battle for life on earth will be won or lost in the urban areas' (Djoghlaf, 2009, p. 2). For primates, over 65% of species are considered threatened with extinction while 93% are considered to have declining populations (Estrada & Garber, 2022). These percentages are alarming. Conversion of forest to urban and associated lands, is one of the drivers of these declines (Torres-Romero et al., 2023). Yet, there are primate species that exhibit behavioural plasticity and persist in urban areas, and for some, they thrive amongst the homes and businesses and the extensive linear infrastructure networks occurring there. While some studies seek to understand how primates adapt to these novel settings and overcome the challenges (Overbeck et al., 2022; Scheun et al., 2015; van Doorn & O'Riain, 2020; Yeo & Neo, 2010), a few seek to understand the unique risks associated with roads and power lines within towns (Corrêa et al., 2018; do Vale et al., 2020; Franquesa-Soler et al., 2023; Goulart et al., 2010), and importantly, how to mitigate these risks (Fan & Lindshield, 2022; Monticelli et al., 2022; Rojas & Gregory, 2022; Teixeira et al., 2013). While this body of literature is growing it remains limited. This thesis aims to fill critical knowledge gaps regarding the risk posed by roads and power lines to urban primates and to develop better strategies to mitigate some of those risks.

1.6 Research location

1.6.1 Colobus Conservation

Colobus Conservation (formally known as Wakuluzu, Friends of the Colobus Trust; Colobus Trust) is a primate and forest conservation organisation based in Diani, Kenya. In 1998, the organisation published the book "Diani's Monkeys." The introduction of that book provides a touching description of the circumstances leading to the organisation becoming established (Eley & Kahumbu, 1998, p. 1).

> *"On September 15th, 1996, the sight of two colobus monkeys mortally wounded by speeding vehicles on the busy Diani Beach Road provoked an emotive response from a small group of Diani residents who resolved to find ways to reduce or even eliminate similar occurrences. Within 24 hours, a rope bridge was suspended over the road at the site of the accident. Despite the provision of this alternative and safer means of passage across the road, over the next three months fifteen more colobus road kills were recorded within two kilometres of the bridge. These numbers convinced us that road kills were indeed a major contributory factor to the apparent decline in the population of this much-loved monkey. More action was essential, and by January 1997, Wakuluzu, Friends of the Colobus Trust, was founded and registered as a charitable organisation in Kenya."*

Since its inception, Colobus Conservation has responded to more than 3,000 primate welfare calls from the local community, recording dead primates and rescuing numerous primates injured by vehicle collisions, electrocutions, dog attacks, snares, and abuse, as well as those that are ill or naturally wounded. The primates are given veterinary care when necessary and in cases of orphans and ex-pets, they are provided with long-term rehabilitation until release. The organisation conducts school education workshops, plants indigenous trees, and carries out advocacy on conservation issues locally, nationally, and internationally. After 25 years of community interventions, Diani's primates and forest trees persist in the face of growing urbanisation, thanks in part to the grassroots work of Colobus Conservation.

1.6.2 Diani, Kenya

Fieldwork for this PhD was undertaken in Diani, Kenya. Diani is a coastal town with an economy based on tourism. The town is linear in shape having developed parallel to the Indian Ocean coastline. It is approximately 10 km long and 500 m wide. Diani is bordered to the north by the Kongo River, to the east by the Indian Ocean, to the west by Ukunda town, and to the south by residential and hotel development (Figure 1.2). The climate is hot and humid, influenced partially by the sea-level altitude and the Indian Ocean monsoon winds (Abuodha, 2003). Typically, there are two dry seasons and two rainy seasons annually. Diani retains trees and forest patches of the original Zanzibar-Inhambane Undifferentiated Forest Floristic Region (White, 1983). This phytogeographical vegetation historically extended from southern Somalia to the Limpopo River in Mozambique. Given its high number of endemic and restricted range flora and fauna species and its highly threatened status, Diani's forests are considered part of the Coastal Forests of Eastern Africa, Global Biodiversity Hotspot (Brooks et al., 2002; Conservation International, 2024; Myers et al., 2000).

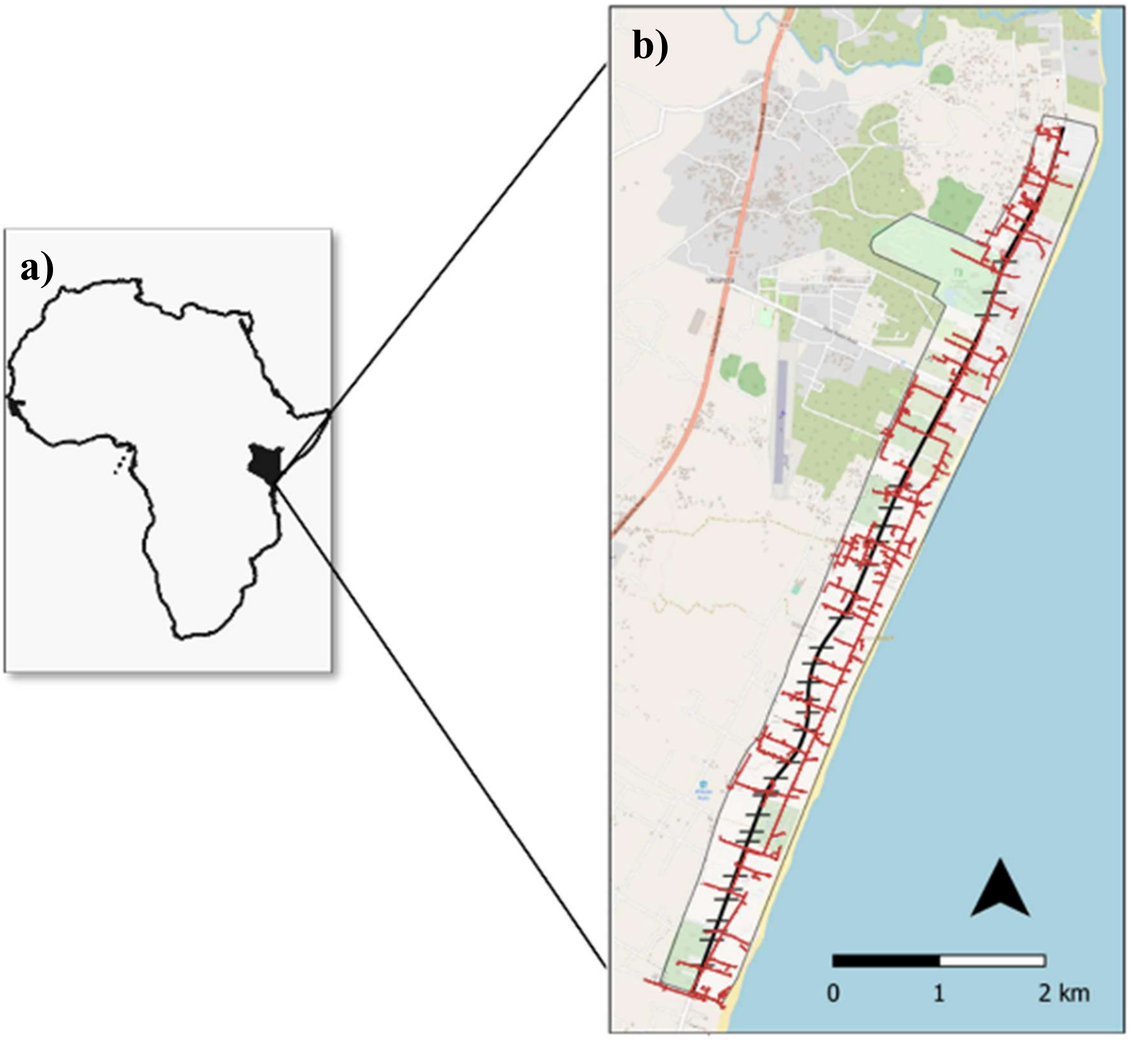

Figure 1.2 The study site: a) Diani is located in southeastern Kenya along the Indian Ocean coastline. b) The data collection area is outlined in grey (-4.267569°, 39.595537° −4.342196°, 39.563738°). Beach Road is denoted as the black line and the power lines are red. The canopy bridges are short lines perpendicular to Beach Road.

1.6.3 Diani's primate species assemblage

Six primates live sympatrically in Diani representing a broad taxonomic range (Figure 1.3): one colobine monkey, Peters' Angola colobus (*Colobus angolensis palliatus*), three cercopithecine monkeys, Zanzibar Sykes' monkey (*Cercopithecus mitis albogularis*), Hilgert's vervet (*Chlorocebus pygerythrus hilgerti*), southern yellow baboon (*Papio cynocephalus cynocephalus*), and two strepsirrhines, white-tailed small-eared galago (greater galago: *Otolemur garnettii lasiotis*) and the Kenya coast (dwarf) galago (*Paragalago cocos*).

Figure 1.3 Diani's six primate species: a) colobus, b) Sykes' monkey, c) vervet, d) baboon, e) greater galago, f) dwarf galago. a) to e) author's photos, f) Colobus Conservation photo library.

1.6.3.1 Colobus monkey

Colobus angolensis palliatus is a forest dependent folivore (Dunham, 2015; Oates, 1994). In Kenya, this subspecies occurs only in the highly fragmented forests in southeastern Kenya, and in Tanzania, it occurs in the coastal forests, the forests along the Rufiji River, and in the northern and central Eastern Arc Mountains (McDonald et al., 2022). These populations are declining due to the conversion of forests to agriculture, and hunting (Anderson et al., 2007) and because of habitat loss and fragmentation, each population is genetically unique (McDonald et al., 2022). Historically, in Kenya, *C. a. palliatus* ranged through the coastal forests north and south of Mombasa with the last recorded colobus north of Mombasa documented in the Arabuko Sokoke Forest Reserve in 1979 (Anderson et al., 2007). In 2020, the global estimate of *C. a. palliatus* was 35,000 individuals. This estimate prompted a reclassification of the subspecies from Least Concern to Vulnerable on the IUCN Red List (Cunneyworth et al., 2020). Approximately 10% of the global population occurs in Kenya, with about 10% of those occurring in Diani (Anderson, 2005a). Therefore, Diani is considered the second most crucial population for sustaining Kenya's colobus metapopulation, after Shimba Hills National Reserve (Anderson, 2005a).

1.6.3.2 Sykes' monkey

Sykes' monkeys are widely distributed across the forests of central, eastern, and southeastern Africa. Across this range, there are 16 subspecies of *Cercopithecus mitis* (Butynski & de Jong, 2022). Although they are an arboreal species in their natural forest habitat (Cords & Chowdhury, 2010), they do well in anthropogenic areas, taking advantage of human-derived foods. Consequently, Sykes' monkeys are often recognised as a nuisance species (Chapman, 1988) and are subjected to retribution killing because of crop foraging in rural areas (Butynski & de Jong, 2021) and stoning in urban areas (Colobus Conservation, unpubl. data). The subspecies of Sykes' monkey found in Diani, *C. m. albogularis*, has a limited range along the coastal forests of Kenya and northeastern Tanzania, extending inland roughly following the forest extent (Butynski & de Jong, 2022). While this subspecies exhibits an overall declining population, it remains listed as Least Concern on the IUCN Red List (Butynski & de Jong, 2022). Twenty-years of census data collected on the Sykes' monkeys in Diani indicate that this urban population is experiencing an annual increase of approximately 2% (Colobus Conservation, unpubl. data). This is likely influenced by the expansion of access to human-derived foods (Macmillan, 2018) associated with growing tourism.

1.6.3.3 Vervet monkey

Five subspecies of vervet monkeys occur in eastern and southern Africa (Butynski & De Jong, 2022b). Vervets naturally occur in savannas and shrubland, and while they use trees extensively, they are considered a semi-terrestrial species (Kiffner et al., 2022). The subspecies found in Diani, *C. p. hilgerti* is wide ranging and though there appears to be a decline in their global numbers, it does not warrant a revision of their Least Concern status in the IUCN Red List (Butynski & De Jong, 2022a). Given their highly adaptive behaviour, vervets are increasing in Diani (Colobus Conservation, unpubl.

data). This is likely because of the growing access to human-derived foods (Macmillan, 2018) and the simultaneous removal of trees for development resulting in irrigated gardens providing year-round foods similar to their natural grassland habitat (Donaldson, 2017). Vervet monkeys are at risk of predation by baboon (*Papio cynocephalus cynocephalus*) in this area (Struhsaker, 1967; Colobus Conservation, pers. obs.) and so the home ranges of these two species in Diani has limited overlap (Donaldson, 2017).

1.6.3.4 Yellow baboon

Yellow baboons inhabit various environments, including savannas, shrubland, and forest (Wallis, 2020). Though they are adaptable and highly terrestrial, baboons require trees as sleeping sites and for foraging and predation refuges. As omnivores, baboons display a versatile diet encompassing leaves, flowers, seeds, fruit, grass, invertebrates, and small mammals (Kitegile, 2016). In anthropogenic environments, baboons often forage on human-derived foods. Crop foraging (Strum, 2010; Taylor et al., 2016), feeding on discarded foods alongside roads (Kitegile et al., 2022), and from kitchens and rubbish pits of homes and hotels (Macmillan, 2018) are well documented. In Diani, the proportion of anthropogenic foods incorporated into the diet of groups within this urban area is estimated to be 15% (Canellys, 2016).

Since baboons are exceptional at adapting to changing environments, their global numbers are stable, and therefore, the IUCN Red List recognises this species as Least Concern (Wallis, 2020). In Diani, likely because of their priority access over other species to human-derived foods and the nutritional and caloric benefits from these foods, the baboon population experiences an annual growth rate of 4% (Cunneyworth, 2023). Given this population growth rate, the number of groups has increased over the past twenty years from three to five. Despite their formidable size (up to 25 kg) and the common perception that they are aggressive (Hill & Webber, 2010), Diani's baboons appear tolerant of the local human population with no reported incidents of baboons biting people in the town (Colobus Conservation, unpubl. data). This is notable as aggression by wild animals toward people is a particularly serious cause of negative interactions between people and wildlife (McLennan & Hockings, 2016).

1.6.3.5 White-tailed small-eared (greater) galago

As described by Harcourt (1984), this nocturnal strepsirrhine with adult males weighing 800 g, occurs predominantly in the upper forest canopy. In Diani, the greater galago incorporates into their range urban development such as rooftops, walls, and kitchens of homes and hotels. Where the opportunity presents itself, they will enter homes in the evening or at night to forage on human foods that are accessible (P. Cunneyworth, pers. obs.). According to the 2018 census, the Diani greater galago population is wide-ranging, with several notable hotspots, suggesting that the population is currently stable (Colobus Conservation, unpubl. data). A recent genetic study of the subspecies indicates that *O. g. lasiotis*, that which occurs in Diani, may have a more restricted range (Penna et al., 2022) compared to that described by the IUCN Red List assessment (Butynski & de Jong, 2020). This may result in a future reclassification of *O. g. lasiotis* to a Vulnerable category on the IUCN Red List.

1.6.3.6 Kenya coast (dwarf) galago

The Kenya coast galago, weighs only 150 g. It is often sympatric with the greater galago, *Otolemur* (Butynski & de Jong, 2019). As described by Harcourt (1984), the dwarf galago inhabits the mid to lower canopy most frequently but has been observed across all forest strata (Rosti et al., 2020). The galago rarely comes to the ground except on occasion when hunting, as they will jump to the ground to catch invertebrates but jump back immediately into the vegetation (Harcourt, 1984). As land developers and homeowners typically remove the forest understory, Diani's 2018 galago census suggests that the restricted distribution of the galago within the town is likely caused by the ongoing removal of their habitat (Colobus Conservation, unpubl. data). Consequently, the forest understory patchiness indicates few dispersal opportunities for the species, and that Diani's population, while unknown, is likely not promising for long-term viability.

1.7 Thesis outline

The aim of this thesis is to examine how linear infrastructure, specifically roads and power lines, impacts the primates living within the urban centre of Diani, Kenya. It also seeks to determine the extent that mitigation measures reduce some of these impacts. Diani is a town that provides a unique opportunity to study this, given the six sympatric species of primates and the availability of long-term datasets.

Chapter 2 examines the extent that Diani's Beach Road causes vehicle collisions across the four species of monkeys. The number of collisions is compared to the local monkey population size to understand the variable impact on each species. Further, species attributes are examined to understand the patterns of these collisions including substrate preference (arboreal versus terrestrial) and their age and sex class. Other factors of hotel bed-nights as a proxy for vehicle volume, and rainfall, were explored as affecting frequency of monkey-vehicle collisions.

Chapter 3 analyses data collected by two-person teams observing primate road crossing, on the ground and on canopy bridges, to determine if canopy bridges reduce the road barrier effect for the four species of monkeys living in Diani. The resulting crossing rates serve as the basis for developing a predictive model for canopy bridge use based on species' attributes of stratum preference and body mass. A cost-effective analysis is conducted to determine whether the annual bridge costs are justified considering the number of bridge crossings.

Chapter 4 analyses the dataset from Chapter 2 using Kernel Density Estimation plus (KDE+) to determine if there are species-specific spatial patterns of monkey-vehicle collisions along Diani's Beach Road. The effectiveness of canopy bridges at reducing collisions is examined carrying out a three-year before and after canopy bridge installation analysis, using the spatiotemporal extension of the KDE+ method.

Chapter 5 analyses the relative proportion of the local population of each species of monkey that has been recorded injured or killed by power lines between 1998 and 2019. Species' attributes of substrate preference and body mass are examined to determine if these explain incident patterns. Comments are made on the mitigation measures of trimming vegetation around power lines and insulating cables to reduce electrocutions.

Chapter 6 describes the spatial patterns of primate injuries and deaths from power lines. This chapter compares electric shock and electrocution occurrence patterns across species and seasons, and examines whether primate population density and power line density predict the location of electrocution hotspots.

Chapter 7 reviews and reflects on the main results of the five analytical chapters in terms of their cumulative contributions, shedding new light on several methodological challenges in the literature, providing practical considerations for installing canopy bridges as a mitigation measure for vehicle collisions and electrocutions, and recommends several avenues for future research to further protect urban primates.

Lastly, **Appendix I** presents publications that I lead or contributed to, throughout the PhD programme and **Appendix II** highlights how the results of this thesis have been used to raise awareness of the impact of roads and power lines on primates, locally, nationally, and internationally.

Chapter 2. Vehicle collisions among four species of monkey between 2000 and 2018 on a suburban road in Diani, Kenya

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2.1 Abstract

The impacts of road infrastructure on wildlife are of mounting concern. Amidst a growing body of literature on vehicle–wildlife collisions, few studies focus on primates. We examined a long-term dataset (2000–2018) of community-reported welfare cases for four species of monkeys: colobus (*Colobus angolensis palliatus*), Sykes' monkey (*Cercopithecus mitis albogularis*), vervet (*Chlorocebus pygerythrus hilgerti*), and baboon (*Papio cynocephalus cynocephalus*). We analysed collision rates using annual census data along a 10-km road section through the suburban town of Diani, Kenya. Vehicle–monkey collisions represented 705 of 1896 cases (37%), which was the most common anthropogenic cause of injury and death. The mean number of monthly vehicle–monkey collisions was 3 (range 0–10), and 83% of collisions led to death of the monkey. We found 1) higher degrees of terrestrialism were associated with lower number of collision cases; 2) no differences in the collision rates between juveniles, subadults, and adults across species, but collisions involving infants occurred at lower rates; 3) similar collision rates for female and male colobus and baboons, whereas Sykes' monkey females and vervet males were more frequently involved in collisions than the other sex; 4) no correlation between the number of hotel bed-nights (a measure of tourist numbers) and vehicle collisions; and 5) drier days correlated with increased rates of vehicle–monkey collisions across all species. This study highlights the risks of roads for monkeys, and that collision rates vary with species, age class, and, in some species, sex and that rainfall is one factor that affects these rates.

Keywords: Diani; Kenya; Primate; Road-crossing behaviour; Road mortality; Wildlife–vehicle collision

2.2 Introduction

The ecological impact of roads is considered a major threat to global biodiversity (Forman & Alexander, 1998; Polak et al., 2014; Trombulak & Frissell, 2000). Studies of the direct impact of vehicle–wildlife collisions suggest that roads are a leading cause of vertebrate fatalities (Forman & Alexander, 1998; Glista et al., 2009). Species-specific rates of vehicle–wildlife collisions reflect differences in the species' response to roads, including variation in attraction to roads and vehicle avoidance behaviour. Collision rates are also affected by vehicle volume and speed (Barrientos & Bolonio, 2009; Ramp et al., 2005; Seiler, 2005), population density (Mysterud, 2004), season (Dodd et al., 2005), degree of terrestrialism (Caceres, 2011; Sosa & Schalk, 2016), and moon phase (Colino-Rabanal et al., 2018).

Understanding differential rates of vehicle collisions provides information on population viability (Dreiss et al., 2010; Olson et al., 2014; Schwab & Zandbergen, 2011) as age and sex survival rates influence population growth and stability in distinct ways (Gaillard et al., 1998; Schindler et al., 2012; Schorcht et al., 2009). For example, in polygynous species, the female contribution to population growth is greater than that of the male (Gaillard et al., 1998; Olson et al., 2014), and juveniles contribute more to population size stability than other age classes (Gaillard et al., 1998; Hatter & Janz, 1994).

The literature on vehicle–wildlife collisions has proliferated since 2000 but the focus on primates has been relatively limited. A scoping review conducted in 2009 identified 131 species in 30 species groups affected by road infrastructure but none of those described involved primates (Fahrig & Rytwinski, 2009). Moreover, a recent article identified 46 primate species affected by road infrastructure (Hetman et al., 2019), yet studies that provide insights into how roads affect primates are entirely lacking.

To address the knowledge gap for vehicle–primate collisions, we examined a long-term dataset for four sympatric monkey species in Diani, Kenya: Peters' Angola colobus (*Colobus angolensis palliatus*), Zanzibar Sykes' monkey (*Cercopithecus mitis albogularis*), Hilgert's vervet (*Chlorocebus pygerythrus hilgerti*), and the southern yellow baboon (*Papio cynocephalus cynocephalus*). We explore the number of vehicle–monkey collisions for the study period, expressed as collision rates exposed to the same 10-km section of road from 2000 to 2018. It is an ideal opportunity for understanding the differential road effects on species with various morphological and social attributes highlighted as risk factors in other wildlife species.

We tested predictions arising from four hypotheses: 1) Arboreal species are at lower risk of vehicle–monkey collisions than terrestrial species because arboreal species do not descend to the ground and therefore avoid crossing road surfaces. Thus, we predict that colobus and Sykes' monkeys, the more arboreal species in Diani, will be involved in vehicle–monkey collisions at lower rates than vervets and baboons, the more terrestrial species in the town. 2) Collision rates differ across the age classes and sex because differences in behaviour put specific age classes and sexes at higher risk. Thus, we predict that juveniles will be involved in vehicle–monkey collisions at higher rates than the other age categories given their inexperience in road crossings. 3) Tourist numbers affect collision rates because they increase vehicle numbers. Thus, we predict that collision rates increase with the number of beds occupied reported by hotels. 4) Rainfall affects collision rates because daily path length increases in the dry season. Thus, we predict more collisions in the dry season than in the wet season.

2.3 Methods

2.3.1 Study site

Diani is an international tourist beach resort in Kwale County, southeastern coastal Kenya (Figure 2.1). The suburban town contains remnant patches of the coastal Zanzibar–Inhambane undifferentiated forest floristic region, which extends from southern Somalia to the mouth of the Limpopo River in Mozambique (Schipper & Burgess, 2004; White, 1983). The climate is bimodal. A shorter dry season occurs between July and September and a longer dry season occurs between December and March, whereas April–June and October–November are the typically rainy months (J. Beakbane, unpubl. data).

We conducted our study along a 10-km paved section of Diani's Beach Road between Southern Palms Beach Resort (−4.267569°, 39.595537°) and KFI Supermarket (−4.342196°, 39.563738°). The Kenyan government constructed this road through primary forest in 1971; it runs parallel to the Indian Ocean 230–1600 m inland. The road is 6 m wide with verge widths of 0–3 m. Some verges are vegetation or dirt paths, whereas others are paved, paving block walkways, or paved driveways. Shrub and forest line the roadside in some areas, and human development occurs along others. The local conservation organisation has installed aerial bridges for primates to cross the road. During the study period, the number of bridges varied between 3 in 2000 and 29 in 2018. Several power cables pass overhead. The road is in reasonable repair with some small potholes. There are eight speed bumps and a few painted lines and traffic signs. The speed limit is 50 km/h.

2.3.2 Study species

Diani has four sympatric species of monkey: one colobine and three cercopithecines. All four species are diurnal, but they vary in habitat use, terrestrial tendencies, food consumption, group structure and size, and body mass (Table 2.1).

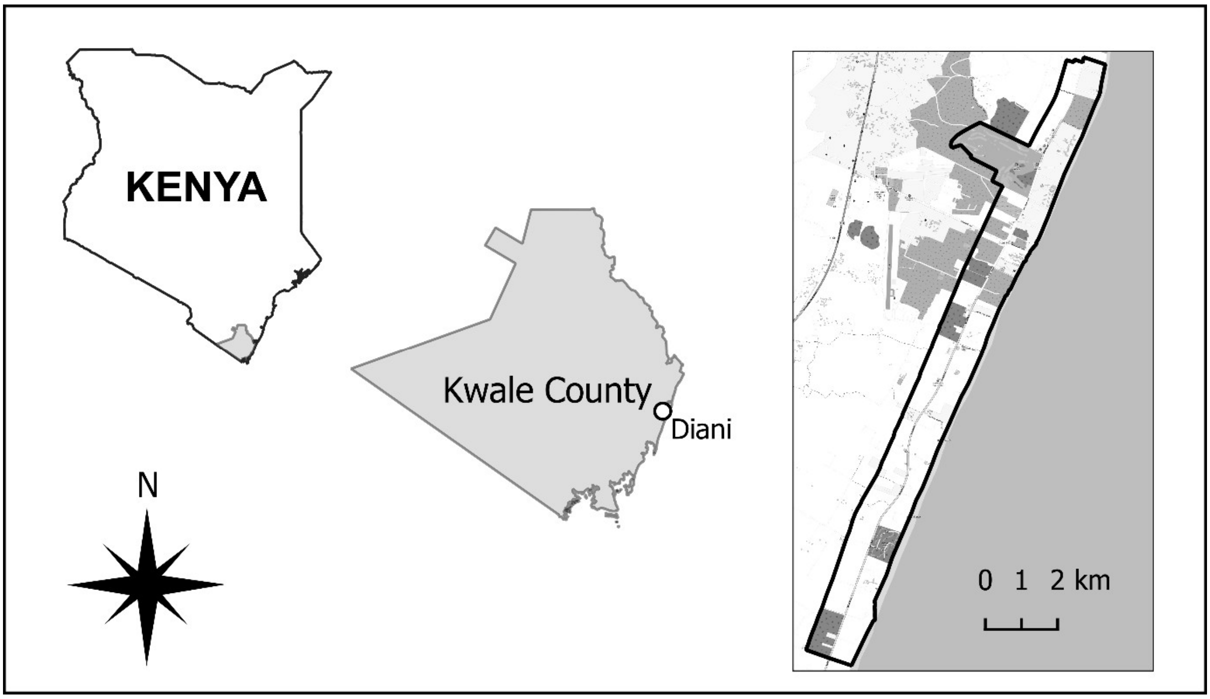

Figure 2.1 Location of the study site in Diani, Kwale County, Kenya. Beach Road is indicated by the thin line bisecting the town. The bold line shows the annual monkey census area from which we derived population data.

2.3.3 Data collection

Vehicle–Monkey Collision Data Colobus Conservation, a local conservation organisation based in Diani, operates a primate rescue service that responds to information provided by members of the community. The research team evaluates each case in the field. The team either collects the remains or captures the animal if it requires care, and the organisation's clinic provides veterinary intervention, as necessary. When an animal recovers, the team releases the individual either near the capture site or to its group if that is known. The team records each case on a standardised report sheet, including date, time, species, age, sex, cause, description of the case, location, and outcome (not found, alive not captured, treated and released, dead, died under treatment, or euthanised), and any clinical symptoms and treatment. We collated the report sheets by cause and created a dataset of vehicle–monkey collisions for the years 2000–2018. We limited the dataset to road locations along a 10-km section of Diani's Beach Road.

Monkey Census Data The conservation organisation carried out a census in October in Diani for the four monkey species for the years 2004–2006 and 2010–2018. The census determined population size and structure. Census area width varied 250–430 m on the east and 400–1230 m on the west side of Diani's Beach Road. For analysis, we matched the census area to the 10-km section of road where Colobus Conservation collected the vehicle–monkey collision data.

For colobus, Sykes' monkey, and vervet, teams of two people visited each property systematically, beginning at the most northerly point of the study area. Four to six teams carried out east-to-west transects. Vegetation type and the location of human structures such as houses, fences, and walls determined the choice of transect width. When a team observed an individual monkey or a group, they moved off the transect line to take a GPS point in the centre of the group, counted the number of individuals in each age class, and recorded the data on a standardised worksheet. Once the team completed the data collection, they returned to the transect line and continued. The teams walked approximately 1–1.5 km/h. The team leader positioned him or herself on the roadside and coordinated the census teams to implement the census of the east and west sides of the road in parallel moving southward. The team leader reviewed data in the field and deleted double counts. The teams conducted the census over three consecutive days. Transects began at 07:00 h and ended at 18:00 h with a break from 12:30 h to 14:00 h. As the census took place during most daylight hours and hours when monkeys are active, we considered the data as near-total counts.

For the baboon census, teams of two people visited all groups in Diani within 1 week. The team positioned themselves ahead of the group and waited for the baboons to pass a stationary linear object such as a road or fence. As the group crossed that object, one researcher stated the age and sex of each baboon to a recording individual. The teams conducted three to six group censuses and used the mode of these repeated counts to determine total counts.

Researchers collected census data at a distance of 5–15 m as the study area is in a suburban environment and the monkeys are typically well habituated. The teams did not approach closer than 5 m. Researchers collected age-class data (infant, juvenile, subadult, and adult) for all species but collected only sex data for juvenile, subadult, and adult colobus and baboons, given the difficulty of accurately identifying sex in all age classes of Sykes' monkeys and vervets and in infants of all four species.

Hotel Bed-Night Data We used monthly hotel bed-night data for Kwale County from January 2010 to December 2018 (Kenya National Bureau of Statistics 2018). Owing to Diani's popularity as an international tourist destination, we used this dataset as a proxy variable for vehicle volume (Saenz-de-Miera & Rosselló, 2012; Þórhallsdóttir & Ólafsson, 2017).

Rainfall Data We used daily rainfall data, measured in mm, collected at ca. 09:00 h during the study period corresponding to the census years 2004–2006 and 2010–2018. The rain gauge was located 1.7 km south of the study site.

Table 2.1 Monkey species of Diani, Kenya with species' attributes.

Common name (*scientific name*)	Habitat	Stratum[a]	Food Consumption	Group structure	Group size	Body Mass	References
Peters' Angola colobus (*Colobus angolensis palliatus*)	Forest	Arboreal	Folivorous	Unimale, multifemale	2–13	Female: 9 kg Male: 10.7 kg	Anderson, 2005; Dunham & McGraw, 2014; Harvey et al., 1987
Zanzibar Sykes' monkey (*Cercopithecus mitis albogularis*)	Forest	Semi-arboreal	Omnivorous	Unimale, multifemale	4–65	Female: 4.4 kg Male: 7.6 kg	Coleman & Hill, 2014; Harvey et al., 1987; Thomas, 1991
Hilgert's vervet monkey (*Chlorocebus pygerythrus hilgerti*)	Woodland	Semi-terrestrial	Omnivorous	Multimale, multifemale	6–20	Female: 3 kg Male: 5.4 kg	Cheney et al., 1988; Harvey et al., 1987; Isbell et al., 2009; Rose, 1979
Southern yellow baboon (*Papio cynocephalus cynocephalus*)	Savanna	Terrestrial	Omnivorous	Multimale, multifemale	27-43	Female: 15 kg Male: 20 kg	Altmann et al., 1985; Harvey et al., 1987; Kitegile, 2016; Napier & Napier, 1985

[a] Based on percentage estimates of terrestrialism from the literature on nonurban groups

2.3.4 Statistical analysis

Using SPSS statistic software (IBM Corp, Version 24), we tested assumptions prior to performing all statistical analyses. We rejected the null hypothesis at a 0.05 significance level. We first calculated the percentage of illness and each type of anthropogenic cause of injury and death in the dataset (vehicle–primate collisions, electrocutions, snares, poison, domestic dog attacks, primate pets, and human abuse) that occurred in the study area surrounding the 10 km section of Diani's Beach Road. We then calculated the Constant Annual Growth Rate to determine the overall population trend of each species. The formula is expressed as follows:

$$Constant\ Annual\ Growth\ Rate = \left(\frac{\text{Final population}}{\text{Beginning population}}\right)\text{^}(1/(15-1)) - 1,$$

where

Beginning population=the number of individuals based on the 2004 annual census; Final population=the number of individuals based on the 2018 annual census; and 15 is the number of years between the beginning population and final population. We tested for species differences in rates of vehicle–monkey collisions by dividing the annual number of cases by the annual population size as determined by the census data for each of the years 2004–2006 and 2010–2018. We used Shapiro–Wilk's test to test normality and Levene's test to test the homogeneity of variance. As the results for both tests were significant, we continued with a Kruskal–Wallis test. As this was significant, we carried out planned post hoc testing for pairwise analyses comparing species using the Wilcoxon rank sum test.

To examine age-class involvement in vehicle collisions, we summed the number of cases of infant, juvenile, subadult, and adult for each species for those years with corresponding census data (2004–2006 and 2010–2018). We also determined the size of each age class in the population for the same years using age-class data collected during the annual census. We then calculated the annual proportion of the population involved in collisions for each age class for each species. We used a

Kruskal–Wallis test to assess the null hypothesis that within species, the mean ranks are equal across age classes. For species that were not consistent with the null hypothesis ($p < 0.05$), we carried out post hoc testing in pairwise comparisons using a Mann–Whitney U test to identify the age classes that were significantly different. We reported the nonadjusted p values as these tests were planned and limited to a small number of tests (Armstrong 2014).

To compare the frequency of collisions between the sexes, we used Pearson's chi-square tests for females and males involved in vehicle–monkey collisions for years 2000–2018 for each species. We assumed a 50:50 ratio of females to males in the population of each species.

We used a two-tailed Pearson's correlation coefficient to compare the number of vehicle–monkey collisions as a percentage of the population and two types of seasonality–tourism and rainfall. We used data from the annual census of each year to determine the proportion of the population involved in collisions in each month of that year. We summed the daily rainfall data by month and conducted the analysis on a month-to-month basis. Hotel bed-night data were available for 2010–2018 (N =108 mo), and rainfall data were available for 2004–2006 and 2010–2018 (N =144 mo).

2.4 Ethical note

We carried out our study with permission from the Kenya Wildlife Service and the National Commission of Science, Technology, and Innovation under permit number NACOSTI/P/17/49217/14501. The study was also approved by the Zoology Department of Anglia Ruskin University. The authors have no conflicts of interest or competing financial interests.

2.5 Supplementary material

The datasets generated and analysed during the current study are available in the supplementary files of the online version of this article https://doi.org/10.1007/s10764-020-00135-w.

2.6 Results

Between January 2000 and December 2018, Colobus Conservation received 1896 reports from the community relevant to primate illnesses, injuries, and deaths. Vehicle–monkey collisions were the most frequent cause reported, accounting for 37% (*N* =705) of the cases. The monthly frequency of vehicle–monkey collisions ranged 0–10 cases with a mean of 3.1 ± SD 2.0 (*N* =228 months) (Figure 2.2). Survival rates were low, as only 15% (104 of 705) of individuals were either alive and not captured or treated and released. Death occurred in 83% of cases (*N* =588); these 588 cases were made up of 80% dying on impact or shortly thereafter, 9% dying during treatment, and 11% euthanised as a result of the injuries. In 2% of cases, the team did not find the monkeys when they followed up on the field report.

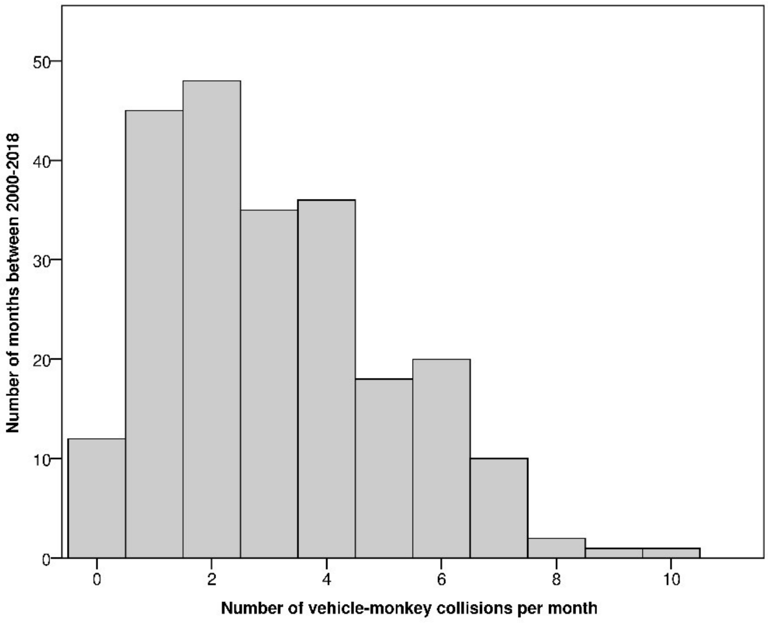

Figure 2.2 Distribution of the monthly number of monkey-vehicle collisions on Beach Road in Diani, Kenya for four monkey species combined (colobus, Sykes' monkey, vervet, and baboon) for 2000–2018 (*N* = 19 yr).

Constant annual growth rate varied between species, with colobus showing negative growth while Sykes' monkeys, vervets, and baboons showed positive growth (Table 2.2). When standardised across years by dividing the number of cases by the annual population size, collision rates differed significantly across species ($\chi2 = 8.451$, N =12, df = 3, p = 0.038) (Figure 2.3). In pairwise post hoc comparisons, we found significant differences only between colobus and Sykes' monkeys, and baboons (colobus–Sykes': $\chi2 = -0.92$, N =12, df = 3, p = 0.87; colobus–vervet $\chi2 = 5.04$, N =12, df = 3, p = 0.37; colobus–baboon: $\chi2 = 13.54$, N =12, df = 3, p = 0.02; Sykes'–vervet: $\chi2 = 5.96$, N =12, df = 3, p = 0.29; Sykes'–baboon: $\chi2 = 14.46$; N =12, df = 3, p = 0.01; vervet–baboon: $\chi2 = 8.5$, N =12, df = 3, p = 0.13).

The pattern of collisions by age class (infant, juvenile, subadult, adult) varied. For colobus and vervets, rates did not differ significantly across age-classes (colobus: $\chi2 = 5.17$, N =48, df = 3, p = 0.16; vervet: $\chi2 = 2.35$, N =48, df = 3, p = 0.50). However, for Sykes' monkeys, infants were involved in collisions more often than the other age classes ($\chi2 = 15.94$, N =48, df = 3, $p = 0.001$) and subadults were involved less often than adults, whereas for baboons, infants were involved less often than all other age classes but this was significant only with juveniles ($\chi2 = 11.2$, N =48, df = 3, $p = 0.011$). There were no statistically significant differences in rates of vehicle–monkey collisions between the sexes in colobus and baboons; however, female Sykes' monkeys were involved in significantly more vehicle–monkey collisions than were males, whereas the opposite was true for vervets (Table 2.3).

Seasonality of hotel bed-nights and rainfall had different effects on collision rates (Table 2.4). Vehicle collisions were not significantly correlated with hotel bed-nights for any species. Vehicle collisions, however, were negatively correlated with rainfall for all species, evidence that more collisions occurred in the drier months. The correlation was significant only for colobus and Sykes' monkeys.

Table 2.2 Population as determined by an annual census of four monkey species in Beach Road study area, Diani, Kenya, 2004–2006 and 2010–2018, with the constant annual growth rate.

Year	Colobus	Sykes'	Vervet	Baboon
2004	258	690	243	118
2005	208	577	244	99
2006	188	375	169	103
2010	321	679	159	108
2011	328	714	223	138
2012	323	734	191	148
2013	310	1104	282	156
2014	296	742	146	160
2015	280	673	212	186
2016	311	709	243	181
2017	225	815	289	190
2018	214	814	274	206
Constant Annual Growth Rate	-0.01	0.01	0.01	0.04

Table 2.3 Monkey-vehicle collisions by sex for four species of monkey on Beach Road in Diani, Kenya, 2000–2018 (N =19 yr).

Species	Female	Male	$\chi 2$	*p value*
Colobus	72	82	0.649	0.420
Sykes'	207	152	8.426	0.004 **
Vervet	35	59	6.128	0.013 *
Baboon	17	22	0.641	0.423

Pearson chi-square analyses assume 50:50 sex ratios.
*$p \leq 0.05$, **$p \leq 0.01$

Table 2.4 Correlations between the monthly number of monkey-vehicle collisions in Diani, Kenya and hotel bed-nights for 2010–2018 (N =108) and rainfall for 2004–2006 and 2010–2018 (N =144).

Variable	Colobus		Sykes'		Vervet		Baboon	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Hotel bed-nights	0.152	0.117	.065	0.502	-0.057	0.560	0.068	0.487
Rainfall	−0.165	0.048*	−0.171	0.041*	−0.001	0.988	−0.030	0.722

* $p \leq 0.05$.

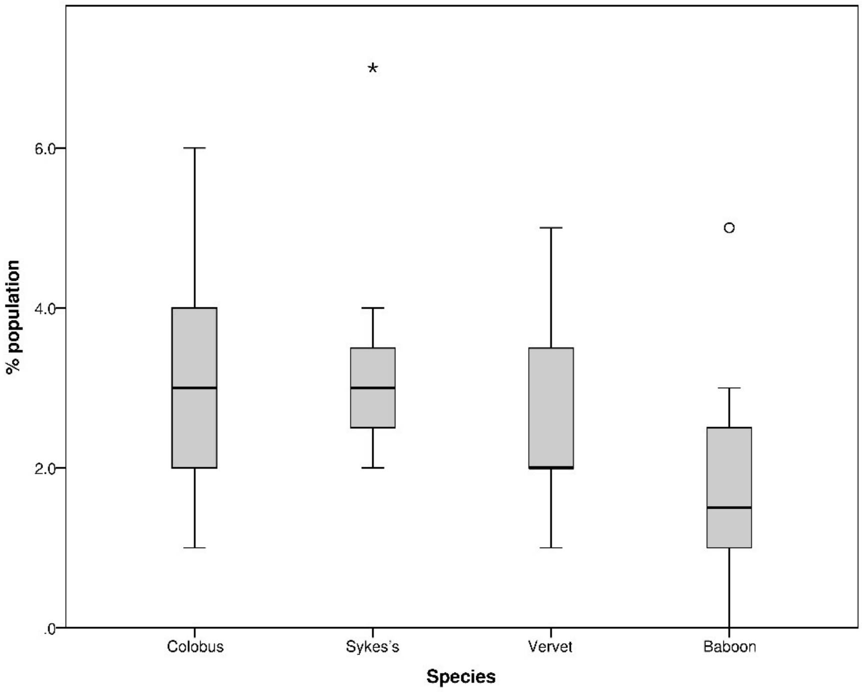

Figure 2.3 Percentage of the population involved in vehicle–monkey collisions on Beach Road in Diani, Kenya, for four monkey species in 2004–2006 and 2010–2018 (N =12 yr). Bars show the median, boxes the interquartile range, whiskers the minimum and maximum values, open circle an outlier, and the asterisk an extreme outlier.

2.7 Discussion

Between 2000 and 2018, vehicle–monkey collisions accounted for 37% of the total number of primate welfare cases reported to Colobus Conservation by members of the community. Furthermore, >80% of the vehicle–monkey collision cases we examined resulted in death of the individual. These results are consistent with studies that describe roads as a leading cause of wildlife fatalities in non-primates (Forman & Alexander, 1998; Glista et al., 2009). We found that vehicle–monkey collisions were almost 2.5 times as common as monkey electrocution cases in Diani. However, three previous studies of suburban monkeys—chacma baboons (*Papio ursinus*), Hanuman langurs (*Semnopithecus entellus entellus*), and Wied's marmosets (*Callithrix kuhlii*)—(Beamish, 2009; Ram et al., 2015; Rodrigues & Martinez, 2014) found that electrocution cases were more common than collisions.

This variation is likely because of the differences in road characteristics such as speed limit, number of curves in the road, and the type of roadside vegetation (Danks & Porter, 2010; Lee et al., 2004; Philcox et al., 1999). Quantification of the infrastructure in future studies would allow comparisons of risk factors across sites.

There is evidence in primates and other taxa that vehicle–wildlife collisions occur at lower rates for arboreal species than for terrestrial species because arboreal species avoid descending to the ground to cross canopy gaps marked by roads (Caceres, 2011; Sosa & Schalk, 2016). However, we found a different pattern that may be particular to the suburban setting: vehicle collisions with the more arboreal species, colobus and Sykes' monkeys, occurred at higher rates than those of the more terrestrial species, vervets and baboons. Baboons, the most terrestrial of the species, experienced the lowest rates of involvement in collisions. We suggest that degree of terrestrialism is the main predictor of collision rates of smaller monkeys (<11 kg). However, it is unclear whether collisions with baboons occurred at the lowest rate due to their high degree of terrestrialism or to their large body mass (>15 kg). The low rate is at least partially due to driver behaviour, as drivers tend to slow down to avoid hitting baboons (Amick, 2018), presumably to prevent damage to the vehicle and injury to the occupants (Kioko et al., 2015).

As noted earlier, collision rates were similar for Sykes' monkeys and vervets; however, we observed higher collision rates for female Sykes' monkeys compared to males whereas the reverse was found to be true for vervets. These species show differences in crossing risk, with Sykes' monkeys crossing at lower vehicle volumes and more quickly than vervets (Amick, 2018). It is possible that, within species, the sexes also differ in crossing behaviours (Hockings, 2011). Further investigation is needed in order to determine whether road crossing behaviour plays a role in the sex biases observed in the current study. Additional contributing factors such as the differences in the social organisation between these two species—one male vs. many male groups—may also need exploring.

In Diani, colobus, Sykes' monkeys and vervets speedily cross the road whereas baboons typically walk along the road (Amick, 2018). Consequently, only baboons socialise during road crossings. Though juvenile, subadult, and adult baboons are equally likely to be hit by a vehicle, the reasons for involvement in collisions may differ across age classes. For example, play behaviour among baboon juveniles is thought to be partially responsible for collisions affecting this age class (Drews, 1995) based on the assumption that play reduces vigilance behaviour. Providing some support for this, one author of this paper (PC) observed a truck hitting a juvenile while it was play-chasing another. An increase in specific age-class risk could also apply to other social interactions such as intermale agonistic behaviour (Ram et al., 2015), but we have not observed this in Diani's baboons. The intentional targeting of baboons observed in Diani (P. Cunneyworth, pers. obs.) and elsewhere (Drews, 1995) raises the possibility that collisions with the largest individuals, the adult males (ca. 20 kg), are because of the negative attitudes of drivers (Kioko et al., 2015) to this species.

Vehicle collisions were not influenced by hotel bed-nights, the variable we used as a proxy for vehicle volume. This was contrary to our prediction and findings for some other species (Laurance et al., 2009; Saeki & Macdonald, 2004; Seiler, 2005). We derived the prediction from the assumption that there is a heightened collision risk when vehicle numbers rise because the distance between vehicles reduces. The weak correlation found between hotel bed-nights and collisions was likely due to changes in the roadside behaviour of the monkeys. We suspect that with higher vehicle volumes, monkeys abort road crossings (Amick, 2018) and use the artificial canopy bridges (Jacobs, 2015) more often than at lower vehicle volumes.

Vehicle collisions increased in frequency during drier months for all species of monkey in Diani. The negative correlation between collisions and rainfall has also been observed for kangaroos (*Macropus rufus*, *M. giganteus*, *M. fuliginosus*, *M. robustus*) in Australia (Klöcker et al., 2006) and across taxa—amphibians, reptiles, birds, and mammals—in Columbia (De La Ossa-Nadjar & De La Ossa, 2015). Authors of both articles linked this pattern to increases in road exposure risks as food resources become scarcer with decreasing rainfall. For kangaroos, vegetation growth near to the roadside persists well into the dry season because of the road drainage properties. As the roadside becomes an increasingly important food resource, this correspondingly increases the exposure of kangaroos to vehicles. For the multiple taxa in Columbia, animals are thought to cross the road more frequently with dry season foraging strategies.

During a road crossing study of monkeys in Diani, the researcher did not observe monkeys crossing the road during rainy events and on one occasion, baboons aborted their road crossing when rain began (Amick, 2018). This indicates that daily rainfall is negatively correlated with daily path length, yet studies have not found that relationship in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), Hilgerti's vervets (*Chlorocebus pygerythrus hilgerti*), and chacma baboons (*Papio ursinus*) (Baoping et al., 2009; Donaldson, 2017; Pebsworth et al., 2012). We suspect that the action and interaction of duration and type of rainfall (drizzle, rain, cloudburst) with daily path length explains the negative relationship between collisions and rainfall for Diani's monkeys and likely some other wildlife species.

Disproportionate impacts on population viability arise from varying rates of age class and sex involvement (Seiler, 2006; Steen & Gibbs, 2004). Infants of all species have a lower impact on population viability, as their deaths lead to shortened interbirth intervals. As only 5% of vehicle–monkey collisions involved infants, this age class has a very low risk; however, the census data may be underreporting infants and obscuring this result in our analysis. Although juveniles are involved at the same rate as subadults and adults, this age class disproportionately contributes to population size stability (Gaillard et al., 1998; Hatter & Janz, 1994) and therefore may have longer-term implications for Diani's population viability. The cumulative impact of adult female involvement across species is also likely substantial, because their deaths result in the loss of their infants and young juveniles, as well as their own breeding potential. By contrast to these age and sex classes, the impact of adult male involvement varies by social structure. For colobus and Sykes' monkeys with one male groups, the loss of the breeding male risks infanticide with the arrival of new males during group takeover, while the loss of nonbreeding males would have little direct impact on the population.

The annual percentages of the population involved in vehicle–monkey collisions in Diani for all four monkey species fall within primate predation rates recorded in natural habitats (Hart, 2007). However, ecologically sustainable mortality is related to population growth rather than the percentage of the population removed. Therefore, we determined the annual growth rate of each species of monkey in order to determine if the number of annual births offsets the number of annual individuals removed, which in suburban areas may be different than for populations living in natural habitats. Sustainable mortality is <4% annually for primates because they reproduce slowly (Robinson & Bodmer, 1999). Rates of vehicle collisions exceed this percentage in 2 yr for colobus and vervets and in 1 yr for

Sykes' monkeys and baboons. Based on the constant annual growth rate, Sykes' monkeys and vervet populations appear to be increasing despite the impact of the road, indicating that these species can withstand the occasional year of higher mortality. The baboon population, which experienced low rates of vehicle collision, showed steady population growth. Vehicle collisions may, however, contribute to the negative population growth rate recorded in colobus.

Assessing cumulative risk from multiple environmental stressors, rather than our single factor analysis, however, would better inform decision-based conservation strategies. In conclusion, we present patterns of vehicle–monkey collisions for four species along a 10-km section of road through a suburban town with a 50 km/h speed limit. This study highlights the risks of roads for monkeys and shows that collision rates vary with species, age class, and, in some species, sex. A spatial analysis of collision locations would further advance the understanding of road-crossing risks to primates.

2.8 Acknowledgements

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Chapter 3. Canopy bridges are an economical mitigation reducing the road barrier effect for three of four species of monkeys in Diani, Kenya

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3.1 Abstract

For primates, canopy bridges can reduce the road barrier effect. Yet little information exists to predict species bridge use. We examined bridge use across a 9 km suburban road in Diani, Kenya, in three survey years ($N_{bridges}$: 21 = 2004, 27 = 2011, 29 = 2020) by four sympatric species of monkeys. The asphalt road is 6 m wide with a 50 km/h speed limit. Roadside observers recorded ground (N =4931) and bridge (N =3413) crossings, crossing direction, and traffic volume. Colobus (*Colobus angolensis palliatus*), Sykes' monkeys (*Cercopithecus mitis albogularis*), and vervets (*Chlorocebus pygerythrus hilgerti*) used the bridges while baboons (*Papio cynocephalus cynocephalus*) rarely did. Crossing rates (Sykes'>vervet>colobus>baboon) did not fit our predictions based on species' attributes of stratum preference (arboreal>terrestrial) or body mass (small>large), while the interaction between these attributes was more informative. Crossings were bidirectional. Colobus crossed bridges during higher traffic volumes than on the ground, whereas we found the opposite for vervets. Sykes' monkeys crossed at similar traffic volumes on the ground and bridges. The mean annual bridge cost was USD 157, deriving a cost per crossing as < USD 0.10, though it undervalues the savings in ecosystem services, tourism benefits, and contributions to protecting colobus, a Vulnerable species. While we consider this highly economical, funders and road engineers will ultimately determine if it is so.

Keywords: Cost-effectiveness analysis; Crossing rate; Horizontal ladder canopy bridge; Road barrier effect; Traffic volume

3.2 Introduction

Roads are a ubiquitous feature of global landscapes and are well documented as physical obstacles to wildlife, acting as barriers between habitat on opposite sides of roads (Bennett, 2017; Weston et al., 2011). As barriers to movement, roads negatively impact wildlife foraging, dispersal, and breeding opportunities (Aresco, 2005; Fitch & Vaidya, 2021; Kelly et al., 2013). However, numerous factors influence the magnitude and direction of the barrier effect, such as road width and surface (Brehme et al., 2013; de Oliveira et al., 2011), road verge habitat and width (Seidler et al., 2015), traffic volume and speed (Diaz-Varela et al., 2011; Seiler, 2005), and noise and lighting (Fahrig & Rytwinski, 2009). Conservationists and engineers install a wide range of road crossing structures to mitigate these factors. These structures fall into one of two general categories: underpasses or overpasses (Smith et al., 2015), chosen based on the road infrastructure type (i.e., highway, connector road, rural road), the attributes and behaviour specific to the target species (Chen & Koprowski, 2019; Smith et al., 2015), and budget (Lindshield, 2016).

For primates, canopy bridge overpasses (horizontal ladder or single pole or rope bridges: Birot et al. 2020) are exclusively used to increase habitat connectivity, such as across agricultural lands (Birot et al., 2020; Das et al., 2009; Nekaris et al., 2020), where intervening habitat is unsuitable (Chan et al., 2020; Hernández-Pérez, 2015), and over roads (Donaldson & Cunneyworth, 2015; Flatt et al., 2022; Langur Project Penang, 2022; Lindshield, 2016; Lokschin et al., 2007; Martín, 2012; Mass et al., 2011; Saralamba & Menpreeda, 2018; Teixeira et al., 2013; Valladares-Padua & Cullen Jr., 1995). Canopy bridges are intended to reduce the impact of landscape fragmentation by increasing the amount and quality of available habitat (Forman et al., 2003; Spellerberg, 1998) while lessening genetic diversity erosion among the subpopulations (Holderegger & Di Giulio, 2010; Reed, 2004).

The plethora of situations where primate canopy bridges reconnect habitat necessitates a better understanding of their functionality. Determining bridge effectiveness (crossings result in reoccurring resource use in habitat on opposite sides of the bridge) is challenging because most studies report a low number of crossings collected (Das et al., 2009; Flatt et al., 2022; Hernández-Pérez, 2015; Kumar et al., 2013). Furthermore, implying habitat connectivity as an outcome of bridge use may be presumptuous as most studies monitor on a short-term basis (van der Grift et al., 2013).

A few studies, however, quantitatively analysed primate bridge use (Javan slow loris, *Nycticebus javanicus*: Birot et al. 2020; Nekaris et al. 2020); Hainan gibbon, *Nomascus hainanus*: Chan et al. 2020; six species of lemur: Mass et al. 2011; brown howler monkey, *Alouatta guariba clamitans*: Teixeira et al. 2013). These studies documented extensive bridge use by the target species, and those seeking to understand resource use in habitat on opposite sides of the bridge demonstrated the incorporation of previously unused foraging trees and patches (Birot et al., 2020; Chan et al., 2020; Das et al., 2009; Hernández-Pérez, 2015). These studies demonstrated bidirectional use of bridges, that is, crossings similar in number in both directions, rather than omnidirectional use representing migration or source to sink movement (Pulliam, 1988).

Some authors discuss increased predation while using crossing structures for primate (Birot et al., 2020; Cuarón, 1995) and non-primate species (Little et al., 2002; Mata Estacio et al., 2015). There is little evidence that this is a substantial risk (Birot et al., 2020; Hernández-Pérez, 2015; Soanes et al., 2017), and a study that attempted to mitigate predation with a box-tunnel design (Australian possums, order: Didelphimorphia), the modification was rarely used (Weston et al., 2011). In contrast, ground movement is fraught with risks from dogs (Anderson, 1986; Riley et al., 2015; Waters et al., 2017), hunters (Linder & Oates, 2011), and vehicles (Hetman et al., 2019). Presumably, at least for arboreal species, ground crossings are perceived as high-risk behaviour (Bicca-Marques & Calegaro-Marques, 1995; Martínez & Wallace, 2011). Accordingly, when wildlife use canopy bridges, there is a reduced risk perception than crossings on the ground. For lemurs, this relative risk may explain the increasing number of bridge crossings as ground crossings decrease (Mass et al., 2011).

Studies on the comparative use of canopy bridges of various designs across primate species have only recently begun. Notably, all four studies found preferences. One field trial testing five designs across three New World monkey species (mantled howler: *Alouatta palliata*, white-faced capuchin: *Cebus capucinus*, Geoffroy's spider monkey: *Ateles geoffroyi*) found that howler and spider monkeys used horizontal nets and ladders more often than single or parallel lianas or bamboo, while capuchins used bamboo more often (Narváez Rivera & Lindshield, 2016). The Javan slow loris used bridges made of waterlines three times as often as bridges made from rubber hoses (Nekaris et al., 2020), and the South African samango monkey (*Cercopithecus albogularis*) also indicated a preference for bridge design when provided with a horizontal ladder or a single pole. In that study, significantly more crossings occurred on the pole (Linden et al., 2020). For black lion tamarins *Leontopithecus chrysopygus*), all crossings occurred on the wood pole bridge, with no crossings observed on the rope net bridge (Garcia et al., 2022). However, there is not enough evidence to predict species use of a particular bridge design or even predict species use of canopy bridges in general. There are hints that smaller species may cross more frequently than larger species on bridges (Aureli et al., 2022; Flatt et al., 2022; Martín, 2012) but these studies do not compare crossing frequency to population size.

Canopy bridge use is becoming a standard mitigation to the barrier effect allowing primates to cross gaps where habitat is unsuitable. Therefore, evaluating bridge efficacy is crucial for decision-making. Bridges are considered an inexpensive strategy (USD 40-600) (Flatt et al., 2022; Garcia et al., 2022; Mass et al., 2011; Nekaris et al., 2020; Teixeira et al., 2013). Still, depending on the design and the materials, some projects report much higher costs (USD 900-1000: Flatt et al. 2022; Garcia et al. 2022; USD 3000-5000: Chan et al. 2020; Mass et al. 2011). A cost-benefit analysis for bridges has yet to be conducted as mitigation measures have for some other taxa (Ascensão et al., 2021; Huijser et al., 2009).

In the suburban town of Diani, southeastern Kenya, Colobus Conservation, a local conservation organisation, installs horizontal ladder canopy bridges across a 9 km section of Beach Road (Donaldson & Cunneyworth, 2015; Eley & Kahumbu, 1998) in response to monkey-vehicle collisions for four sympatric species of monkeys: colobus (*Colobus angolensis palliatus*), Sykes' monkey *Cercopithecus mitis albogularis*), vervet (*Chlorocebus pygerythrus hilgerti*), and baboon (*Papio cynocephalus cynocephalus*) (Cunneyworth & Duke, 2020). While crossing structures over and under roads are typically installed to reduce both wildlife-vehicle collisions and the barrier effect, we limited our study to evaluate whether the canopy bridges reduced the road barrier effect and whether this was an economical mitigation to do so. To achieve our aim, we observed monkey road crossings on the ground and the canopy bridges in three survey years (2004, 2011, 2020). We tested predictions arising from the following hypotheses: 1) Terrestrial species use bridges less frequently than arboreal species because terrestrial species are already on the ground and cross directly rather than move to a bridge to cross the road. Thus, we predict bridge use to vary according to the species substrate preference, where arboreal species use bridges more often than those that are terrestrial. 2) As body mass increases, the centre of gravity shifts higher, and therefore an individual's stability on a bridge decreases. Thus, we predict more frequent bridge use among smaller species than larger species. 3) Foraging areas, water, and sleeping sites occur on opposite sides of the road, and therefore, monkeys cross the bridges bidirectionally to access these spatially discrete resources. Thus, we predict that the number of bridge crossings east-west and west-east did not differ significantly. 4) Monkeys perceive higher road crossing risk on the ground than on bridges because individuals on the ground are closer to the oncoming vehicles. Thus, we predict that bridges facilitate crossings at higher traffic volumes than ground crossings. Lastly, we assessed the financial costs of bridges against the frequency of use to determine if bridges were an economically viable mitigation strategy to the road barrier effect.

3.3 Materials and methods

3.3.1 Study species and site

Four species of monkeys occur sympatrically in the suburban town of Diani, on the southeastern coast of Kenya (−4.26757°, 39.59554°): Peters' Angolan colobus (colobus), Zanzibar Sykes' monkey (Sykes' monkey), Hilgert's vervet (vervet), and the southern yellow baboon (baboon). These species crosscut a broad taxonomic range, and amongst other variables, they vary in the degree of arborealism and body mass, with all species being sexually dimorphic (Table 3.1).

Table 3.1 Attributes of Diani's four sympatric species of monkeys.

Species	% time arboreal	Substrate preference[b]	Body mass (kg)[c]	Size[b]	Reference
Colobus	99	Primarily arboreal	Female: 10 Male: 12	Large	Cunneyworth and Slade, 2021, Dunham & McGraw, 2014
Sykes'	95[a]	Semi-arboreal	Female: 6 Male: 8	Medium	Coleman & Hill, 2014; Thomas, 1991
Vervet	81[a]	Semi-terrestrial	Female: 5 Male: 6	Small	Cheney et al., 1988; Isbell et al., 2009; Rose, 1979
Baboon	40[a]	Primarily terrestrial	Female: 16 Male: 25	Very large	Altmann et al., 1985; Kitegile, 2016; Napier & Napier, 1985

[a] Based on nonurban data from the literature.
[b] Lay term categories used for predictions given in this study.
[c] Based on Colobus Conservation, unpubl. data. Body mass is based on the typical maximum adult from necropsy reports.

The economic base of Diani is beach tourism, and consequently, there are many hotels of which most retain some original forest trees, forest patches, and other vegetation. As typical for an anthropogenically modified area, the monkeys move around their range above the ground using vegetation as well as electrical and telephone cables, building roofs, fences, and walls. Beach Road was built in 1971 through Diani's primary forest, part of the Coastal Forests of East Africa, Global Biodiversity Hotspot (Myers et al., 2000). Set inland 200-450 m, the road bisects the town approximately north to south. The asphalt road is 6 m wide, and the speed limit is 50 km/h.

3.3.2 Canopy bridge design

All of the canopy bridges in this study are horizontal ladder-style design (Figure 3.1). The team chooses trees offset from the road's verge and secures the bridges to the trees using T-bars and anchors. They install additional bridge segments with support poles and platforms when the tree line occurs far from the road's edge.

Figure 3.1 Horizontal ladder canopy bridges over Diani's Beach Road. a) Sykes' monkey crossing with bridge rungs visible, b) two Sykes' monkeys crossing, c) bridge components are: i) 30 cm rubber pipe, ii) 30 cm PVC conduit pipe, iii) 45 cm pressure pipe, iv) 3/16" galvanized wire rope grips, v) 3/16" galvanized wire, vi) turnbuckle. Photos a) and b) by 2nd author Andrea Donaldson, photo c) Colobus Conservation photo library.

3.3.3 Data collection

3.3.3.1 Road crossings on the ground and canopy bridges

In 2004, 2011, and 2020, we conducted road crossing surveys of the colobus, Sykes' monkey, vervet, and baboon along a 9 km section of Diani's Beach Road. We standardised the methods and included all canopy bridges present on the road in each survey year. While we observed all bridges on the road, the number of bridges varied across the survey years (2004: $N_{\text{bridges}} = 21$; 2011: $N_{\text{bridges}} = 27$; 2020: $N_{\text{bridges}} = 29$) (Figure 3.2). Eighteen bridges occurred in a similar location across all three survey years, ten bridges occurred in a similar location across two survey years, and three bridge locations were surveyed only in one year. We defined similar locations across years as situations when bridges were relocated to within 50 m. This occurred when a tree could no longer safely support a bridge (died, lost branches, cut down).

Figure 3.2 Maps of the canopy bridge locations in each survey year (2004, 2011, 2020) on Diani's Beach Road, Kenya. Beach Road is denoted as the bold line approximately north to south, and the lighter polygon defines the monkey census area, which determines the population size for each species in this study. The short black lines across the road indicate bridge locations.

Two-person teams sat on the roadside and recorded ground and canopy bridge crossings for two twelve-hour days (06:00 h-17:59 h) for each bridge (Table 3.2). The teams sat near the roadside where the road transect and the bridge were visible but where their presence did not appear to influence road crossings. On datasheets, the teams recorded information for each individual that crossed the road: the species of monkey, whether the crossing was on the ground or the bridge, the time to the minute of the start of the crossing, and the crossing direction (east-west, west-east).

Table 3.2 Sampling effort by survey year (2004, 2011, 2020), noting the standardised number of survey days and hours for each bridge while the sampling effort varied by year.

Year	Number of bridges	Survey days by bridge (by year)	Survey hours by bridge (by year)
2004	21	2 (42)	12 (504)
2011	27	2 (54)	12 (648)
2020	29	2 (58)	12 (696)
Total	77	(154)	(1848)

To record ground crossings, we created road transects at each canopy bridge, within which the teams limited the recording of crossings (Figure 3.3). Using a tape measure, we measured the transects along the road north and south of each bridge and used rocks as markings on the road verge visible to the observation team demarcating the transect extent. The road transect length was standardised as 200 m (100 m north and 100 m south) at each bridge; however, the transect lengths varied from 22 m to 100 m on either side of the bridge because of the varying proximity of the bridges to each other and where some road features such as the S-curve limited visibility. Where bridges were <200 m from one another, we allocated half of the total distance to each bridge as their respective transect length. Accordingly, with the increase in canopy bridges over the survey years, the percentage of the 9 km road included within the road transects also increased (2004: $N_{\%\ road} = 39$; 2011: $N_{\%\ road} = 53$; 2020: $N_{\%\ road} = 56$).

3.3.3.2 Traffic volume

At the same time that the team carried out the road crossing survey, they counted the number of vehicles that passed under the bridge that they were observing. The teams recorded the vehicles as tallies on a datasheet sectioned into 48 15-minute blocks, representing the twelve-hour survey day. The teams limited the count to three- and four-wheeled vehicles regardless of type or direction of travel (north-south, south-north). This dataset provided the specific traffic volume during the 15 minutes of each road crossing (ground and bridge) at the location of the crossing.

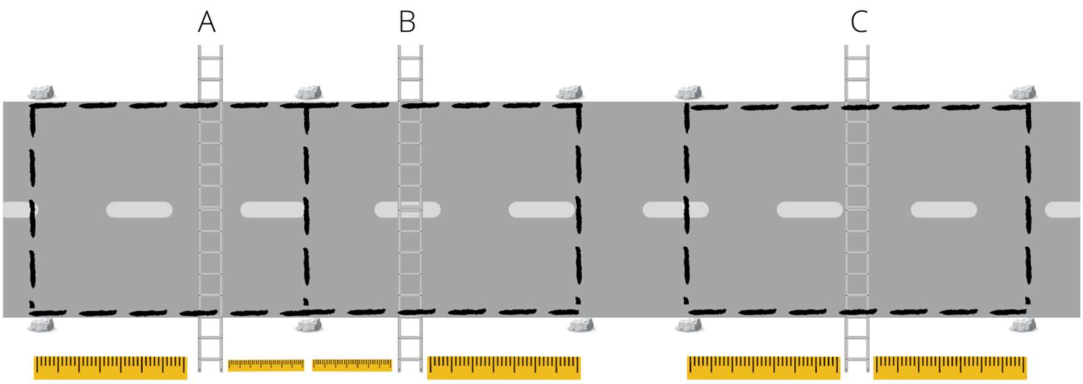

Figure 3.3 Method for determining road transects for recording ground crossings. Grey ladders indicate canopy bridges, and bold dashed boxes indicate the associated transects with the rock symbols denoting how the transect extents were marked on the road. The large yellow tape measures denote the standardised 100 m transect on either side of the bridge (bridge C) where bridges were greater than 100 m apart, and the smaller yellow tape measures measure half the distance between the two bridges (bridge A and B) where bridges were less than 100 m apart.

3.3.3.3 Monkey population size

Censuses of Diani's monkeys were conducted in each survey year (2004, 2011, 2020). These censuses applied survey methods standardised across the years within a defined 7 km2 area (ref. polygon in Figure 3.2). The censuses surveyed the east and west sides of the 9 km section of Diani's Beach Road, where the teams recorded the road crossing and traffic volume data. The census distance varied between 200-450 m on either side of the road (east: between the road and the Indian Ocean beach, west: between the road and the edge of the town). In only one location (golf course), the census distance extended beyond this width to 1250 m.

We could not find a standardised method to census suburban primates in the literature. As this is a town, properties are privately owned and individually demarcated. Therefore, we modified the traditional line transect methodology (Struhsaker, 1981) by entering properties and censused by conducting east-west line transects where possible, walking around buildings and other features where necessary. The censuses took place on three consecutive days in October in each survey year between 06:00-12:30 h and 14:00-18:00 h, as these are the times monkeys are typically more active and, therefore, more easily observed.

Four to six two-person survey teams carried out the census by walking 1-1.5 km/h. When the team observed monkeys, they moved off the transect, took a GPS (Global Positioning System) waypoint at the approximate centre of the group, and recorded the property name, the species, and the number of individuals observed. They then returned to the transect to continue. If the property was large or had dense vegetation, multiple teams simultaneously censused it, with the teams remaining in visual contact while walking the transects to ensure that they observed all areas of the property. The survey moved relatively evenly on both sides of the road, from the northern limit of the survey area (−4.267562°, 39.595575°) to the southern limit (−4.342272°, 39.563768°). A census supervisor remained on the roadside, moving southward with the teams, directing the teams to the next appropriate property to be censused. The supervisor reviewed the census data as the teams completed the property censuses to delete double counts.

We compiled the census data and calculated the population size of each species for each survey year (2004, 2011, 2020). As the teams used standardised census methods across the properties and removed double counts, we considered the dataset to estimate the minimum population size.

Situations where estimating complete counts are rare (Plumptre et al., 2013) but given the unique nature of our census area and its relatively small size, made this practical. Furthermore, Diani's monkeys are bound to the east by the Indian Ocean, the north by the Kongo River, and the west by Ukunda town. There are limited opportunities for immigration and emigration to the area south of Diani because of the highly fragmented habitat due to small-scale agriculture, informal businesses, and urban development. Given these ranging constraints, their exposure to the census area is relatively stable across seasons and years, as corroborated by several longer-term studies (Donaldson, 2017; Dunham, 2017).

3.3.4 Data analysis

We combined the results across survey years and reported the number of road crossings on the ground and the canopy bridges for each species of monkey (colobus, Sykes' monkeys, vervet, baboon). For analysis, we used individual rather than group crossings. Structuring the data by group crossings did not provide a clear resolution. We provide three examples of group crossing: 1) 8 bridge crossings appeared to be made by 2 individuals, 2) a group of 7 crossed, but only 1 individual used the bridge, the others used the ground, and 3) over two hours, a group moved back and forth and back again, but each time, there was a different number of individuals crossing. These crossing types were the norm, not the exception in our dataset. Therefore, given the complexity of defining a group crossing, absolute crossing numbers were used.

3.3.4.1 Crossings by substrate preference and body mass

As bridge numbers increased on Beach Road over time, we created a data subset for those bridges in a similar location in all three survey years ($N_{bridges} = 18$), which standardised the time base for the crossing rate. We calculated species crossing rates (number of crossings/population size) for each species in each survey year, where the higher the rate, the more effective the bridges were in facilitating crossings for that species. We performed pairwise comparisons for each survey year (2004, 2011, 2020) by testing the null hypothesis that crossing rates did not differ between species. We performed a Poisson exact test, reported the 95% confidence interval, and applied a Bonferroni correction for multiple tests ($\alpha = 0.05/9 = 0.006$).

3.3.4.2 Bridge crossing direction

We compared the bridge crossing directions, east-west and west-east. Using a chi-squared test for each species for each survey year, we tested the null hypothesis for bidirectional movement, with expected values of 50% in each direction. We applied a Bonferroni correction for multiple tests ($\alpha = 0.05/9 = 0.006$).

3.3.4.3 Traffic volume

We combined the traffic volume (at the crossing location) taken within the 15-minute time block during each crossing in all three survey years, categorised by species, then by road crossing type – on the ground or the bridges. Using a Mann-Whitney U test for each species, we tested the null hypothesis that the traffic volume distribution was equal between road crossing types.

3.3.4.4 Cost-effectiveness

Lastly, we calculated a cost-effectiveness ratio (Boardman et al., 2018) to determine the cost per crossing in USD. We defined the cost as bridge capital expenses, installation, and maintenance, and effectiveness as the number of annual bridge crossings by extrapolating the observed crossings from our survey for all species combined for each survey year. We used the following cost-effectiveness formula:

$$\boldsymbol{cost\ (USD)^{-crossing} = exch\left(\frac{\left(\frac{ce + ie}{5\ years}\right) + ame}{cr * 182.5}\right)}$$

where, exch = mean annual exchange rate of Kenya shillings to USD according to the Central Bank of Kenya, ce = capital expense including procurement, materials, and labour; ie = installation expense; ame = annual maintenance expense for bridges based on quarterly checking and repairs; cr = number of observed crossings for the two survey days. We amortised the projected life span of the bridges over five years.

3.4 Ethical note

Kenya Wildlife Service and the National Commission of Science, Technology, and Innovation granted the permits for this study (permit number: NACOSTI/P/18/13412/26289). The funder of the 2020 bridge survey had no involvement in writing this manuscript.

3.5 Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.20058974

3.6 Results

For all survey years combined (2004, 2011, 2020), we observed 8344 road crossings by the four species of monkeys (colobus, Sykes' monkey, vervet, baboon). Of these, 4931 were ground crossings (colobus: *N* =42, 1%; Sykes': *N* =1187, 24%; vervet: *N* =622, 13%; baboon: *N* =3080, 62%) and

3413 were canopy bridge crossings (colobus: *N* =159, 5%; Sykes': *N* =2982, 87%; vervet: *N* =269, 8%; baboon: *N* =3, 0%).

3.6.1 Crossings by substrate preference and body mass

We compared the bridge crossing rate between species based on their population sizes (Figure 3.4). All nine tests were significantly different (Table 3.3). Yet, bridge use (result: Sykes'>vervet>colobus>baboon) did not follow the predicted order based on stratum preference, arboreal to terrestrial (prediction: colobus>Sykes'>vervet>baboon) or body mass, smallest to largest (prediction: vervet> Sykes'>colobus>baboon). There was some ranking ambiguity in the crossing rate between colobus and vervets because, in one survey year (2004), colobus used the bridges more than vervets; and in the other two years (2011, 2020), vervets used the bridges more than colobus. Yet, the mean crossing rate over the three survey years for colobus is 0.1 and for vervets is 0.2.

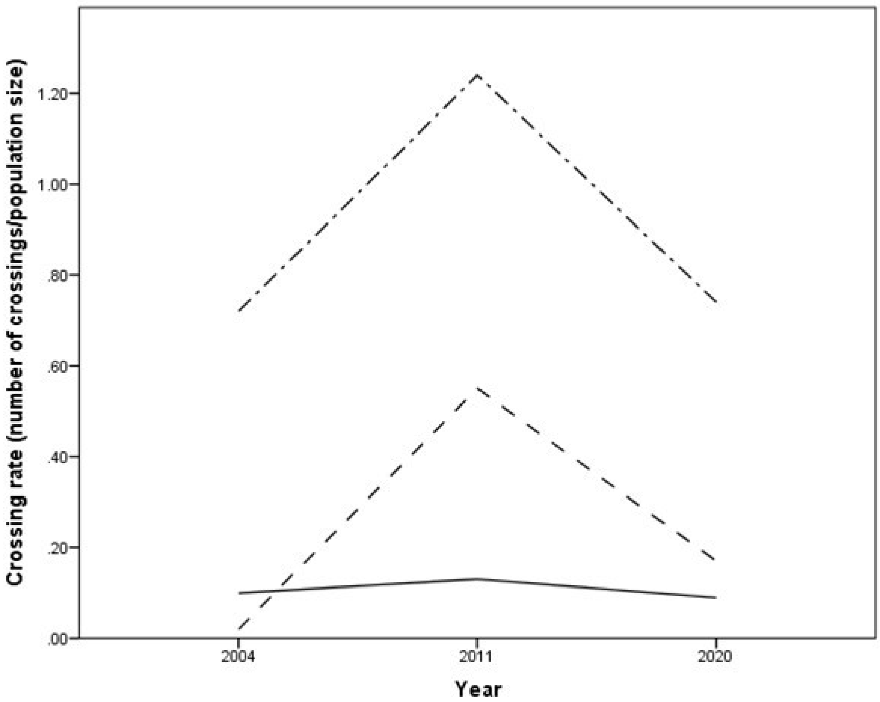

Figure 3.4 Crossing rate expressed as the number of bridge crossings by population size for each species (colobus, Sykes' monkey, vervet) in the three survey years (2004, 2011, 2020). The crossing rate for baboons equals 0. Colobus = solid, Sykes' monkey = dash-dot, vervet = dash.

3.6.2 Bridge crossing direction

The direction of bridge crossings within each survey year, east-west and west-east, was not statistically different after applying the Bonferroni correction (Table 3.4). The number of crossings for vervets in 2004 (east-west: 4; west-east: 3) was too low to analyse. The results indicate bidirectional movement for bridge crossings.

3.6.3 Traffic volume

Differences in traffic volume at the location of the crossing (Figure 3.5) were significant for colobus and vervets yet in the opposite direction. For colobus, the mean rank of traffic volume at the time of bridge crossings was higher than ground crossings ($U = -3.5$, $N = 84$, $p < 0.001$), and for vervet, the mean rank of traffic volume at the time of bridge crossings was lower than ground crossings ($U = 6.46$, $N = 538$, $p < 0.001$). For Sykes' monkeys, the mean rank of traffic volume during ground and bridge crossings was not significantly different ($U = -0.467$, $N = 2372$, $p = 0.64$). We did not analyse the baboon data due to the low number of bridge crossings ($N = 3$).

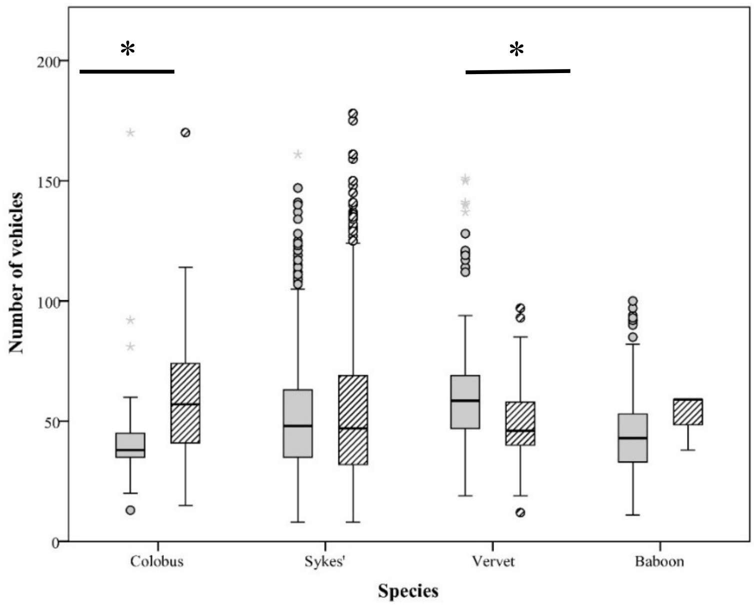

Figure 3.5 For each crossing, the number of vehicles passing at the crossing location (ground: solid; bridge: hatched) counted as a 15-minute block, categorised by species (colobus, Sykes' monkey, vervet, baboon). The data were combined for the three survey years (2004, 2011, 2020). Significant results are denoted with an underlined asterisk.

Table 3.3 Poisson exact test comparing the rate (number of bridge crossings/population size (Pop)) for species (sp) pairs (colobus, Sykes' monkey, vervet) by survey year (2004, 2011, 2020). The 95% confidence interval (CI) is given. The direction of the result is displayed as < where the crossing rate of species 1 is less than that of species 2, or > where the crossing rate of species 1 is greater than that of species 2. Asterisks indicate where the direction of the result between species 1 and species 2 is significant.

Year	Species	Bridge crossings/ Pop sp 1	Direction of the result	Bridge crossings/ Pop sp 2	Crossing rate ratio between sp 1 and sp 2 (95% CI)	*p*-value
2004	Colobus/Sykes'	26/258	<	500/690	7.19 (4.85-11.12)	<0.001*
	Colobus/Vervet	26/258	>	5/243	4.90 (1.85-16.33)	<0.001*
	Sykes'/Vervet	500/690	>	5/243	35.22 (14.99-108.94)	<0.001*
2011	Colobus/Sykes'	41/328	<	886/714	9.927 (7.26-13.93)	<0.001*
	Colobus/Vervet	41/328	<	122/223	4.38 (3.05-6.40)	<0.001*
	Sykes'/Vervet	886/714	>	122/223	2.27 (1.88-2.76)	<0.001*
2020	Colobus/Sykes'	21/226	<	599/814	7.92 (5.13-12.89)	<0.001*
	Colobus/Vervet	21/226	<	41/217	2.03 (1.17-3.62)	<0.001*
	Sykes'/Vervet	599/814	>	41/217	3.90 (2.84-5.48)	<0.001*

Table 3.4 Number of bridge crossings for colobus, Sykes' monkeys, and vervets in each direction, east to west and west to east, by year. The significance value is 0.006 for multiple tests.

Year	Species	χ^2	Bridge crossing direction E→W – W→E	*p*-value
2004	Colobus	0.04	12–14	0.84
	Sykes'	1.70	267–299	0.19
	Vervet	–	4–3	–
2011	Colobus	2.22	26–39	0.14
	Sykes'	1.30	653–611	0.25
	Vervet	0.56	85–96	0.45
2020	Colobus	0.36	75–84	0.55
	Sykes'	6.88	531–621	0.009
	Vervet	4.94	140–129	0.03

3.6.4 Cost-effectiveness

The mean cost of each bridge was USD 157. The cost increased with fewer crossings, yet the cost per crossing was < USD 0.10 in all three survey years (Table 3.5).

Table 3.5 Cost-effectiveness analysis in USD, estimating the cost of construction, installation, and maintenance of the canopy bridges in each survey year (2004, 2011, 2020) amortised over 5 years, measured against the extrapolated number of annual crossings for all species combined (colobus, Sykes' monkeys, vervet).

Survey year	Number of bridges	Construction	Installation	Maintenance	Number of crossings	Cost$^{-\text{crossing}}$ USD
2004	21	6150	1175	3831	109 317	9 ¢
2011	27	7680	1539	4422	275 575	5 ¢
2020	29	6330	1225	3955	237 433	4 ¢

3.7 Discussion

We observed the four species of monkeys living sympatrically in Diani–colobus, Sykes' monkey, vervet, and baboon – crossing Beach Road on the ground, but only colobus, Sykes' monkey, and vervet regularly used the canopy bridges.

3.7.1 Crossings by substrate preference and body mass

Bridges facilitated road crossings for Sykes' monkeys at higher rates than colobus and vervets and vervets at higher rates than colobus. We observed baboons using the bridges only three times. Our results did not meet the predictions of bridge use by species' attributes of either stratum preference or body mass; however, both predictions ranked baboons as the species with the lowest bridge use.

We suggest the interaction between stratum preference and body mass may be more informative (Figure 3.6). While our results are, to some extent, consistent with these predictions, the addition of crossing rates for other species will determine if stratum preference and body mass together are predictive of species canopy bridge use. We note that there are additional factors that possibly constrain bridge use. For example, the colobus hand does not have a thumb, the typical morphology of the African colobines (Oates & Davies, 1994), which with their larger body size, may contribute to greater instability on the bridges resulting in a lower crossing rate than otherwise would be expected.

Interestingly, but perhaps coincidentally, the spider monkey (*Ateles* spp.), a genus also lacking a thumb, has not been observed to use bridges (Aureli et al., 2022). While we observed baboons crossing the road frequently on the ground, we only recorded three bridge crossings. These were observed in 2004; within 8 minutes, 2 individuals crossed west, and 1 crossed east. Although the bridges do not mitigate the road barrier effect for this species, the annual proportion of the population involved in vehicle collisions on Diani's Beach Road is <1.75% (Cunneyworth & Duke, 2020), which

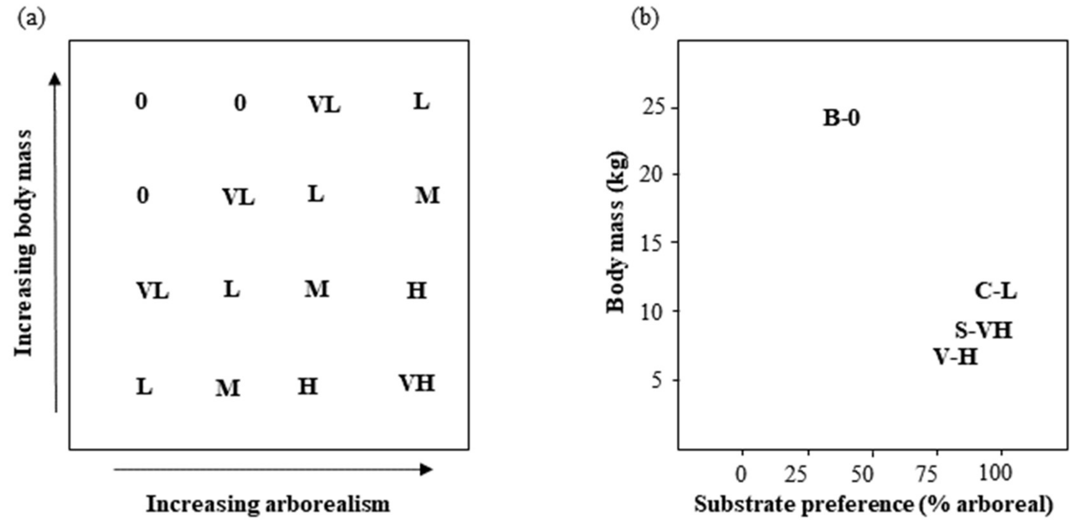

Figure 3.6 Representation of species' attributes, substrate preference and body mass (kg of Diani's adult males), hypothesised to constrain the canopy bridge crossing rate (a) predictions, and (b) our results (C = colobus, S = Sykes' monkey, V = vervet, B = baboon). Crossing rates (number of bridge crossings/population size) defined as 0 = few to no crossings, VL (Very Low) = 0.1, L (Low) = 0.25, M (Medium) = 0.5, H (High) = 0.75, VH (Very High) = 0.9.

is likely sustainable (Robinson & Bodmer, 1999). We found only one reference of bridge use by baboons elsewhere. Subadult chacma baboons (*Papio ursinus*) in South Africa infrequently used pole bridges (Linden et al., 2020). Baboons are a large, highly terrestrial species, and together these attributes may contribute to their lack of bridge use. Perhaps at higher traffic volumes, baboons will use the bridges. Yet, testing various bridge designs is warranted for baboons (and other large, terrestrial species). Specifically, the overall width of the bridge (side to side) could mitigate the larger body mass, and incorporating netting from the ground to the top end of the canopy bridge, could mitigate the high degree of terrestrialism by providing access to the bridge from the ground (P. Cunneyworth & B. Linden, pers. comm.). Alternatively, speed calming measures (speed bumps) may also mitigate the road barrier effect for large, terrestrial primates.

Two papers discuss speed bumps but to mitigate primate-vehicle collisions rather than reduce the road barrier effect (Zanzibar red colobus (*Piliocolobus kirkii*): Struhsaker and Siex 1996; chimpanzees (*Pan troglodytes schweinfurthii*): Cibot et al. 2015).

3.7.2 Bridge crossing direction

Although we found species-specific road crossing patterns, bridge use was bidirectional for the three species across the survey years. These results provide evidence that bridge use facilitated reoccurring resource use in habitat on opposite sides of the road for colobus, Sykes' monkeys, and vervets, but not for baboons.

Landscape genetics (Sunnucks & Balkenhol, 2015) has not been conducted to characterise Diani's monkey populations. We studied the movement of individuals across the road, which precludes direct evidence of gene flow, an important aspect of the road barrier effect (Reed, 2004). We do not expect evidence of genetic population structuring present on opposite sides of the road for Sykes' monkeys, vervets, and baboons as we observed large numbers of road crossings on the ground for these species. Colobus present an interesting case as the crossings on the ground were frequent in 2004 but rarely occurred in 2011 and 2020, suggesting increased road avoidance in the latter two survey years. We postulate that this is due to increasing traffic volume due to the continued development in the town. Because colobus primarily cross the road on the bridges, we expect that bridges have a role in lessening the genetic diversity erosion of the subpopulations on opposite sides of Beach Road. In the absence of genetic studies, we expect future behavioural research to identify individuals moving from their natal group on one side of the road to a breeding group on the other side.

3.7.3 Traffic volume

Bridges facilitated road crossings at higher traffic volumes than crossings on the ground only for colobus. For Sykes' monkeys, there was no difference in traffic volume between crossing types (ground, bridge), and the more terrestrial vervets crossed the road on the ground at higher traffic volumes than on the bridges.

Once on the road, the ability to avoid vehicles factors into the magnitude and direction of the barrier effect (Fahrig & Rytwinski, 2009; Forman et al., 2003). While this effect is generally taxon-specific, differences among species within a taxon are evident. For example, two kangaroo rats, *Dipodomys merriami* and *D. microps*, showed neutral versus positive responses to the presence of roads (Garland & Bradley, 1984; Rosa & Bissonette, 2007). For primates, some data alludes to an awareness of risks from oncoming traffic that may factor into our observed differences. Vervets on the roadside of Diani's Beach Road looked toward the road and oncoming traffic before crossing (Amick, 2018). Colobus and Sykes' monkeys were rarely observed to do this. Another colobine, the Zanzibar red colobus, also does not look for vehicles before crossing the road (Struhsaker & Siex, 1996). However, among chimpanzees of the Sebitoli area, Uganda, most individuals look right and left before and during road crossings (Cibot et al., 2015). In Diani, vervets, a more terrestrial species, are at lower risk of vehicle collisions (~2% of the annual population) than the more arboreal colobus and Sykes' monkeys (~3% of the annual population of each species) (Cunneyworth & Duke, 2020) which may be because of this increased road awareness. Accordingly, this may explain the lower risk of vehicle collisions for vervets even though they cross the road on the ground at higher traffic volumes than bridge crossings.

3.7.4 Cost-effectiveness

A study calculated a cost-benefit analysis for 13 various mitigation measures against the costs of large ungulate vehicle collisions (Huijser et al., 2009). That study calculated the difference between construction, installation, and maintenance costs of the mitigations and the costs associated with collisions such as vehicle damage, human injury and death, loss of the hunting value of the animal, carcass removal and disposal, and towing and investigation. We, instead, calculated a cost-effectiveness analysis calculating the cost of the mitigation (construction, installation, and maintenance) against the cost of each crossing. We did not do a cost-benefit analysis because, of the collision costs associated with the large ungulate study, only carcass removal and disposal applied to our study. We chose not to include carcass removal and disposal because while Colobus Conservation carries out these activities, it would not necessarily be a service available at other study sites. We calculated the cost of each crossing as USD <0.10. A cost-benefit analysis places a net benefit in a dollar value of the program (= cost of mitigation less cost of collisions). In other words, the program is cost-effective when the net benefit is greater than zero. In contrast, the result of a cost-effectiveness analysis (= cost/outcome) is open to interpretation. We consider Diani's bridge project as an economical mitigation to the road barrier effect for the three species of monkeys that use the bridges, but ultimately donors and road engineers will determine if it is so. Within the primate canopy bridge literature, some studies include the bridge cost (construction and installation), but none include the annual maintenance cost or the bridge's life span before replacement. We encourage authors to include this information in their reporting so that cost-effectiveness analyses can be compared across sites.

Diani's bridges are different lengths, and additional sections are added with support poles for longer bridges. Because of these differences, there is some variability in individual bridge costs. However, the mean cost per bridge per year is USD 157. Diani's bridges are within the range of inexpensive bridges constructed in other areas(Garcia et al., 2022; Mass et al., 2011; Nekaris et al., 2020; Teixeira et al., 2013) even though the materials chosen must withstand the rapid rusting effects due to atmospheric humidity and salinity in the ocean-side town. Single-strand bridges are likely sufficient and less expensive for Sykes' monkeys and vervets, given our observations of their frequent use of telephone and electricity cables to cross the road. In Quepos, Costa Rica, a shift from a horizontal ladder to rope bridges was done strictly based on financial considerations (Lindshield, 2016). And, for samangos (a subspecies of *Cercopithecus mitis*, a species to which Diani's Sykes' monkey also belongs), poles were used more often than ladder bridges (Linden et al., 2020). Our observations of colobus walking on insulated electrical cables show that they use only short sections (<5 m) and, given their near-continuous exaggerated tail swings for balance, strongly suggest that single-strand bridges are insufficient as a bridge design for this species.

The cost-effectiveness analysis formula did not incorporate the non-tangible value of bridge use, which economists largely ignore (Chardonnet et al., 2002). For example, primates are crucial seed dispersers in tropical forests, spreading seeds either by spitting them out or through their faeces (Chaves et al., 2011; Sengupta et al., 2020). To date, the role of Diani's primates in dispersing seeds of rare and endemic tree species across the road has been unrecognized in cost-benefit analyses for road and power line mitigations. But as Diani's indigenous forest is part of the Coastal Forests of East Africa, a Global Biodiversity Hotspot (Myers et al., 2000), this benefit may be substantial. Other benefits such as from tourism (Ampumuza & Kaburu, 2023) should also be considered to improve the accuracy of the analysis.

3.7.5 Survey limitations and recommendations for future studies

Colobus Conservation installed the first canopy bridge across Diani's Beach Road in 1996, and within three years, 15 bridges were added (Colobus Conservation, unpubl. data). The rapid increase in the number of bridges in the organisation's early days prevents a pre- and post-mitigation installation study design (van der Grift et al., 2013). We, therefore, selected data for this study that is replicable and comparable to other study sites. As this is a population-level study, identifying the individuals crossing was impossible. We could not determine the contribution of specific individuals to the total number of crossings, yet as crossings occurred on multiple bridges for each species, these likely represent different individuals. Understanding how groups use bridges will inform on best practices for the choice of bridge spacing and location along the road.

While we collected a large sample of crossings, we recognise three limitations of our study. 1) The study was conducted on only two days in each survey year. Our assumption is that these days represent an ‘average’ crossing day in that year though we were unlikely to record all species that crossed each bridge. We do not expect substantial differences from what we observed because the species are closely bound to the study area and likely remain close to the bridges throughout the year. 2) In general, Diani’s monkeys appear habituated to the suburban sights and sounds. The monkeys display indicators of high levels of habituation to the bridges. For example, across the years, we have observed matings, playing, grooming, and resting on bridges, and individuals crossing back and forth and immediately back again. However, future studies should consider including variables such as traffic noise, the presence of pedestrians, and including motorcycles as vehicles, as we recognise that some monkeys will be more fearful than others, on a species and an individual level. These additional variables may help further to explain differences in crossing rates within and across species. 3) Other studies report periods of bridge habituation. An early Colobus Conservation report writes that, of Diani’s monkeys, only colobus delayed using the first bridge (Eley & Kahumbu, 1998). Though the report does not specify the habituation time for colobus, it indicates that colobus were using them regularly at least by eight months post-installation. None of our bridges were installed less than eight months before the survey; therefore, we believe that bridge habituation does not factor into our results.

Camera traps are a standard method for assessing canopy bridge use (Chan et al., 2020; Nekaris et al., 2020; Ow et al., 2022). We chose to use roadside observers because we were interested in understanding how traffic volume affected road crossings, data not available using camera traps. In addition, from a practical perspective, in a suburban area, the vandalism risk to camera traps is high.

3.8 Conclusion

Diani's Beach Road is an asphalt road with a speed limit of 50 km/h, and of the four sympatrically occurring species of monkeys, the horizontal ladder canopy bridges connect habitats on opposite sides of the road for three: colobus, Sykes' monkey, and vervet. Many studies assume that primate canopy bridge use reduces the road barrier effect, and our study provides evidence that they do so, but in a species-specific manner. Colobus, Sykes' monkeys, and vervets use the bridges bidirectionally, enabling individuals and groups to access spatially discrete resources. The interaction between stratum preference and body mass, and bridge use remains elusive and deserves further study. In addition, we wait to confirm if baboons will use bridges when traffic volume is higher than that currently on Beach Road or if a bridge redesign that distributes their body mass over a wider area and provides access from ground level promotes bridge use.

Cost-effective bridges are of particular interest to conservationists needing to justify mitigation investments to government agencies or non-governmental funders. Considering our results, conservation managers and road engineers can estimate the effectiveness of canopy bridges on populations across various monkey species and traffic volumes. This study fills knowledge gaps in this understudied mitigation, of which the urgency increases annually as road networks expand across primate range countries.

3.9 Acknowledgements

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Chapter 4. An effect of canopy bridges on monkey-vehicle collision hotspots: Spatial and spatiotemporal analyses

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4.1 Abstract

Almost one-quarter of primate species are reported to be involved in vehicle collisions. To mitigate these collisions, canopy bridges are used though their effectiveness is not broadly substantiated. We studied bridge impact on 23 years of vehicle collisions (2000–2022: *N* =765) with colobus (*Colobus angolensis palliatus*), Sykes' (*Cercopithecus mitis albogularis*), and vervet (*Chlorocebus pygerythrus hilgerti*) monkeys in Diani, Kenya. Along a 9 km road, collisions did not decrease over the study duration, although bridges increased from 8 to 30. Using the kernel density estimation plus (KDE+) method, collisions appeared highly concentrated at some locations. These concentrations, called hotspots, represent hazardous road segments, though the hotspots for all three species overlapped for only 3% of the road length. We then inspected the collision hotspots over time, using the spatiotemporal extension of the KDE+ method. We compared hotspot presence in the 3 years before and after bridge installation to determine if bridges mitigated these hotspots. Hotspots disappeared for ~60% of bridges post-installation, suggesting that bridges effectively reduce some collisions. However, of the bridges installed in locations that were not hotspots, 13% had hotspots emerge. Surprisingly, regardless of pre-installation hotspot occurrence, almost one-fifth of bridges had post-installation hotspots. To understand the extent to which bridges mitigate collisions, other factors need consideration, including species attributes and crossing behaviour, and road features and vehicle volume. We used the novel analytical method because it best suited our dataset, given the challenges of determining the bridge impact zone and the low collision frequency.

Keywords: Before–after study design, Diani Kenya, Horizontal-ladder design, Road overpass mitigation; STKDE+

4.2 Introduction

Roads are an unparalleled component of the environment, used by some wildlife species, but not others (e.g., Coffin 2007; Forman and Alexander 1998; Spellerberg 1998; Trombulak and Frissell 2000). Though roads, particularly paved roads, are separate from the biotic system, their most obvious influence on the surrounding community of living organisms is injuries and deaths from vehicle collisions (Jackson & Fahrig, 2011; Pagany, 2020). Although there is strong evidence of a negative impact of roads on wildlife populations, the effect is often species-specific and broadly varies given the taxa, their ability to avoid roads, and if they cross roads, their capacity to avoid vehicles, intentionally or unintentionally (Fahrig & Rytwinski, 2009; Jacobson et al., 2016).

Among the primates, almost one-quarter of species are reported to be involved in vehicle collisions (Galea & Humle, 2022; Hetman et al., 2019). In attempts to reduce this impact, artificial canopy bridges are used to encourage primates to cross roads aerially. There is an increasing number of publications describing bridge installation in primate range countries for this purpose (Buss et al., 2022; Corrêa et al., 2018; Flatt et al., 2022; Hidalgo-Mihart et al., 2022; Linden et al., 2020; Lindshield, 2016; Lokschin et al., 2007; Maria et al., 2022; Monticelli et al., 2022; Ow et al., 2022; Teixeira et al., 2013; Valladares-Padua & Cullen Jr., 1995).

Though bridge installation is increasing globally, information remains scanty regarding canopy bridge effectiveness in reducing primate-vehicle collisions. Only five papers quantify the extent that they do so. Four of these report the number of incidents before and after bridge installation, and all recorded a substantial reduction in collisions (Al-Razi et al., 2019; Maria et al., 2022; Monticelli et al., 2022; Rojas & Gregory, 2022; Yap et al., 2022). A fifth paper used 2D Ripley's *K* statistics to analyse a collision hotspot for marmosets (*Callithrix geoffroyi*) and showed that the hotspot did not disappear but remained stable after bridge installation (Franceschi et al., 2022).

In a study conducted between 2000 and 2018 in the suburban town of Diani, Kenya, community members reported to Colobus Conservation, a local conservation organisation, monkey-vehicle collisions along a 9 km section of Beach Road (Cunneyworth and Duke 2020). These reports involved injuries and deaths of colobus (*Colobus angolensis palliatus*), Sykes' (*Cercopithecus mitis albogularis*), and vervet (*Chlorocebus pygerythrus hilgerti*) monkeys. Compared with their local populations, ~3% of colobus and Sykes' monkeys and ~2% of vervets were injured or killed by vehicles annually (Cunneyworth and Duke 2020). Colobus Conservation began installing canopy bridges in 1996 across Beach Road to mitigate these collisions (Eley & Kahumbu, 1998).

Diani's canopy bridges effectively reduce the road barrier effect for colobus, Sykes' monkeys, and vervets but in a species-specific way (Cunneyworth et al. 2022). The effect was considerable for colobus because, at higher vehicle volumes, colobus almost exclusively crossed the road using the bridges rather than crossing on the ground. The impact was lowest for vervets as they are often terrestrial (Rose, 1979) and cross the road on the ground if they are already on the roadside.

While canopy bridges reduce the road barrier effect in Diani, whether they reduce monkey-vehicle collisions has yet to be demonstrated. We addressed this gap using the same long-term dataset (2000–2018: N =646) as previously analysed of monkey injuries and deaths (Cunneyworth & Duke, 2020), with an additional 119 cases (N =765) collected from 2019 to 2022. We hypothesised that when a canopy bridge is installed, monkeys preferentially cross the road on the bridge, resulting in fewer crossings on the ground and, therefore, fewer collisions. Therefore, for each species (colobus, Sykes' monkey, vervet), we predicted that the number of collisions would decrease over time because of the increasing number of canopy bridges installed across the road throughout the study duration (2000: 8, 2022: 30). We then modelled the data using the KDE+ method (Kernel Density Estimation plus) to understand the extent to which these collisions were spatially concentrated (i.e., forming hotspots). If collisions are concentrated, then these hotspots identify the hazardous road segments for each species.

We then employed a Before–After study design using a 3-year window. We modelled the data using the STKDE+ approach (Spatiotemporal extension of the KDE+ method) by adding the temporal variable, collision date, to the analysis. We superimposed the canopy bridge locations by the year of occurrence onto the STKDE+ output graphs. We hypothesised that if the canopy bridges effectively reduced monkey-vehicle collisions, collision hotspots occurring 3 years before installation would disappear at the mitigated locations in the 3 years after installation.

4.3 Methods

4.3.1 Study site and species

The original forest of Diani, a suburban town on the southeastern coast of Kenya (−4.290496°, 39.585727°), is part of the East Africa Coastal Forest, Global Biodiversity Hotspot (Myers et al., 2000). Diani has developed along the Indian Ocean coastline (Figure 4.1), with its economy based on the hospitality industry. Though development continues, original forest trees and patches remain interspersed with exotic vegetation. The study area of the town is only 7 km^2, yet ~1500 monkeys are occurring in proximity to the homes, hotels, and businesses (Cunneyworth and Duke 2020). Of the four species of monkeys sympatrically occurring in Diani, three use canopy bridges (Cunneyworth et al. 2022): Peters' Angolan colobus (colobus), Zanzibar Sykes' monkey (Sykes' monkey), and Hilgert's vervet (vervet). These species have varying attributes: colobus are arboreal folivores (Anderson 2005; Dunham 2017), Sykes' monkeys are arboreal frugivores (Takahashi et al., 2019), and vervets are semi-terrestrial omnivores (Cheney et al., 1988; Rose, 1979). All three species are sexually dimorphic, with adult males reaching 11, 8, and 5 kg, respectively (Harvey et al., 1987). southern yellow baboons (*Papio cynocephalus cynocephalus*), which also occur in Diani, rarely use the canopy bridges.

4.3.2 Road features

In 1971, Diani's Beach Road was built through primary forest. It runs north to south, bisecting the town 200–450 m inland. The 6 m wide asphalt road is flat, has a single lane in each direction, and has a 50 km/h speed limit. As Beach Road is the only main road in Diani, vehicles use this road almost exclusively to travel between destinations within the town. We limited our study to the 9 km road section (−4.26762°, 39.59553° to −4.34224°, 39.56377°) where Colobus Conservation installed the canopy bridges.

We highlight three road features (Figure 4.1). (1) The road is fairly straight with one S-curve ~2.1 km long (−4.30918°, 39.57709° to −4.32524°, 39.57000°). Driver visibility to see monkeys on the road and roadside and monkey visibility to see oncoming vehicles are limited on approaches to tighter bends. However, visibility is markedly reduced on the 130 m southernmost section of the S-curve because of the trees growing near the roadside. (2) One major intersection occurs on Beach Road (−4.29053°, 39.58592°), which links Diani with Ukunda town, located on the main Mombasa highway to Tanzania. Most vehicles entering or leaving Diani pass through this T-intersection. While there are numerous intersections along Beach Road–dirt roads, beach accesses, and driveways–vehicle volume at these intersections is lower than at the T-intersection. (3) On a property 300 m long, trees and most of the other bushy vegetation were removed to install electrical infrastructure alongside the road, creating a 30 m wide gap between the trees on opposite sides of the road (−4.32950°, 39.56843° to −4.33216°, 39.56746°).

Figure 4.1 Study site in Diani, Kenya, showing highlighted road features: (a) S-curve, (b) T-intersection, and (c) 30 m vegetation gap where the road and electrical infrastructure are co-aligned. Photos from Google Earth Pro, Street View, imagery date 03/2018.

4.3.3 Canopy bridges

All canopy bridges installed along Diani's Beach Road are of the horizontal-ladder design (Figure 4.2) (Cunneyworth et al. 2022). Colobus Conservation developed this bridge design in 1996 to facilitate colobus crossings, given that they lack a thumb, which is the typical hand morphology of African colobines (Oates & Davies, 1994). Our observations indicate that pole bridges, which may be effective for Sykes' monkeys (Linden et al., 2020) and vervets, do not provide sufficient stability for colobus, especially for distances necessary to cross roads.

The number of canopy bridges increased over time (Figure 4.3) when funding became available. Four criteria determine the installation site: (1) a bridge cannot be near electrical infrastructure; (2) anchor trees on opposite sides of the road must be large enough to support the bridge; (3) canopy cover must extend beyond the anchor trees; and (4) bridge length must be ≤40 m. There is no consideration for a minimum distance between bridges if a site meets the criteria. Distances between bridges range from 40 to 1650 m. On four occasions, Colobus Conservation removed bridges when at least one selection

Figure 4.2 A canopy bridge (a) anchored in a roadside tree, (b) across Diani's Beach Road, (c) used by a Sykes' monkey with the horizontal ladder bridge design visible. Colobus Conservation photo library.

criterion was no longer valid. One bridge was removed when the national power company installed electrical cables at the bridge location, and consequently, there were wildlife electrocution concerns. One bridge was removed because the vegetation of the adjacent property was clear-cut in preparation for development, one was removed because a bridge's anchor tree was cut down, and one became unsafe to use when the supporting wooden pole rotted. In an additional four cases, the bridge was shifted less than 20 m, which occurred when the anchor tree or main branches of the anchor tree died or the tree was cut down. Maintenance is carried out on each bridge four times annually, with bridges rebuilt approximately every 5 years.

4.3.4 Monkey-vehicle collisions

The local community reports primate welfare incidents to Colobus Conservation. The Colobus Conservation team immediately responds to investigate these reports. If they find a dead monkey, they retrieve and dispose of it. If the monkey is injured or sick and requires veterinary care, they capture the individual, provide care, and then release it back to its group or the location where they found it. For each incident, the team writes notes on standardised datasheets listing the species, date, case description, incidence location described by landmarks, and a GPS (Global Positioning System) waypoint.

We created a subset of these welfare incidents limited to monkey-vehicle collisions (injuries and deaths), 2000–2022, and along the 9 km section of Diani's Beach Road, where the canopy bridges occur. We included only incidents for the three species of monkeys that use the canopy bridges (colobus, Sykes' monkey, vervet) (Cunneyworth et al. 2022). When only a landmark was noted for the collision location on the datasheets, we estimated the GPS waypoint based on a site survey or using Google Earth Pro Street View.

4.3.5 Data analysis

We predicted that the collision number would decrease given the increase in canopy bridges (from 8 to 30) over the study duration (2000–2022; N =23 years). Using a one-sided Mann–Kendall trend test for each species (colobus, Sykes' monkey, vervet), we tested the null hypothesis that there was a nondecreasing trend in the number of collisions, against the alternative that there was a decreasing trend in the number of collisions. The significance level was set to 0.05/3 = 0.0167 using the Bonferroni correction for multiple comparisons. Any p value below this threshold indicates a statistically significant decrease in collisions.

We analysed the extent to which vehicle collisions are spatially clustered for each species using the KDE+ (Bíl et al., 2016) downloadable software (http://kdeplus.cz/en/method). If hotspots are identified, it would indicate that the respective road segments had a significantly higher frequency of collisions than expected (i.e., according to a random uniform distribution). The threshold for statistically significant hotspots was estimated by the Monte Carlo method (Bíl et al., 2013). We uploaded shapefiles for the 9 km study section of Beach Road and the collision GPS waypoints for each species. The software identified the hotspots and reported the number of collisions within each hotspot and each hotspot's length (m). The analysis accounts for the collision number in a hotspot and total number of collisions on the road, and the hotspot length and total road length (Bíl et al., 2013). Instead of a 150 m kernel size bandwidth used for collision modelling on highways, we chose a 100 m bandwidth recommended for rural road studies (Bíl et al., 2013) because, in the urban setting, vehicle breaking distances and driver visibility ranges are also shorter.

We calculated the percentage of the road length where hotspots overlapped between species to determine the extent that hazardous road segments were species-specific. We visualised the collision hotspots from the KDE+ output shapefiles in QGIS v. 3.18 and annotated the three highlighted road features on the resulting maps (S-curve, T-intersection, and the road segment with the 30 m vegetation gap where the road and electrical infrastructure are co-aligned).

We then compared the data 3 years before and after bridge installation to determine if bridges effectively reduce collision hotspots. We chose a 3-year window because longer time frames would likely introduce confounding effects as the urban environment changes (Cheng & Washington, 2005; Elvik, 2008). We added the temporal variable to the KDE+ method using the downloadable STKDE+ toolbox for ArcGIS (http://kdeplus.cz/en/stmethod) (Bíl et al., 2019). We uploaded the files we used for the KDE+ model with the date for each collision added. The analysis generated output graphs visualising the collision hotspots resulting from the combination of the spatial variable (collision location along the 9 km road section) and the temporal variable (collision date from 2000 to 2022). As with KDE+, the STKDE+ threshold for statistically significant hotspots was estimated by the Monte Carlo method (Bíl et al., 2013).

We superimposed onto the STKDE+ output graphs bridge locations for their years of occurrence. We summarised the impact of the canopy bridges on the monkey-vehicle collision hotspots for each of the three species (colobus, Sykes' monkey, vervet). We recorded whether a collision hotspot was present before the installation of each bridge. If yes, we recorded if the hotspot disappeared or remained stable for the 3 years after installation. If the location did not have a hotspot before bridge installation, we recorded whether a hotspot emerged after installation. The STKDE+ method calculates collision hotspots based on a moving window throughout the study duration, which we chose to be 3 years. Accordingly, collisions of the previous 3 years are reflected in the hotspot occurrence precisely at the end of each time window (Bíl et al., 2019). Out of the 34 bridges (30 currently installed + 4 previously removed) that occurred along Diani's Beach Road, only 13 had 3 years before and after data available.

4.4 Ethical note

Kenya Wildlife Service and the National Commission of Science, Technology, and Innovation granted the permits for this study (permit number: NACOSTI/P/18/13412/26289). This was a desk-based analysis; as such, no animals were handled during this study. This research adhered to the American Society of Primatology's Principles for Ethical Treatment of Nonhuman primates.

4.5 Supplementary material

The data that supports the findings of this study are available in the supplementary material: https://onlinelibrary.wiley.com/action/downloadSupplement?doi=10.1002%2Fajp.23492&file=ajp23492-sup-0001-Supplemental_data_Revision_2.docx.

4.6 Results

Between 2000 and 2022, there were 765 vehicle collisions involving the three species of monkeys that use canopy bridges on Diani's each Road (colobus: N =184, 24%; Sykes' monkey: N =455, 60%; vervet: N =126, 16%). The results of the one-sided Mann–Kendall trend test showed that there were no significant declines in the time series for any of the species suggesting that the frequency of collisions did not decrease over time (Figure 4.3) (colobus: $\tau = -0.20$, N =23 years, $p = 0.11$; Sykes' monkey: $\tau = 0.18$, N =23 years, $p = 0.88$; vervet: $\tau = 0.01$, N =23 years, $p = 0.51$). Applying the KDE+ model, 547 of the 765 collisions (72%) occurred within hotspots (Table 4.1). These hotspots were species-specific (Figure 4.4). Hotspots of colobus and Sykes' monkeys overlapped for 16% of the road length (1453 m), colobus and vervets overlapped for 6% (551 m), and Sykes' monkeys and vervets overlapped for 8% (672 m). Approximately 3% (249 m) of the road had overlapping hotspots for all three species.

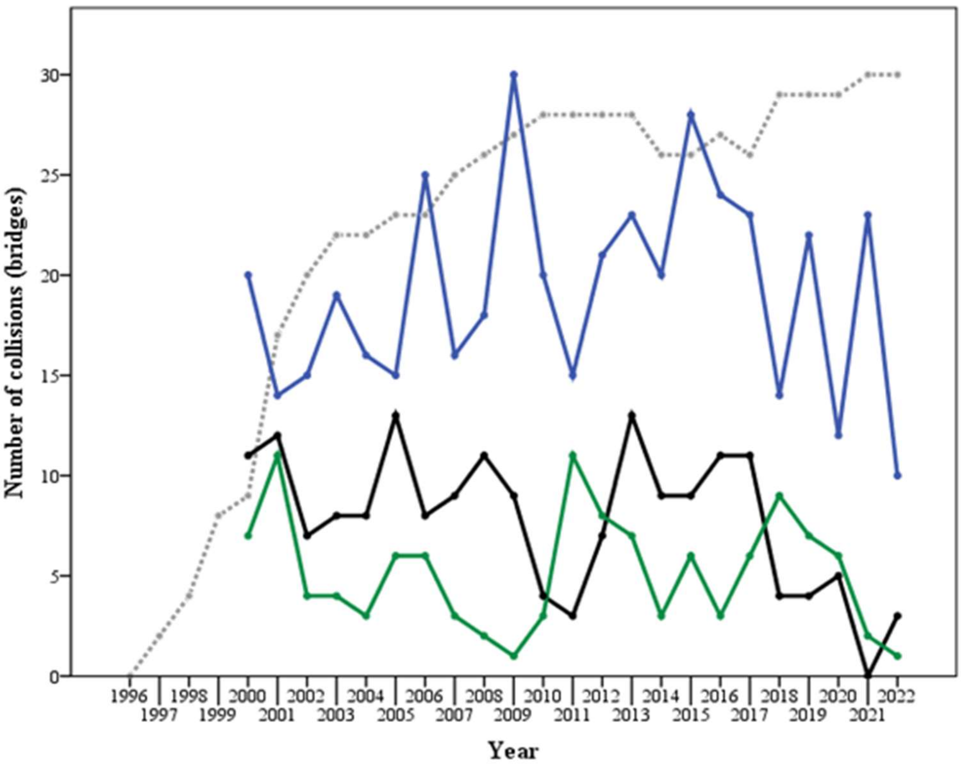

Figure 4.3 Along the 9 km section of Diani's Beach Road, the number of injuries and deaths reported for each species of monkey (colobus: black, Sykes' monkey: blue, vervet: green), 2000–2022. Also displayed is the number of canopy bridges present each year along the same road section (dashed line).

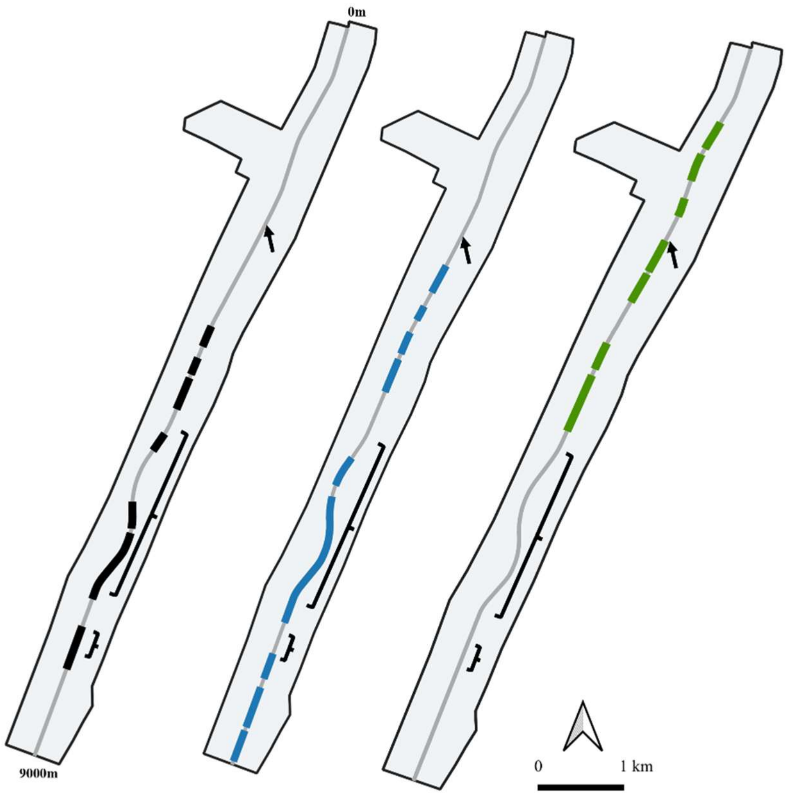

Figure 4.4 Kernel density estimation plus visualisations of the collision hotspots along the 9 km section of Diani's Beach Road (light grey line, 0–9000 m), 2000–2022, for each species, colobus (left), Sykes' monkey (middle), vervet (right). Highlighted road features are noted as S-curve = wide bracket, T-intersection =arrow, 30 m vegetation gap caused by the road and electrical infrastructure co-alignment = narrow bracket.

Table 4.1 Results of the KDE+ analyses by species (colobus, Sykes' monkey, vervet) indicating hotspot characteristics for the monkey-vehicle collisions (*N* =765) along the 9 km section of Diani's Beach Road, 2000–2022.

Species	Total collisions	Number of hotspots	Number of collisions in hotspots	% of total collisions in hotspots	Road length (m) of hotspots	% of road with hotspots
Colobus	171	7	107	63	2050	23
Sykes’	422	10	312	74	3265	36
Vervet	119	7	88	74	1539	17

The STKDE+ analyses identified collision hotspot changes over time (Figure 4.5). Canopy bridge installation had some impact on these hotspots (Table 4.2). When bridges were installed in locations within hotspots, the majority of hotspots disappeared within 3 years after installation (cases hotspots disappeared/total cases bridges installed in hotspots: N =5/8, 62.5%). Some hotspots emerged when bridges were installed in locations that were not hotspots in the 3 years before installation (cases hotspots emerged/total cases bridges installed in locations that were not hotspots: N =4/31, 13%). Surprisingly, 18% (7/39) of bridges had hotspots after installation (four emerging hotspots + three stable hotspots). Similarly, when we considered all bridges with 3 years of post-installation data (N =39), 18% had collision hotspots after installation (colobus: 4, Sykes': 2, vervet: 1).

Table 4.2 Results of the 3-year before and after comparison of the impact of canopy bridge installation on vehicle collision hotspots along Diani's Beach Road, 2000–2022, for colobus, Sykes' monkey, and vervet.

Bridge installed:	No hotspot $N = 31$		Hotspot $N = 8$		Total bridges
Bridge impact:	No change	Hotspot emerged	Hotspot disappeared	Hotspot stable	
Colobus	8	3	1	1	13
Sykes’	9	1	2	1	13
Vervet	10	0	2	1	13
Total	27	4	5	3	

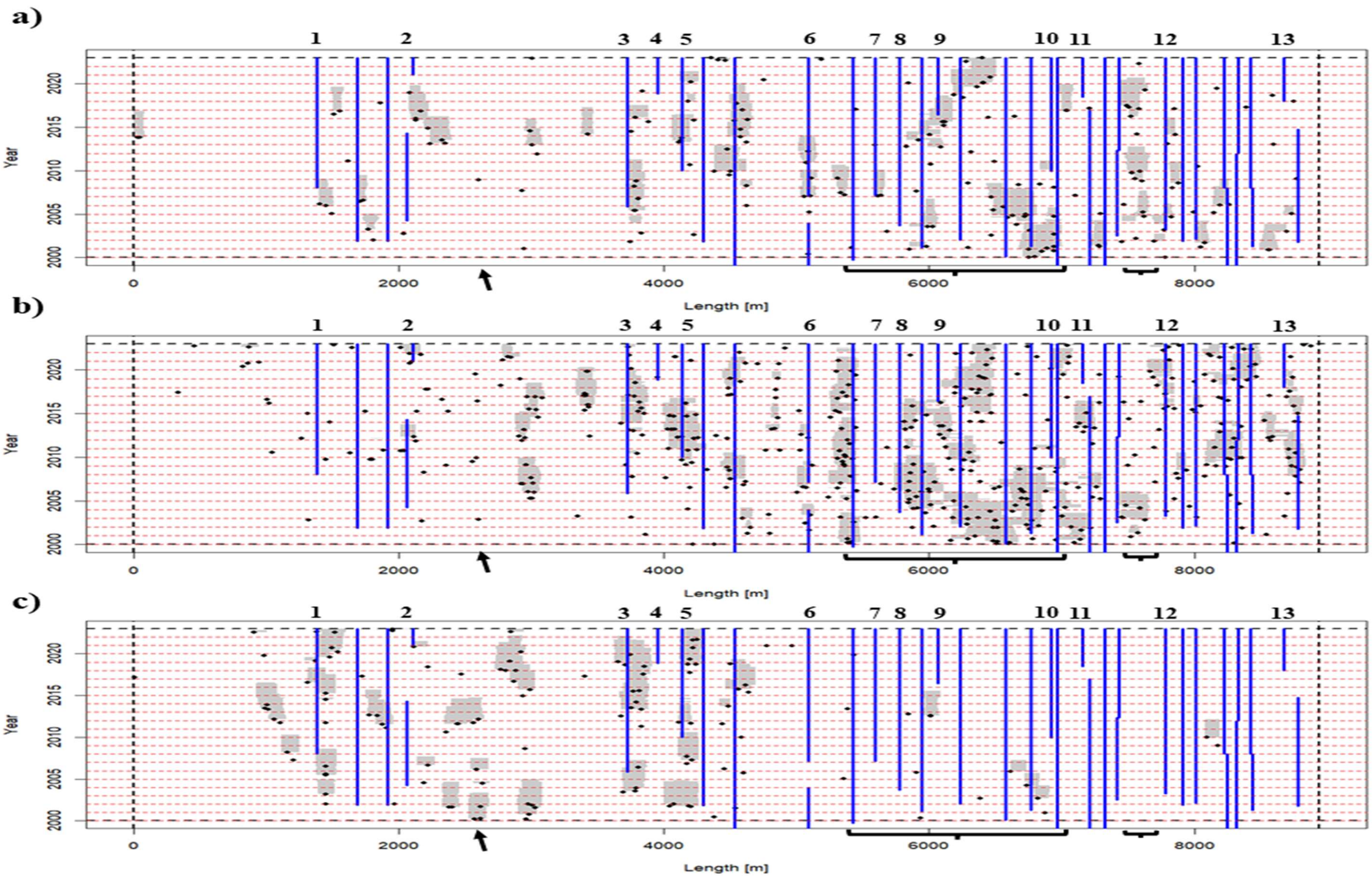
a)
b)
c)
1 2 3 4 5 6 7 8 9 10 11 12 13
Year
2000
2005
2010
2015
2020
0
2000
4000
6000
8000
Length [m]

Figure 4.5 Spatiotemporal kernel density estimation plus modelling for each species, (a) colobus, (b) Sykes' monkey, (c) vervet, north to south, along the 9 km section of Diani's Beach Road (0–9000 m). Black dots indicate monkey-vehicle collisions in space (horizontal axis) and collision date as time 2000–2022 (vertical axis). Gray shading indicates collision clustering. Vertical blue lines represent canopy bridge locations over time. Highlighted road features are noted as S-curve = wide bracket, T-intersection = arrow, 30 m vegetation gap caused by the road and electrical infrastructure co-alignment = narrow bracket. Bridges noted as 1-13 were used for the before-after collision hotspot analysis.

4.7 Discussion

The annual number of vehicle collisions with colobus, Sykes' monkeys, and vervets on Diani's Beach Road did not show a downward trend even though the number of canopy bridges increased from 8 to 30 over the 23-year study. However, the collisions were not random along the road, as ~70% occurred in hotspots. These hotspots represent hazardous road segments but were species-specific, as only 3% of the road length overlapped across the three species. There is evidence that canopy bridges reduce vehicle collision hotspots because when bridges were installed in collision hotspots, the majority of hotspots disappeared in the 3 years after installation. Surprisingly, however, some hotspots remained stable when bridges were installed in hotspots, and some hotspots emerged after bridge installation in locations that did not have hotspots. Overall, almost one-fifth of bridges had hotspots 3 years post-installation.

4.7.1 Collision clustering

Studies of wildlife-vehicle collisions found that these incidents cluster (Kronprasert et al., 2021; Shilling & Waetjen, 2015). Collision clustering also appears to be the case for primates (Corrêa et al., 2018; Franceschi et al., 2022; Linden et al., 2020). It is, therefore, unsurprising that Diani's monkey-vehicle collisions occur in hotspots and that these hotspots are species-specific. The low hotspot overlap across species is likely because of attribute differences (i.e., substrate preference–arboreal vs. terrestrial and diet–folivore, frugivore, omnivore) which leads to varying population densities proximate to the urban road and each species' ability to cross the road while avoiding vehicles. These differences highlight additional considerations when planning mitigations that target multiple species, even within a single taxon.

4.7.2 Bridge effectiveness

Our results show that bridges can reduce vehicle collision hotspots in some cases. We presume that when bridges become available, individuals preferentially use bridges rather than continue crossing the road on the ground. However, the presence of collision hotspots for almost one-fifth of the bridges after the installation was unexpected. Regardless of collisions continuing near bridges, bridges can lessen the overall population risk of extirpation. For example, the median proportion of Diani's population of colobus and Sykes' monkeys involved in collisions annually over the past two decades is 3% (Cunneyworth and Duke 2020). Extrapolation of crossing data on Diani's bridges suggests that >200,000 occur annually (Cunneyworth et al., 2022). Without the bridges, the annual mortality rate would almost certainly exceed 4% for these species, which is considered the maximum rate for sustainable replacement in primates (Robinson & Bodmer, 1999).

Canopy bridge studies often present bridge crossing frequency to evaluate bridge effectiveness in mitigating vehicle collisions (Flatt et al., 2022; Ow et al., 2022; Saralamba et al., 2022). However, bridge use does not directly measure their effectiveness in reducing collisions (van der Grift et al., 2013). There appears to be an assumption in the literature that the number of bridge crossings inversely correlates with collision number. Bridge crossings, however, are a more reliable measure of the road barrier effect (van der Ree et al., 2007) than a measure of collision risk.

Future studies should investigate whether bridge use reduces the road barrier effect while concurrently increasing collision risk through an associated increase in the frequency of ground crossings. In other words, as more individuals and groups cross the road on a bridge, it may be that there is an increase of individuals crossing the road on the ground during the same crossing event. In Diani, for all three species that use bridges, it is regularly observed that during group crossings, some individuals cross on the bridge and some cross on the ground (P. Cunneyworth, pers. obs.). This behaviour may explain why the increase of bridges in Diani over the study duration did not show a downward trend in collisions and why hotspots exist for almost one-fifth of the bridges after installation. Fencing is commonly used to prevent wildlife road access except at crossing structures (van der Ree et al. 2015). However, for monkeys with exceptional climbing ability, an effective fence design blocking ground crossings would be challenging. But perhaps even more challenging are the practicalities of fence installation in an urban area, such as acquiring permits, inconvenience to pedestrians, and fence gaps from adjoining roads and driveways.

The reason why road crossings continue to occur on the ground after bridge installation is unknown. It is also unknown whether this road-crossing behaviour occurs in other primate species. These unanswered questions highlight the importance of continued monitoring of road crossings on the bridges and ground and that camera traps used for tabulating bridge crossings (Garcia et al., 2022; Prasetyo et al., 2022; Yap et al., 2022) collect only part of the dataset necessary to understand the extent to which bridges are effective in reducing collisions.

4.7.3 Road features

We highlight three road features, the S-curve, T-intersection, and the 30 m vegetation gap for the co-alignment of the road and electrical infrastructure. Though all three road features have collision hotspots, the S-curve has bridges, while the T-intersection and the vegetation gap do not.

The 2.1 km long S-curve has 10 bridges; all except one were installed in the earlier years of the study. The potential for vehicle accidents on road curves is established (Kronprasert et al., 2021; Mićić et al., 2022), but even with many bridges along the S-curve, there are numerous hotspots for colobus and Sykes' monkeys. Driver visibility of monkeys on the road and roadside and monkey visibility of oncoming vehicles are limited on parts of the S-curve, which may explain the long-standing collision hotspots. Collision hotspots for colobus and Sykes' monkeys on the curve's southernmost section exemplify this, as trees near the roadside markedly reduce visibility for both drivers and monkeys.

On the southernmost section of the S-curve, collision hotspots for colobus and Sykes' monkeys were reduced by 2010. Our analyses did not consider the increasing vehicle volume over time, even though the relationship between vehicle volume and wildlife-vehicle collisions is well-known (Bíl et al., 2020; Kruuse et al., 2016; Ng et al., 2008; Zuberogoitia et al., 2014). Diani's colobus, and to a lesser extent, Sykes' monkeys, appear to have upper limits on vehicle numbers passing, above which ground crossings are considerably reduced (Cunneyworth et al. 2022). Because of the vehicle volume effect on ground crossings, we suspect an increasing road barrier effect caused the collision hotspots to disappear from 2010 onwards, rather than bridge effectiveness reducing the monkey-vehicle collision hotspots.

All three species showed collision hotspots on the southern approach towards the T-intersection at some point during the study period. Almost all vehicles pass through this intersection as they enter and exit Diani, so the vehicle volume is higher than in other areas along the road. No canopy bridges exist in this area because the selection criteria cannot be fulfilled as this area has extensive development. Other mitigations, such as signage and speed bumps, should be considered in urban areas under similar conditions. However, studies of their effectiveness for primates remain little studied as there are no qualitative analyses on signage to prevent primate-vehicle collisions, and only one study on speed bumps (which found them effective) (Olgun et al., 2021).

An example of a cumulative effect of two types of infrastructure is a location where the electrical infrastructure is co-aligned with Beach Road, and the trees that would otherwise have anchored canopy bridges were removed. In this case, colobus collision hotspots exist, which begs the question of the motivation for this folivorous, highly arboreal, forest-dependent species to cross this 30 m gap. High-level bridges placed above the power cables are an option, as installed for howler monkeys (*Alouatta palliata*) in Costa Rica (Lindshield, 2016).

4.7.4 Bridge site selection criteria

Our bridge site selection criteria focuses on the immediate installation requirements. Extensive site selection criteria have been drafted for canopy bridges across pipeline rights-of-way (Gregory et al., 2013), but only scattered information is available for bridges over roads that target primates. Several studies (Flatt et al., 2022; Hidalgo-Mihart et al., 2022) describe similar criteria as ourselves, while others installed bridges in locations where primates cross the road (Buss et al., 2022; Rojas & Gregory, 2022; Teixeira et al., 2013; Valladares-Padua & Cullen Jr., 1995). Some ensured that primates were present in the surrounding area, and that landowners were willing to have bridges on their properties (Narváez Rivera & Lindshield, 2016; Valladares-Padua & Cullen Jr., 1995), and several publications stated that the main criterion was a collision hotspot (Lokschin et al., 2007; Maria et al., 2022; Ow et al., 2022; Teixeira et al., 2013).

Using our bridge site selection criteria, at the end of our study (December 31, 2022), five opportunities were missed for placing bridges in hotspots. Yet, our study and others (Teixeira et al., 2017) indicate that restricting bridges to collision hotspot locations misses bridge opportunities. Guidelines are needed outlining the range of requirements to be considered for selecting bridge installation locations to ensure their highest possible frequency of use.

4.7.5 Study design

We considered the recommended BACI (Before, After, Control, Impact) study design to determine if the canopy bridges reduced the monkey-vehicle collisions as suggested for these types of studies (van der Grift et al., 2015). For several reasons, our dataset was best suited to only the before and after aspect with a STKDE + hotspot analysis, noting that the KDE+ analysis, which is the core of the STKDE+ analysis, has been used to study road collisions across a range of taxa (amphibians and reptiles: Heigl et al. 2017; ungulates: Favilli et al. 2018; range of mammals: (Bartonička et al., 2018; Périquet et al., 2018).

(1) Collision numbers 3 years before and after bridge installation were few, negating the use of *t* tests on the differences. In contrast, the STKDE+ analyses generated hotspots based on a statistically significant deviation from a random uniform distribution providing an objective method for comparison. We simply identified if bridges intersected with hotspots on the output graph. (2) Counting collisions before and after a bridge installation requires a subjectively chosen road segment length from which collisions are included (Bíl et al., 2016). The four previous studies that presented before and after monkey-vehicle collision numbers (Maria et al., 2022; Montilla et al., 2020; Rojas & Gregory, 2022; Yap et al., 2022) were ambiguous on the road segment length used and the relationship between the bridge impact zone and the location of the collisions. The STKDE+ analysis eliminates the subjectivity introduced when deciding which collisions to include in the analysis. In other words, the STKDE+ analysis does not use road segments. Instead, it requires a smoothing parameter called bandwidth to estimate the probability density function. This parameter is not completely subjectively chosen as it stems from the driver visibility range and the braking distance of a vehicle. The results are not, however, sensitive to this parameter (a slight change of this parameter has only a negligible effect on the results). Collision counts, on the other hand, are sensitive to the chosen segment length because it determines whether a collision is counted or not (a slight change in the segment length may significantly change the results). (3) One primate study presented a collision

clustering analysis using 2D Ripley's K statistic (Franceschi et al., 2022). While that type of analysis measures the general tendency of collision clustering through one dimension (space) (Gunson et al., 2009), the STKDE+ method identifies the exact positions of hotspots based on time and space. Thus, the STKDE+ method better reflects our aims at determining whether a specific bridge mitigates a collision hotspot.

Furthermore, using the control and impact study design is complex because in the growing town of Diani, monkey access to human-derived foods and other resources, such as sleeping sites and water, changes frequently. These changes, in turn, affect the motivation for monkeys to cross the road at any specific location. We chose a 3-year window before and after bridge installation to reduce these confounding factors and avoid reporting false positives. While we recognise the importance of the control-impact study design, it is perhaps more suited to highways or established towns, for example, with greater environmental uniformity in time and space.

4.7.6 Study limitations

This study assumes that all monkey-vehicle collisions were reported over the past 23 years. While this cannot be the case, our confidence that the dataset is robust is high. Colobus Conservation is well known in the area and has been since the organisation's inception in 1996 when Diani was a much smaller town. Our team continually interacts with the community and provides contact details for reporting welfare cases. We also are confident that the proportion of missed monkey-vehicle collisions is similar across the study years because, throughout the study duration, the staff have driven the road numerous times daily while commuting between their homes and work and carrying out the project activities. These are opportunities to detect incidents without relying on the community to report them.

The dataset began before GPS devices became widely available. Even when available, the devices sometimes had technical issues. These limitations reduced the number of incidences with exact locations of the monkey-vehicle collisions. In these cases, we used the landmark described in the datasheet, lowering the spatial variable's overall accuracy (Gunson et al., 2009). We used the KDE+ and STKDE+ software 100 m bandwidth smoothing parameter, reducing this impact on our results as the bandwidth means, spreading the collision risk along the road (Anderson, 2009).

The population size for each species in Diani has remained remarkably stable over the study years (Cunneyworth and Duke 2020), suggesting that the changes in collision hotspots were not an effect of demographic variables. We also considered that groups might shift in range resulting in a corresponding shift in the crossing points (Yap et al., 2022). Multiyear studies in Diani indicate that ranges are also stable over time (Donaldson, 2017; Dunham, 2017). However, home ranges are expected to change as properties are clear-cut and developed and vegetation regrows or is planted. For this reason, we limited the before and after window to 3 years.

4.8 Conclusion

We present a novel approach for analysing the impact of canopy bridges on monkey-vehicle collisions. The main advantages of the STKDE+ method are that we did not need to determine the bridge impact zone, and it overcame the analytical challenges from low collision occurrences before and after bridge installation. The STKDE+ hotspot analysis indicates that bridges over Diani's 2-lane road sometimes mitigate collisions. But determining bridge effectiveness to reduce monkey-vehicle collisions is not as simple as one might expect. It involves exploring the impact of species' attributes and road-crossing behaviours, and road features and vehicle volume on where and when collisions continue to occur. Without this, continued collisions may be confused with bridge ineffectiveness, although it seems unrealistic to expect that canopy bridges can completely eliminate primate-vehicle collisions.

4.9 Acknowledgements

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Chapter 5. Impact of electric shock and electrocution on populations of four monkey species in the suburban town of Diani, Kenya

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5.1 Abstract

Electric shock and electrocution affect at least 31 primate species, but studies of how electrical infrastructure affects primate populations are rare. We investigated 320 cases of electric shock and electrocution in four sympatric monkey species in Diani, Kenya, 1998–2019: Peters' Angola colobus (*Colobus angolensis palliatus*), Zanzibar Sykes' monkey (*Cercopithecus mitis albogularis*), Hilgert's vervet (*Chlorocebus pygerythrus hilgerti*), and the southern yellow baboon (*Papio cynocephalus cynocephalus*). These represent 16% of the total welfare cases reported to a local conservation organisation. Deaths occurred in 73% of cases. The number of cases did not increase through the study period, presumably because mitigations implemented by the power distribution company and a local conservation organisation offset the risks associated with the electrical infrastructure expansion. Colobus accounted for 80% (*N* =256) of cases, representing ca. 4.6% of the population annually, which is likely unsustainable. Adult male colobus were shocked or electrocuted more than expected, while all other age–sex classes were involved in proportion to the population structure. The number of cases was low for Sykes' monkey (13%, *N* =42), vervets (5%, *N* =16), and baboons (2%, N= 6). Our findings show that electrical infrastructure affects species differentially; larger arboreal species with individuals ≥8 kg are at higher risk of injury and death than smaller arboreal species and terrestrial species. Other organisations can estimate risks in their areas based on the factors we reviewed. Further understanding of how body mass impacts risk will have implications for designing electrical infrastructure as part of conservation planning.

Keywords: *Colobus angolensis palliatus*; Electrical infrastructure; Electric shock; Electrocution; Monkey; Power lines; Primate; Urban environment

5.2 Introduction

Urbanisation is a major cause of wildlife extinction (McKinney, 2006). Although many species of wildlife have adapted to urban habitats (Hulme-Beaman et al., 2016), they are exposed to novel threats in doing so (Beamish & O'Riain, 2014; Sol et al., 2013). One of these threats results from the electrical infrastructure (Dwyer et al., 2014; Katsis et al., 2018), as some species use electricity cables, poles, and transformers as aerial pathways due to limited tree coverage (Rodrigues & Martinez, 2014), This enables them to remain arboreal while accessing food resources and sleeping sites, searching for mates, and dispersing (Ram et al., 2015).

The likelihood of wildlife surviving electrical injuries is low because the unique pathophysiology affects the whole body (Schulze et al., 2016). In severe cases, these injuries present as tissue burns where the current enters and exits the body, respiratory paralysis, cardiac arrest, muscle necrosis, systemic infections, and organ damage (Fish & Geddes, 2009; Koumbourlis, 2002)). The severity of an injury varies with voltage, type of current and amperage, and duration of exposure. Secondary trauma often occurs when the individual falls from the infrastructure (Fish & Geddes, 2009; Koumbourlis, 2002; Kumar & Kumar, 2015).

The literature records injuries and deaths from electrical infrastructure in 10 families and 31 species of primates. Social media, especially the YouTube platform, and websites of conservation organisations, document species injured or killed by the electrical infrastructure undescribed in the scientific literature. Published reports typically note that the electrical infrastructure is a threat to a species (Boinski et al., 1998; Kumara et al., 2006; Nowak et al., 2017) or report a small number of cases (Goulart et al., 2010; Lokschin et al., 2007; Montilla et al., 2020; Moore et al., 2010; Printes, 1999). Some studies found that electrical infrastructure is a major source of injury and death for arboreal primates (Al-Razi et al., 2019; Ampuero & Sá Lilian, 2012; Montilla et al., 2020), while other studies found that electrical infrastructure had a considerable impact on terrestrial species (chacma baboons *Papio ursinus*: Beamish 2009 and Hanuman langur, *Semnopithecus entellus*: Ram et al. 2015). One study of the spatiotemporal location of incidents within an electrical infrastructure grid found that injuries and deaths occurred on specific sections in a suburban area, and these remained relatively constant over time and across seasons (Katsis et al., 2018). Several other studies also showed that particular sections of the infrastructure caused most cases (Printes, 1999; Ram et al., 2015).

Four species of monkeys occur sympatrically in the oceanside suburban town of Diani, in southeast Kenya: Peters' Angola colobus (*Colobus angolensis palliatus*), Zanzibar Sykes' monkey (*Cercopithecus mitis albogularis*), Hilgert's vervet (*Chlorocebus pygerythrus hilgerti*), and the southern yellow baboon (*Papio cynocephalus cynocephalus*). Colobus Conservation is a local primate conservation organisation that investigates primate welfare cases reported by members of the community, offering an opportunity to study electric shock and electrocution trends at one site across species varying in behavioural and morphological attributes. We analysed 22 years of records for injuries from electric shock and deaths from electrocution (1998–2019) and investigated the impact on the populations of these species using annual population census data. We combined cases of electric shock, which occurs when an organism serves as a pathway for electric current but is not killed by that current, and electrocution, which occurs when the organism is killed by that current.

Although electrical infrastructure related injuries and deaths affect a broad range of primate species, little is known about its impact on the populations. To gauge the severity of the problem in Diani, we first examined the percentage of shock and electrocution cases compared to the total reported cases and the percentage of reported cases that resulted in the death of the monkey. We then tested several hypotheses and predictions: 1) If the expansion of the electrical infrastructure increases the risk of electric shock and electrocution cases, we predict that the number of annual cases reported would increase through the study period concurrently with Diani's growth. 2) If arboreal and terrestrial species experience different risks, we predict more cases involving the arboreal colobus and Sykes' monkeys than the terrestrial vervets and baboons. 3) If large individuals are more likely to be affected because they can contact multiple elements of the electrical infrastructure simultaneously, creating a short circuit, we predict more cases involving individuals with higher body masses; particularly adults and especially adult males. Finally, we explored the relationship between the number of electric shock and electrocution cases with rainfall.

5.3 Methods

5.3.1 Study site

We conducted our study in Diani, an oceanside suburban town in southeastern Kenya between Southern Palms Beach Resort (−4.267569°, 39.595537°) and KFI Supermarket (−4.342196°, 39.563738°), an area of ca. 6.5 km^2 (Figure 5.1). Diani is a linear development lying parallel to the Indian Ocean coastline, with an economy based on beach tourism. Phytogeographically, this area lies within the Zanzibar–Inhambane Undifferentiated floristic region, which historically extended from southern Somalia to the Limpopo River in Mozambique (White 1983). Diani retains original forest trees and fragments interspersed with exotic vegetation planted among the houses, hotels, and shopping areas.

Kenya Power is responsible for transmitting and distributing electricity in Kenya. In Diani, the company positioned the medium voltage distribution line alongside Beach Road, which bisects the town from north to south. Along some sections of the road, the company placed the powerline within the roadside vegetation. Older utility poles are wood, while more recently installed poles are concrete. These poles route either two, three or four cables, or a combination. The cables are placed vertically or horizontally towards the top of the poles. Transformers with uninsulated terminals step down the voltage from medium to low voltage distribution lines, connecting the utility to the consumer. The cables are uninsulated except where Kenya Power and Colobus Conservation have jointly added insulation to mitigate the risk of primate electrocutions.

Diani's climate is hot and humid, influenced by the sea-level altitude and the monsoon winds from the Indian Ocean. Although variable, typically, there are two dry seasons and two rainy seasons annually. The long rains occur from April to June, and the short rains occur from October to November. The dry seasons occur from July to September and December to March (J. Beakbane, unpubl. data).

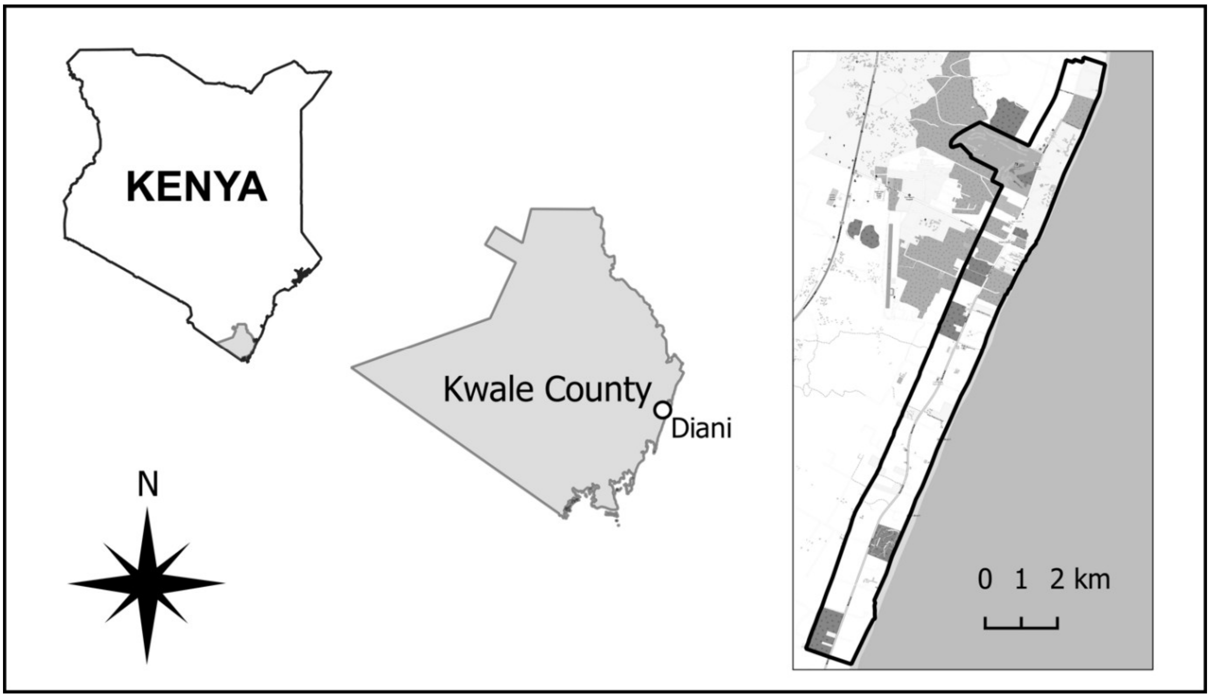

Figure 5.1 The study area within the oceanside suburban town of Diani, located in Kwale County, southeastern Kenya (Cunneyworth and Duke 2020).

5.3.2 Study species

(Dunham, 2017; Oates & Davies, 1994)The four species of monkey in Diani vary in habitat use, social organisation, and morphology, and are all sexually dimorphic. Peters' Angola colobus (colobus) is a medium-sized primate; adult female body mass is 9 kg, and adult male body mass is 11 kg (Harvey et al., 1987). They are highly arboreal and folivorous (Dunham, 2017; Oates & Davies, 1994). Groups typically consist of six individuals: a single adult male, multiple adult females, and offspring (Anderson 2005).

The genera of the Zanzibar Sykes' monkey (Sykes' monkey) and Hilgert's vervet (vervet) are closely related. Molecular studies propose that Sykes' monkeys and vervets belong to different phylogenetic clades; Sykes' monkeys are in the arboreal clade, and vervets are in the terrestrial clade (Xing et al., 2007). In Sykes' monkeys, adult female body mass is 4 kg, and adult male body mass is 8 kg. In vervets, adult female body mass is 3 kg, and adult male body mass is 5 kg (Harvey et al., 1987). Both species are omnivorous. Sykes' monkeys live in one-male, multifemale groups, and vervets live in multimale, multifemale (Mugatha et al., 2007; Struhsaker & Siex, 1996).

The southern yellow baboon (baboon) is the largest primate in Diani; adult female body mass is 15 kg, and adult male body mass is 20 kg (Harvey et al., 1987). Baboons are omnivorous, primarily terrestrial, and live in multimale, multifemale groups (Altmann et al., 1993).

5.3.3 Data collection

Members of the community report primate welfare cases to Colobus Conservation. This local conservation organisation operates an emergency rescue service for injured and ill primates. The staff follow up on each report in the field and provide veterinary care when appropriate or collect the carcass if the individual is dead. The staff inputs each case into a database as part of the organisation's internal reporting. The information recorded includes species, date, cause and description of the incident, age class, sex, body mass, the clinical presentation of the individual, and case outcome (alive not captured, treated and released, dead on arrival, died under treatment, euthanised, not found, or unknown). The veterinarian or field assistant categorises electric shocks and electrocutions at the time of the incident by physical presentation of the monkey and/or proximity of the injured or dead individual to electricity cables, poles, or transformers.

We used previously published population census data for each species (Cunneyworth & Duke, 2020). These data were available for 2004–2006 and 2010–2019. We delineated the census study area, then reviewed the location information in each case report and created a subset of cases in the census area for analysis. A Diani resident provided rainfall data collected at ca. 09:00 h daily for the entire study period. A standard rainfall gauge measured the rainfall in mm. The rainfall gauge was 1.7 km south of the study area (−4.3556°, 39.5615°).

5.3.4 Statistical analysis

We analysed data using IBM SPSS version 23. For all tests, the probability level of significance was 0.05. We tested assumptions and used Shapiro–Wilk's test to test for normally distributed data and the Levene's test to test for homogeneity of variance. We analysed 22 years of the organisation's records from January 1998 to December 2019. We calculated 1) the number of electric shock and electrocution reports for all species of monkeys as a percentage of the total number of welfare reports of monkeys for the same area and time frame, 2) the mean and standard deviation for the number of monthly electric shock and electrocution reports (N =264 mo), and 3) the percentage of each category of case outcome for the monkey (alive not captured, treated and released, dead on arrival, died under treatment, euthanised, not found, or unknown).

We used a Pearson's correlation to test for an association between study year and the number of reported cases. We chose a one-tailed test, as we predicted that the number of reported cases would increase over time as Diani's electrical infrastructure expanded. We investigated the impact of electric shocks and electrocutions on the population of each species using the annual census data. We calculated the number of cases annually as a percentage of the population size in that year. We used a Kruskal–Wallis test to determine whether the distributions of annual percentage of the population that were shocked or electrocuted differed across species. As this test was significant, we used a Mann–Whitney U test to carry out planned pairwise comparisons. We determined which pairs of species were statistically different and reported the results of the adjusted α level (0.05/6 = 0.008) using the Bonferroni correction for multiple tests to protect against type I error.

We tested if the age–sex classes were shocked or electrocuted in proportion to their occurrence in the population. We carried this test out only for colobus due to the low number of cases for the other species. We first established the population's structure by determining the proportion of the population for each age class (infant, juvenile, subadult, and adult) for each census year (2004–2006, 2010–2019) and then calculated a mean across the years. We assumed an equal number of females and males in each age class (Bronikowski et al., 2016). Using the chi-square goodness of fit test, we tested if the proportion of each age–sex class involved in electric shock and electrocution cases differed from its mean proportion in the population. As this test was significant, we carried out planned post hoc tests to calculate the z-scores based on the adjusted residuals and used a one-tailed test with a Bonferroni adjusted α level (0.05/8 = 0.006).

For colobus, we compared the distribution of body mass (kg) in cases of electric shock and electrocution with that for all other colobus welfare cases (i.e., vehicle–monkey collisions, abuse, dog attacks, illness, and injuries) ($N_{\text{shocks and electrocutions}} = 144$; $N_{\text{other causes}} = 243$). We then compared the body mass (kg) of colobus females and males involved in electrical infrastructure related incidents ($N_{\text{females}} = 51$; $N_{\text{males}} = 93$). We used Mann–Whitney U tests for both tests. Lastly, we used a two-tailed Spearman's ρ correlation for all the cases to test whether the monthly number of electric shock and electrocution cases (N =264 mo) was associated with the monthly rainfall (mm). We used the monthly values because we could not attribute a specific day to the incident for half of the cases given that individuals that receive electric shock often live with their injuries for some time before being reported.

5.4 Ethical note

Our study adhered to the legal requirements of Kenya with permission from the Kenya Wildlife Service. NACOSTI granted this research permission through permit number NACOSTI/P/16/10434/11346. The University of Bristol ethics committee approved the protocols. The authors have no conflicts of interest or competing financial interests to declare.

5.5 Supplementary material

The online version contains supplementary material available at https://doi.org/10.1007/s10764-020-00194-z.

5.6 Results

Within the study area, members of the community reported 2017 welfare cases involving monkeys from January 1998 to December 2019. Of these, 320 cases (16%) were either electric shock injuries or electrocutions. The mean number of cases reported was 1.2 per month (range = 0–6, N =264 mo, SD = 1.3). The case outcomes show low survival: only 25% (N =79) of the shocked or electrocuted individuals were alive and not captured or treated and released. Death occurred in 73% of cases (N =233), and of those cases, 149 died at the time of the incident, 31 died under veterinary care, and 53 were euthanised because of extensive injuries. The team did not find the monkey in the field in six cases and did not note the case conclusion in two cases.

The annual number of electric shock and electrocution cases ranged 6–23 (X = 15, SD = 4) (Figure 5.2) and did not increase over the study period (one-tailed Pearson's correlation = −0.005, *N* =22 yr, $p = 0.49$). The number of incidents reported by members of the community varied by species: colobus, *N* =256 (80%), Sykes' monkeys, *N* =42 (13%), vervets, *N* =16 (5%), and baboons, *N* =6 (2%). We found significant differences between the four species in the percentage of the annual population involved in electric shock and electrocution incidents ($\chi 2 = 32.2$, N= 52; df = 3, $p < 0.001$) (Figure 5.3). In planned pairwise comparisons (Table 5.1), the annual percentage of the colobus population shocked or electrocuted was significantly higher than that for the other species, while the percentages of the population involved were similar for Sykes' monkeys, vervets, and baboons.

Table 5.1 Results of pairwise Mann–Whitney tests comparing the annual percentage of the population involved in electric shock or electrocution cases in four species of monkey in Diani, Kenya, 2004–2006, 2010–2019 (N= 13 yr).

Species	X^2	***N***	**df**	***p***
Colobus–Sykes'	21.9	13	1	0.001**
Colobus–Vervet	25.5	13	1	<0.001**
Colobus–Baboon	30.6	13	1	<0.001**
Sykes'–Vervet	3.7	13	1	1.00
Sykes'–Baboon	8.8	13	1	0.789
Vervet–Baboon	5.1	13	1	1.00

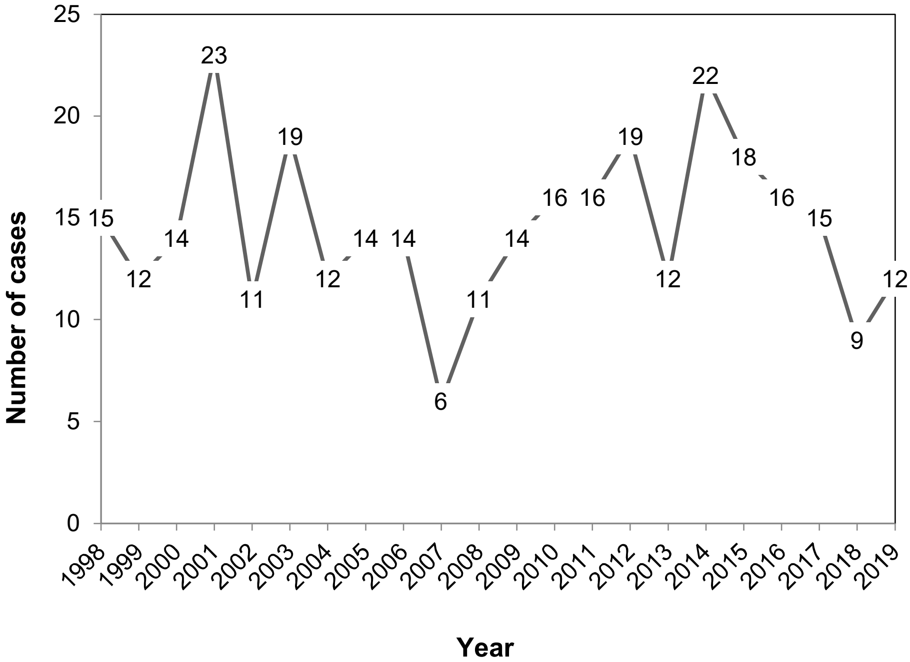

Figure 5.2 The number of electric shock and electrocution cases reported by members of the community in Diani, Kenya, 1998–2019 (*N* =22 yr), in four monkey species combined (colobus, Sykes' monkey, vervet, and baboon).

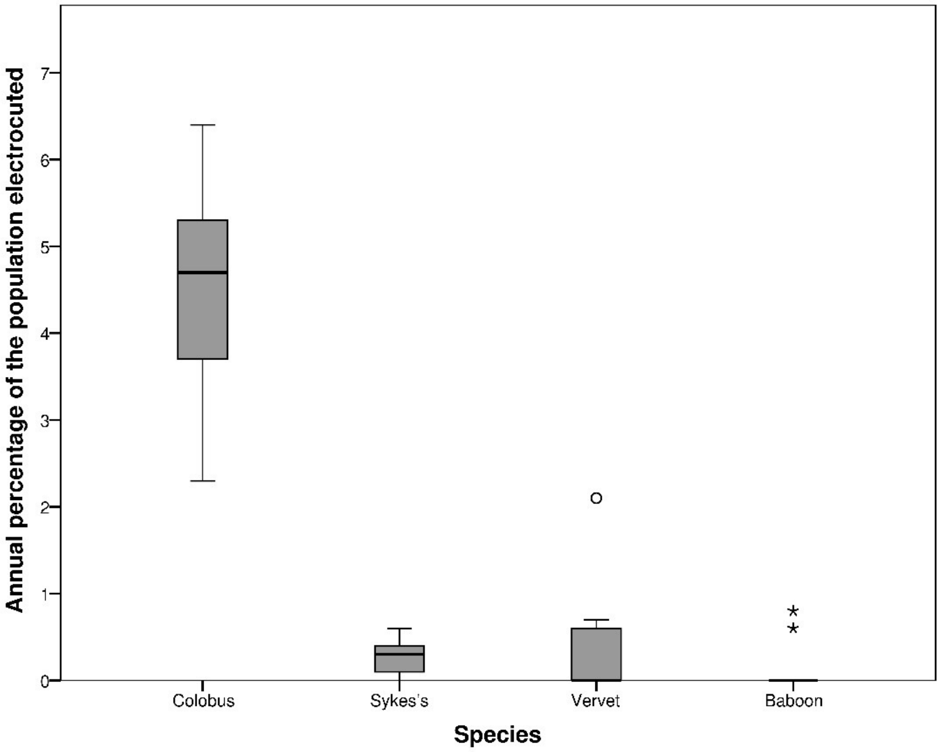

Figure 5.3 Annual percentage of the population reported as electric shock or electrocution cases in four species of monkey in Diani, Kenya, 2004–2006, 2010–2019 (*N* =13 yr). Boxes represent 50% of the dataset, with the line indicating the median value. The whiskers represent the top and bottom quartiles. The circle indicates an outlier, and asterisks indicate extreme outliers.

We reviewed the number of cases by age–sex class for all four species (Figure 5.4); however, we carried out the age–sex class and body mass analyses only for colobus, as the number of electric shock and electrocution cases was low for the other species. For colobus, the proportion of each age–sex class affected differed significantly from the proportion of each age–sex class in the population ($\chi 2 = 15.9$, $N = 227$, df = 7, $p = 0.03$). Post hoc tests show that colobus adult males were affected significantly more than expected given their presence in the population. The proportion of all other colobus age–sex classes shocked or electrocuted did not differ significantly from the population structure (Table 5.2) after applying the adjusted α level for multiple tests.

Colobus individuals involved in electrical infrastructure related cases were larger than those involved in other welfare incident types (Mann–Whitney $U = 12{,}095$, $p < 0.001$, Figure 5.5). The percentage of reports that recorded a body mass was similar in shock and electrocution cases (56%) and other causes (58%). There were significant differences in body mass between colobus males and females who were shocked or electrocuted ($U = 3638$, $N = 144$, $p < 0.001$), with females showing a population distribution and males being larger (Figure 5.6).

Table 5.2 Results of post hoc tests comparing the observed proportion of each colobus age–sex class involved in electric shock and electrocution cases with that expected from the mean proportion of the colobus population represented by that age–sex class, in Diani, Kenya, 2004–2006, 2010–2019 (N =13 yr).

Age-class	Female				Male			
	Exp.	Obs.	*z*-score	*p*	Exp.	Obs.	*z*-score	*p*
Infant	0.06	0.03	-1.5	0.07	0.06	0.02	-2.41	0.01
Juvenile	0.08	0.07	-0.71	0.24	0.08	0.08	-0.07	0.47
Subadult	0.10	0.11	0.10	0.46	0.10	0.07	-1.54	0.06
Adult	0.26	0.20	-2.33	0.01	0.26	0.42	8.00	<0.001**
Total	0.50	0.41			0.50	0.59		

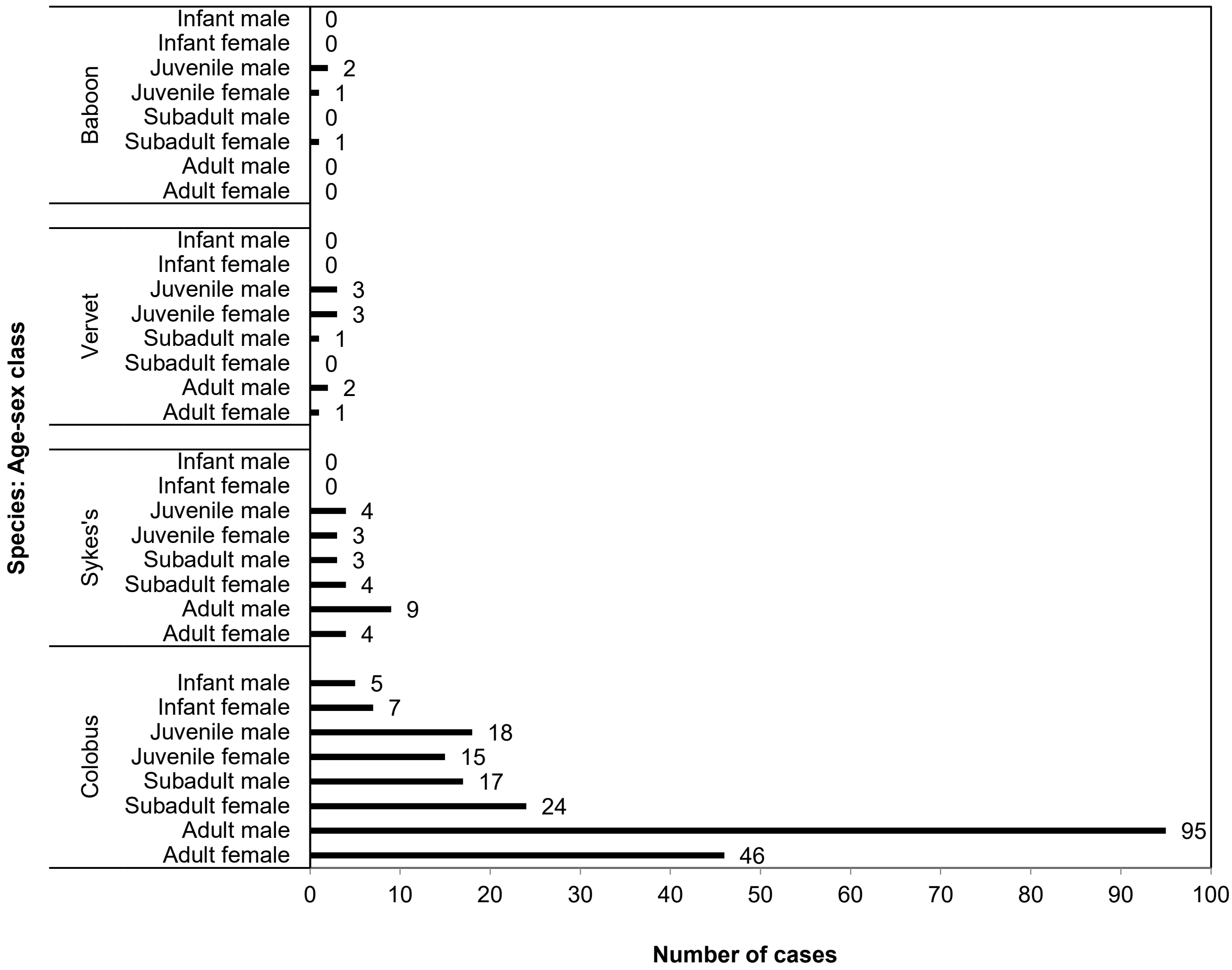

Figure 5.4 Number of cases of electric shock and electrocution reported by age–sex class in four species of monkey in Diani, Kenya, 1998–2019 (N =22 yr). Only cases with recorded age–sex class are included (N =268).

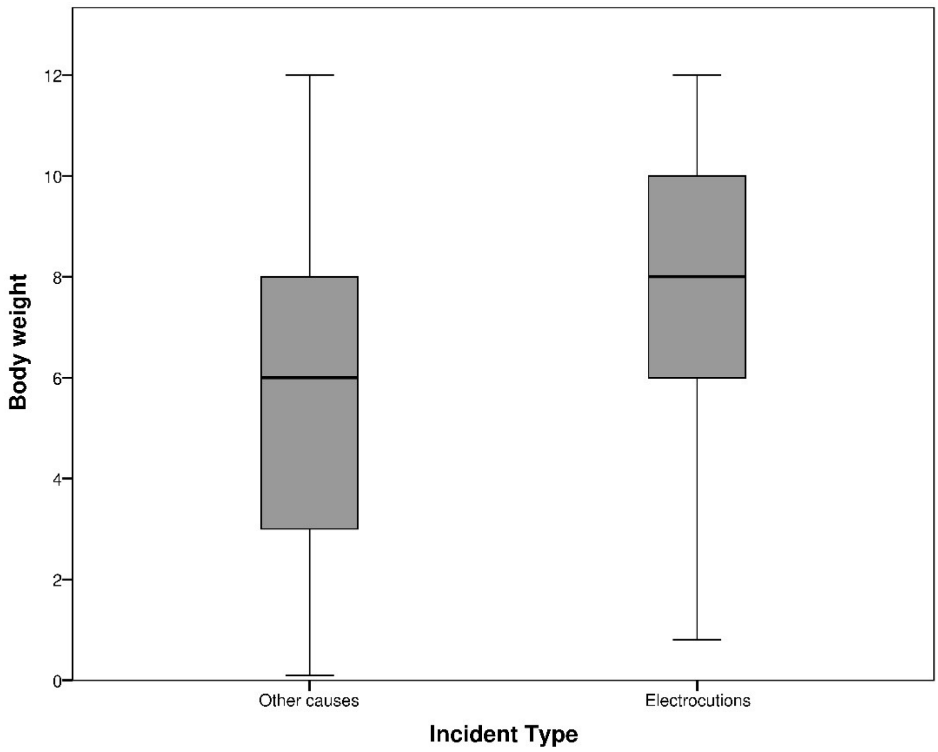

Figure 5.5 Body mass of colobus individuals involved in electric shock and electrocution cases (N =144) compared with all other colobus welfare causes (N =243), 1998–2019. Boxes represent 50% of the dataset, with the line indicating the median value. The whiskers represent the top and bottom quartiles.

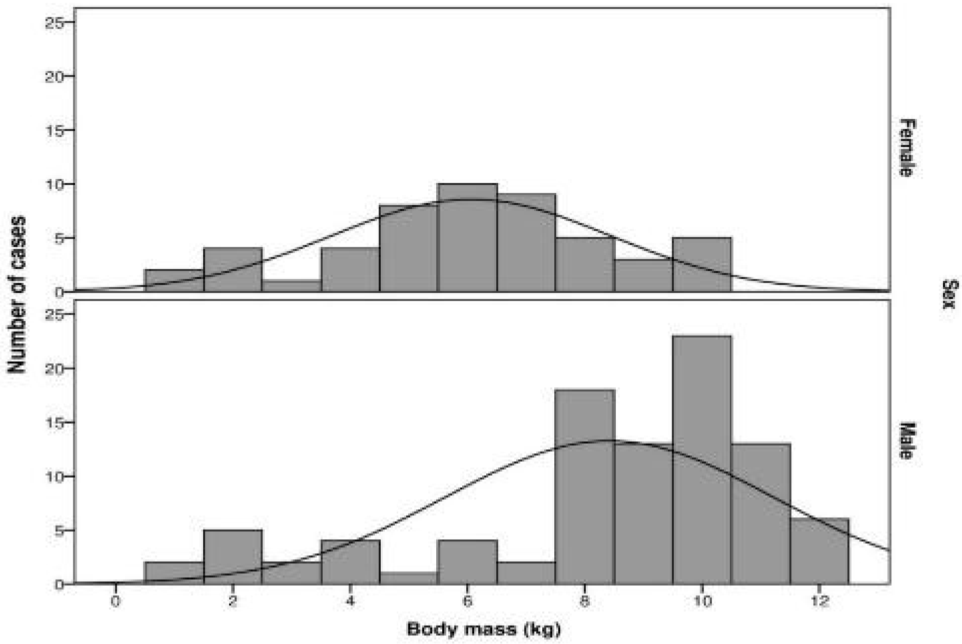

Figure 5.6 Number of electric shock and electrocution cases for colobus body mass categories and indicating the normal curve, for females (N =51) and males (N =93) in Diani, Kenya, 1998–2019 (N =22 yr).

Monthly rainfall and the monthly number of electric shock and electrocution cases were significantly negatively correlated ($r = -0.16$, N =264 mo, N =320 ca0ses, $p = 0.009$). In months with lower rainfall, there were more electric shock and electrocution cases (Figure 5.7).

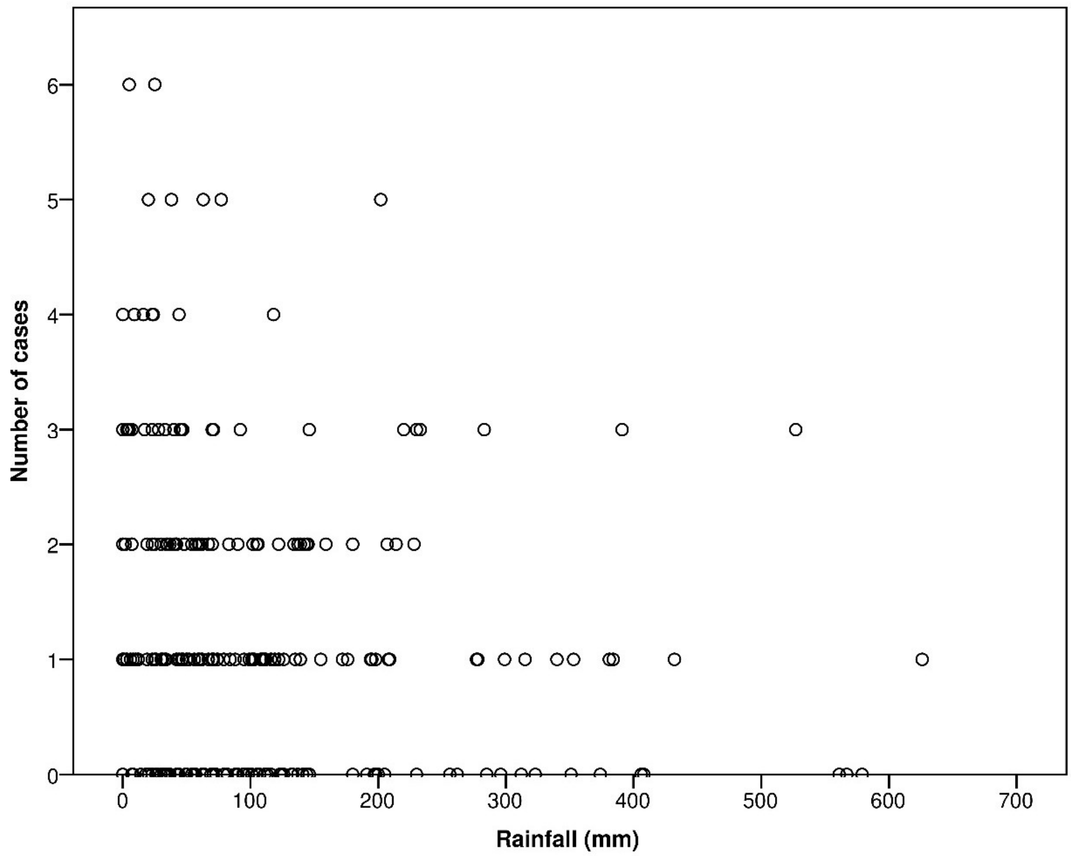

Figure 5.7 The number of electric shock and electrocution cases by month (N =320 cases) compared to monthly rainfall in Diani, Kenya, 1998–2019 (N =264 mo) in four species of monkeys combined (colobus, Sykes' monkey, vervet, and baboon).

5.7 Discussion

Of the 2017 welfare incidents reported to the conservation organisation in 1998–2019, 16% were electric shock or electrocution cases, considerably fewer than the 34% of vehicle–monkey collision cases reported for the same study area (Cunneyworth & Duke, 2020). The number of cases of electric shock and electrocution of monkeys was consistent across the years but more community reports occurred in months with rainfall ≤50 mm than in other months. Almost three-quarters of cases resulted in death. This is not surprising, because of the delay between the incident and its reporting by members of the community (Kumar & Kumar, 2015). We found species differences, and of the two arboreal species in Diani (colobus and Sykes' monkeys), colobus made up most cases, with ca. 4.6% of the colobus population involved annually. Cases involving Sykes' monkeys, vervets, and baboons were low, and the percentage of the population involved annually was low. For colobus, the body mass of the individuals involved in shock and electrocution cases was higher than that of colobus involved in other causes of welfare incidents. Of all the colobus age–sex classes, only adult males were involved more than expected given their proportion in the population. This was reflected in the higher body mass of colobus males involved than colobus females.

Reports of injuries and deaths due to the electrical infrastructure did not increase over time as we predicted given Diani's growth during the study years. We attribute this to the mitigation strategies that the power distribution company and the conservation organisation implemented to reduce such cases. Since 2002, these organisations, in partnership, have trimmed vegetation growing around electricity cables, poles, and transformers. The amount trimmed has varied by month and by year, but typically, the teams cut ca. 500 m twice a month. In 2010, long-term mitigations began by insulating electricity cables and moving transformers known to cause electric shocks and electrocutions. While the efficacy of these tree-trimming and insulation mitigations remains to be tested in detail, our findings suggest that they may contribute to reducing injuries and deaths, as cases have not increased over time, although the electrical infrastructure has expanded.

We suspect that electric shock cases are underrepresented in our dataset. A study of 3 colobus groups in our study area with 21 study subjects found 5 electrical infrastructure related incidents occurred in 336 study days (N. Dunham, unpubl. data). These cases included one electrocution case (an adult male) and four electric shock cases (two adult males, one adult female, one juvenile female). In the electric shock cases, the individuals sustained burn injuries but the incidents were not reported by members of the community. If electric shock cases are as frequent as those observations suggest, this presents substantial welfare concerns regarding the installation of uninsulated electrical infrastructure in primate areas (Printes et al., 2010).

We found that species of monkeys differ in their risk of electric shock and electrocution. Of the four species of monkeys that live sympatrically in Diani, Kenya, three—Sykes' monkeys, vervets, and baboons—experienced injuries and deaths infrequently, indicating that the electrical infrastructure is a negligible conservation threat to these populations. However, the reports of colobus injured or killed consistently exceeded 4% of the annual population, which is the upper limit of sustainable mortality for primates (Robinson & Bodmer, 1999). The annual censuses of colobus in Diani indicate that their numbers are decreasing (Cunneyworth & Duke, 2020). The Diani colobus are the second largest population in Kenya (Anderson, 2005a), making electrical infrastructure an ongoing conservation threat to this Vulnerable species (Cunneyworth et al., 2020; de Jong et al., 2020).

We hypothesised that stratum use—arboreal vs. terrestrial—influenced species risk from the electrical infrastructure, where arboreal species are at high risk of involvement in electrical infrastructure incidents and terrestrial species are at low risk of involvement. Our results support the prediction that terrestrial species are at low risk of electric shock and electrocution, as there were no cases for either vervets or baboons in many study years. In years with cases, the annual percentage of the population affected was well within the range of sustainable mortality (Robinson & Bodmer, 1999). However, the data do not entirely support the prediction that arboreal species are at high risk of electric shock and electrocution, as the annual percentage of the Sykes' monkey population reported to be involved was similar to that of the terrestrial species. This result is surprising, as both colobus and Sykes' monkeys are primarily arboreal (ca. 1% and ca. 6% terrestrial, respectively) (Coleman & Hill, 2014; Dunham, 2017), and their distributions overlap extensively in Diani due to the compact nature of suitable habitat in the town. This difference between colobus and Sykes' monkeys indicates that stratum use is not the only factor determining electrical infrastructure risk for arboreal species.

Differences in habitat use are an unlikely explanation as the Diani hotspots of electric shock and electrocution of these two species are strongly correlated (Katsis et al., 2018), presumably because they negotiate the suburban environment in similar ways. In addition, differences in the size of the home range and daily path length are also unlikely explanations as colobus are folivores and rest for 50–70% of the day (Wijtten et al., 2012), meaning that they should be at lower risk of shock and electrocution due to less time spent moving and consequently less time in potential contact with the electrical infrastructure than Sykes' monkeys.

We suspect that body mass is an important factor in understanding electrical infrastructure risk. The distribution of cases across age–sex classes follow the same pattern for colobus and Sykes' monkey, with adult males more often shocked or electrocuted. Both species are sexually dimorphic, suggesting that larger individuals are at greater risk of electric shock and electrocution than smaller individuals. Other primate studies also indicate that adult (and subadult) males are more likely to be electrocuted than immature individuals or females (Montilla et al., 2020; Pereira et al., 2020). We suggest that the risks become greater when individuals of the arboreal species reach 8 kg, given the distribution of our data.

We found only one other study that provided data on the number of electrocutions of two sympatric arboreal species of monkey of different adult body mass—capped langur (*Trachypithecus pileatus*) with a body mass of 9.5–14 kg and Phayre's langur (*Trachypithecus phayrei*) with a body mass of 6.5–7.5 kg (Al-Razi et al., 2019). The number of electrocution cases in the capped langur was more than twice that of Phayre's langur, consistent with our hypothesis, although relative population size was not presented. While that study implicated the langur's long tail as the short-circuit contact point between two parallel cables, this may not be the case. Investigations of electric shock and electrocution injuries of black-tufted marmosets (*Callithrix penicillata*), brown howlers (*Alouatta* *guariba clamitans*), and rhesus macaques (*Macaca mulatta*) indicate that tails were rarely affected (Ampuero and Sá Lilian 2012; Kumar and Kumar 2015; Pereira et al. 2020).

A brief examination reveals multiple scenarios for how electric shocks and electrocutions occur, such as vegetation to phase, phase to phase, between pole terminals and phase, and between transformer terminals, each with varying likelihoods. We suggest that spacing distances between cables and the cable arrangement—horizontal or vertical—are likely to affect the relationship between body size and risk. Additionally, we suspect that risk increases for colobus and perhaps other larger-bodied monkeys due to their locomotion mode of quadrupedal walking: climbing through rather than jumping past specific infrastructure elements (i.e., uninsulated terminals) may predispose them to higher risk. Given the paucity of previously published data on the specifics of incidents, we suggest that authors include, when possible, the body mass of individuals involved in the incidents and a complete description of the structural elements of the electrical infrastructure where the incident occurred. Furthermore, how species navigate the various structural elements of the electrical infrastructure is an area for further investigation.

Electric shocks and electrocutions were more frequent in months with lower rainfall than in months with higher rainfall. One might expect that this result occurs because daily path lengths are longer during the drier months, when food is less readily available, meaning that monkeys spend more time using the electrical infrastructure moving between foraging areas. However, in Diani, colobus home ranges are small (ca.6–11 ha: Dunham 2017), and daily path lengths are not correlated with rainfall (N. Dunham, unpubl. data; Santarsieri 2019). In comparison, no seasonal pattern of electrocutions was found in black-tufted marmosets (Pereira et al., 2020), and a higher percentage of cases occurred in the rainy months than in drier months in rhesus macaques (Kumar and Kumar 2015), the opposite to the pattern we found. Further investigation is needed to determine if these differences are due to study methodology, environmental factors, or species differences.

In conclusion, we reviewed electric shock and electrocution reports in four sympatric species of monkeys. Our study shows that species differ in their risk of injury and death related to electrical infrastructure. Based on our findings, we suggest that more susceptible species are arboreal, with greater risk to individuals ≥8 kg compared to more terrestrial species, and arboreal species with smaller individuals. Electricity cable spacing and arrangement may differ across sites, affecting which species or size individuals are at higher risk. Electric shocks are likely much more common than reported, raising welfare concerns relating to poor site selection for electrical infrastructure and installation of uninsulated electrical hardware. Other organisations can estimate risks based on the factors reviewed in this article, even when the impact of electrical infrastructure on populations is not known. Further understanding of how body mass affects the risk of electric shock and electrocution can inform infrastructure design and consequently have far-reaching implications for primate conservation planning.

5.8 Acknowledgements

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Chapter 6. Spatial patterns of primate electrocutions in Diani, Kenya

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6.1 Abstract

Electrocution from power infrastructure threatens many primate species, yet knowledge of effective evidence-based mitigation strategies is limited. Mitigation planning requires an understanding of the spatial distribution of electrocutions to prioritise high-risk areas. In Diani, a coastal Kenyan town, electrocution is an important cause of death for five primate species. In this study we aim to describe the spatial patterns of electrocutions and electric shock incidents (collectively referred to as electrocutions hereafter) and identify electrocution hotspots to guide an effective primate conservation approach in Diani. Colobus Conservation, a not-for-profit organisation, has recorded electrocutions and annual primate census data since 1998. We georeferenced 329 electrocution data points and analysed them using QGIS. We identified and compared hotspots across species, seasons, and time using kernel density estimation and Getis-Ord-Gi*. We employed spatial regression models to test whether primate population density and power line density predicted the location of electrocution hotspots. Electrocutions occurred in hotspots that showed little variation in location between species and seasons. The limited variation in hotspot location over time likely occurred as a result of new building development in Diani and variability in primate detection rates by community members. Primate density and power line density were significant predictors of electrocution density for Angolan black-and-white colobus (*Colobus angolensis palliatus*) and Sykes' monkeys (*Cercopithecus mitis albogularis*), but the relationship was weak, suggesting the presence of additional risk factors. This study provides a framework for systematic spatial prioritisation of power lines that can be used to reduce primate electrocutions in Diani, and can be adopted in other areas of the world where primates are at risk from electrocution.

Keywords: Electrocution; GIS; Hotspots; Power lines; Spatial analysis

6.2 Introduction

Primates are at high risk of extinction as a result of unsustainable human activity, which is causing extensive habitat loss and degradation (Estrada et al., 2017). Consequently, many species are restricted to human dominated landscapes (Arroyo-Rodríguez & Fahrig, 2014), where their survival is threatened by novel risks including electrocution from overhead power lines (Parker et al., 2008; Ram et al., 2015; Slade, 2016). Primates are exposed to power lines as they use them to travel across the landscape, especially between isolated tree patches, and to escape from aggressors (Boinski et al. 1998; Dittus 1986; Goulart et al. 2010; Ram et al. 2015). As cables are rarely insulated, this behaviour poses a high risk of electrocution (lethal) or electric shock injury (not immediately lethal) (Dwyer, 2006) when individuals simultaneously grasp two conductors, or a conductor and an earthed device (Bevanger, 1998). Similarly, injury can result from wet vegetation contacting energised components, creating short circuits from power lines to the ground (Kumar and Kumar 2015). Reported death rates after electric shock range from 31% to 36% (Kumar and Kumar 2015; Slade 2016), with individuals dying from the effects of electric current passing through the body (Schulze et al., 2016), or from the subsequent impact of falling from a height (Kumar and Kumar 2015). Survivors of electric shocks are frequently left with injuries to the hands, head, and chest, and may later die from secondary infection (Kumar and Kumar 2015). In addition, these incidents cause power outages, equipment damage, and fires, which affect human communities (APLIC, 2006; Dwyer et al., 2014; Harness & Wilson, 2001; Printes, 1999).

Electrocutions are documented for a range of primate species across Asia (Kumar and Kumar 2015; Nekaris and Jayewardene 2004; Roscoe et al. 2013), Africa (Maibeche et al., 2015; Slade, 2016), and Latin America (Goulart et al., 2010; Printes, 1999; Rodrigues & Martinez, 2014). They are a principal mortality factor for the Endangered Central American squirrel monkey subspecies *Saimiri oerstedii citrinellus* and *Saimiri oerstedii oerstedii* (Boinski et al., 1998), and were found to be the most common cause of death for a population of Hanuman langurs (*Semnopithecus entellus*) (Ram et al., 2015). There is limited knowledge about population-level effects of electrocution on primates, but avian studies have shown that even low electrocution rates can drive declining populations to local extinction (Hernández-Matías et al., 2015). Therefore, evidence of electrocutions of Critically Endangered species including the Javan slow loris (*Nycticebus javanicus*) (Moore et al., 2014) and the western purple-faced langur (*Trachypithecus vetulus nestor*) (Moore et al., 2010; Parker et al., 2008) is a cause for conservation concern.

As habitat encroachment increases and power line networks rapidly expand, this problem is likely to escalate in the future (Bevanger, 1998; Jenkins et al., 2010), and development of effective evidence-based mitigation strategies is crucial (Sutherland et al., 2004). Current strategies to reduce electrocution include power line insulation, tree-trimming around power lines, artificial canopy bridges, and braiding of power lines (Lokschin et al., 2007; Printes, 1999; Roscoe et al., 2013); however, their effectiveness in reducing electrocutions is rarely evaluated (Teixeira et al., 2013). Limited funding makes mitigation measures across the entire power grid unfeasible; therefore, measures must be targeted to high-risk areas (Dwyer et al., 2014; Lokschin et al., 2007). This requires an understanding of the spatial distribution of electrocutions (Guil et al., 2011; Malo et al., 2004), which is rarely studied for primates.

In the Kenyan town of Diani, electrocution contributes to mortality for five of the six primate species: Angolan black-and-white colobus (*Colobus angolensis palliatus*), Sykes' monkeys (*Cercopithecus mitis albogularis*), vervet monkeys (*Chlorocebus pygerythrus hilgerti*), southern yellow baboons (*Papio cynocephalus cynocephalus*), and white-tailed small-eared galagos (*Otolemur garnettii lasiotis*). No electrocutions have been recorded for the Kenya coast galago (*Paragalago cocos*), possibly because of their small body size (Slade, 2016). Angolan black-and-white colobus monkeys are particularly affected, with annual mortality estimates ranging from 1.7% to 7.9% (Slade, 2016). We aim to describe the spatial patterns of primate electrocutions and electric shock incidents (collectively referred to as electrocutions hereafter) in Diani and to identify electrocution hotspots to inform an effective evidence-based mitigation strategy. Our hypothesis is that particular locations will be more likely to result in reported electrocutions than others, owing to landscape features (e.g., proximity of power lines to trees), behavioural factors (e.g., habitually used routes), or demographic factors (e.g., locations with higher densities of primates). We predict that 1) electrocutions will occur in hotspots, 2) hotspots will be species specific, 3) hotspots will differ between seasons, 4) hotspots will change over time, 5) hotspots will be associated with high primate density, and 6) hotspots will be associated with high power line density.

6.3 Methods

6.3.1 Study site

Diani is a touristic coastal town in southern Kenya, located 30 km south of Mombasa in Kwale County (Figure 6.1). It is in the fragmented Diani Forest, a narrow strip of coastal rag forest ca. 10 km long by 0.5 km wide (Dunham & McGraw, 2014). This forest is part of the Zanzibar–Inhambane Undifferentiated Floristic Region (White, 1983), a global biodiversity hotspot undergoing extensive habitat loss (Brooks et al., 2002; Myers et al., 2000). Rainfall is bimodal, with long rains occurring from April to June and short rains from October to November (Colobus Conservation, unpubl. data).

As a result of expansive human development in Diani, a high proportion of forest cover has been lost and the remaining forest is highly fragmented by roads, resorts, developed land, and overhead power lines (Kanga & Heidi, 1999; Moreno-Black, 1977). Consequently, primates are often threatened by human activity, and a local conservation organisation, Colobus Conservation, operates a primate rescue centre in this area.

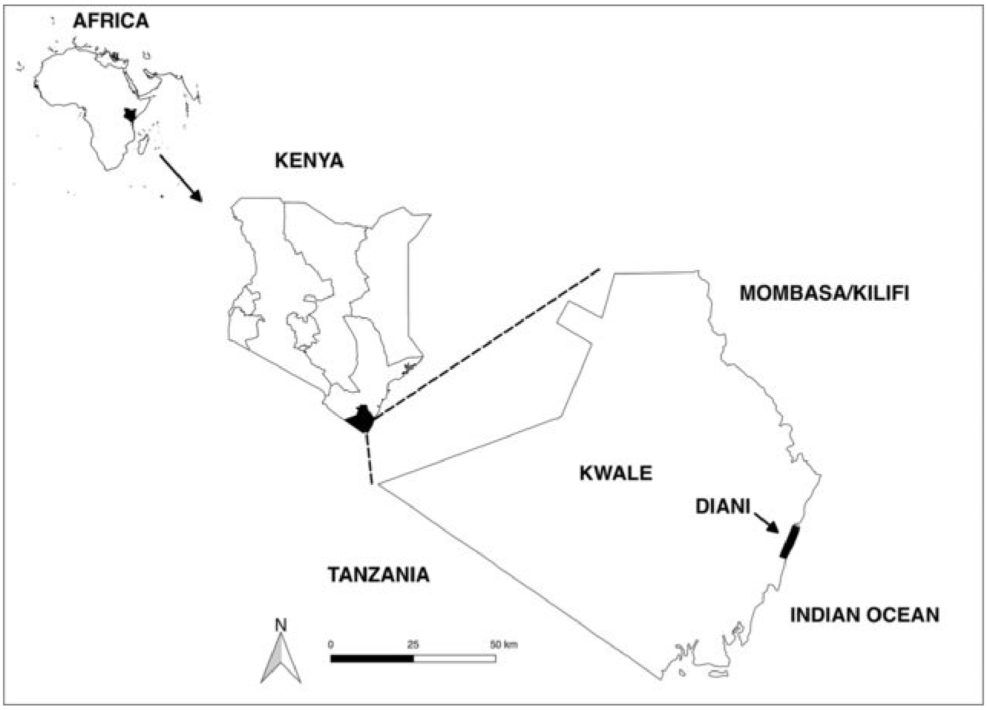

Figure 6.1 Map of southern Kenya, indicating location of study site (Diani).

6.3.2 Data collection

Kenya Power provided the power infrastructure data in digital CAD format (an image file format used by the software AutoCad). We extracted from the CAD files all above ground power lines within the study area and verified power line location against logical pathways down major highways and against shadows cast in high-resolution imagery in nonpopulated places. We also tracked the power infrastructure the power lines entered and exited, such as substations, from the imagery and the CAD file. We converted the power line data from the provided projection EPSG:21307 to the more standard EPSG:32737, which is compatible with current GPS standards. We used the Kenya datum conversion information provided by the American Society for Photogrammetry and Remote Sensing (ASPRS 1983) to complete this transformation.

Colobus Conservation provided electrocution and electric shock data from 1998 to the end of 2016. Community members report welfare cases and dead animals to the Colobus Conservation emergency response team, which attends to the cases and records data. Data include each reported electrocution case, primate species, description of the incident, and incident GPS location since 2010. Colobus Conservation logs these data onto a record sheet and enters it into an electronic database. We collated and crosschecked welfare reports against the electronic database to compile a dataset of 370 electrocution incidents. We validated all location coordinates against a base map and updated incorrect locations. Of 370 incident reports, 266 were associated with a specific location and valid GPS location (Garmin eTrex 30×); 63 only provided the name of the property where the incident occurred, so we took coordinates for all power lines associated with the property, and assigned a random point to the power line using the QGIS random points tool; the remaining 41 reports did not contain sufficient information to assign a GPS location and we excluded them from the analysis.

Since 1997 Colobus Conservation has conducted annual primate censuses in Diani for southern yellow baboons, Sykes' monkeys, vervet monkeys, and Angolan black and white colobus, and provided this population data for our study. They did not collect census data for either galago species. They conduct the census each year in October. For southern yellow baboons, Colobus Conservation visited each known group in Diani three to six times within a week and determined the group size as the mode of repeated counts. They calculated the census figure as the total of all groups. For Sykes' monkeys, vervet monkeys, and Angolan black-and-white colobus, they conducted line transect surveys throughout every property in Diani and the remaining forest over 3–4 days. At each plot, observers spread themselves at intervals and moved along a prescribed route at 1–1.5 km per hour, stopping periodically to watch and listen for primates. Distance between observers varied at each plot depending on the density of the foliage, but ranged from 10 to 200 m. They walked transects in east to west direction, and then returned in west to east direction until they covered the entire plot. When they encountered a group of monkeys, observers joined together and recorded the GPS location, time of discovery, species, number of primates, sex composition, age composition, and direction of movement. They then returned to their last survey mark to complete the census walk. The conservation manager checked each data sheet to identify any repeated counts. The observers determined the census figure as the total of these raw counts. As the primates in Diani are habituated, the observers recorded data at distances of 10–20 m from the primates. We checked the coordinates of census group locations against a base map to identify incorrect locations, and removed data from years with inaccurate readings. This left 10 years of accurate census data for Angolan black-and-white colobus, 9 years of accurate data for vervet monkeys, and 8 years of accurate data for Sykes' monkeys.

6.3.3 Statistical analysis

Electrocution Hotspots To visualise electrocution hotspots we used two techniques: 1) kernel density estimation (KDE) and 2) Getis-Ord-Gi*. KDE is a common technique used in ecological studies (Kernohan et al. 2001) and is used to identify wildlife road traffic accident hotspots (Gomes et al. 2009). We implemented KDE using the QGIS Heatmap plugin, which creates a density surface of the electrocution points based on the number of points per unit area. A moving function weights points within a region of influence based on the distance of each point to the location of interest. The area of influence is determined by the bandwidth, with larger bandwidths resulting in a smoother surface (Gatrell et al. 1996). We used a bandwidth of 500 m for each heatmap, as it enabled good resolution of hotspots and allowed for comparison between data subsets. We then visualised hotspots for all electrocution records, for individual species, and for different seasons. The KDE algorithm we used was developed for planar analysis, but the dataset we analysed occurred along the power line network. Therefore we performed an additional KDE developed for network analysis using the v.kernel tool from GRASS GIS (GRASS Development Team, 2017). For this analysis we used the split nodes method and the suggested bandwidth of 10 map units and multiplied the result by the number of input points as specified in the user manual (GRASS Development Team, 2018).

As KDE does not provide a measure of statistical significance of hotspots, we used the QGIS Hotspot Analysis plugin to calculate Getis-Ord-Gi* statistics (Getis & Ord, 1992; Oxoli et al., 2016). We aggregated electrocution points into a 150 m by 150 m grid, with each cell containing a value representing the number of electrocutions. To account for the network nature of power lines and the tendency of electrocution events to cluster around them we applied Getis-Ord-Gi* using two methods. For the first method (hereafter Getis-Ord-Gi*1) we removed all cells that were not intersected by power lines and performed the hotspot analysis only along the power line network. This decreased the sample size, as some of the electrocution points fell outside these cells. For the second method we performed hotspot analysis along the power line network and corrected for the power line length in each cell. We calculated the linear distance of power lines in each cell (network length of power lines for each cell) and divided the number of electrocutions by the length of power lines per cell. We compared these two methods by assessing the percentage of electrocutions occurring in the resulting hotspots and found that Getis-Ord-Gi*1 accounted for a higher percentage of electrocutions. Therefore, for the remainder of the analysis we used only the Getis-Ord-Gi*1 method.

The hotspot analysis finds clustering by comparing values of each cell and its neighbours to the sum of all cells. Resultant *z*-scores give a measure of clustering, with large positive *z*-scores indicating clustering of large values (hotspot) and large negative *z*-scores indicating clustering of small values (coldspot). We overlaid hotspots identified by planar KDE and Getis-Ord-Gi* onto the power line map to calculate the percentage of power lines and electrocutions each hotspot is associated with.

Comparison of Electrocution Hotspots Between Species and Seasons To compare electrocution hotspots between species and seasons, we used the planar KDE and Getis-Ord-Gi*1 outputs. We used the planar KDE results as opposed to those from the network KDE, as they allowed for better visualisation of overlap of hotspots. Using the KDE, we divided each heatmap into five equal interval levels of density and extracted the highest two levels to create a vector outline of hotspots. We overlaid the hotspot outlines for each species onto one map to visualise hotspot overlap and repeated this to visualise overlap between seasons.

To quantitatively assess similarity between the locations of hotspots we transformed the Getis-Ord-Gi*1 output into a binary variable representing electrocution hotspot presence or absence, including only hotspots with $p \leq 0.05$ in the hotspot presence category. With these data we used Pearson's correlation tests in R. 3.2.3 (R Core Team 2015) to test the association between species-specific hotspots and between seasonal hotspots (Teixeira et al., 2017).

Electrocution Hotspots Over Time To assess change in electrocution rate over time, we performed an ordinary least squares regression (OLS) of yearly electrocution rate against year using R 3.2.3. To account for varying population sizes, we repeated the OLS using electrocutions year^{-1} population^{-1} for each species excluding the white-tailed small-eared galago, for which we did not have census data.

To visualise change in electrocution hotspots over time, we divided the dataset into three study periods: 1998–2003, 2004–2009, and 2010–2016. We chose these study periods to illustrate changes over time, while retaining sufficient electrocution events in each approximately equal time period. We created a KDE overlay map of hotspots as described in the foregoing for species and seasons.

Electrocution Hotspots and Primate and Power Line Density To assess whether electrocution density was associated with primate density and power line density we applied spatial regression analyses using GeoDa 1.10 (Anselin et al., 2006). We could assess only Angolan black-and-white colobus, Sykes' monkeys, and vervet monkeys, as georeferenced census data were not available for southern yellow baboons and white-tailed small-eared galagos. For each species we aggregated census and electrocution data onto a 150 m by 150 m grid and calculated the mean density of monkeys per cell across the total number of years of census data, and the mean density of electrocutions per cell across all years. We calculated the density of power lines within each cell by dividing the length of power line by the area of each cell. We removed all cells that did not have power lines to restrict the analysis to the power line network. Because the spatial autocorrelation violates the independence assumption of OLS, we employed spatial regression models using the maximum likelihood approach and a queen's contiguity spatial weights matrix and selected the most appropriate models based on Akaike's information criterion (AIC), which gives a measure of relative fit of statistical models (Akaike, 1974). We compared the spatial lag and spatial error models for each species because both improved the original OLS model, and consequently selected spatial lag models for Angolan black-and-white colobus and Sykes' monkeys, and a spatial error model for vervet monkeys. The specification of the spatial lag model is given by

$$\gamma = \beta o + X\beta + \ \rho W\gamma + \ \varepsilon$$

In this model the values of the dependent variable in neighbouring locations (Wγ) are included as an extra explanatory variable or the Bspatial lag^ of γ. The second model used, the spatial error model, is given by

$$\gamma = \beta o + X\beta + \ \rho W\varepsilon + \ \varepsilon$$

In this model the values of the residuals in neighbouring locations (Wε) are included as an extra term in the equation, which are considered the Bspatial error.^ W is the spatial weights matrix in both models. To visualise the relationship, we overlaid electrocution hotspots identified by planar KDE onto a heatmap of mean population density for each species.

6.4 Ethical note

The Kenyan government granted permission to conduct this study (permit number NACOSTI/P/17/46068/16586). All research protocols reported in this article were reviewed and approved by the Animal Welfare Review Body at the University of Bristol, Bristol, UK. The authors declare that they have no conflict of interest.

6.5 Supplementary material

The datasets analysed during the current study are deposited and available from: https://mdsoar.org/handle/11603/10940. The online version of this article contains supplementary material, which is available to authorised users.

6.6 Results

In Diani, between 1998 and the end of 2016, community members reported 370 electrocutions, 329 of which we georeferenced. The most commonly observed species was Angolan black-and-white colobus, followed by Sykes' monkeys, white-tailed small-eared galagos, vervet monkeys, and southern yellow baboons (Table 6.1). We found that the 54% of cells had no power lines, hence a network distance of 0 m. Of all cells with power lines, the mean length was 200 ± SD 156 m, with a maximum power line length of 738 m. The power line lengths were longer in urbanised areas and near major roads.

6.6.1 Electrocution hotspots

Across all species, planar KDE showed that 51% of electrocutions occurred within hotspots on 10% of the power line network (Table 6.1, Figure 6.2). We could not calculate percentage of electrocutions or power line network percentages from the results of the network KDE (Figure 6.2). Getis-Ord-Gi*1, which did not correct for power line length, showed that 56% of electrocutions occurred within hotspots on 10% of the power line network (Table 6.1, Figure 6.2). The second Getis-Ord-Gi* method, which corrected for power line length within each cell, showed that 36% of electrocutions occurred within hotspots on 7% of the power line network (Figure 6.2).

Hotspots for individual species identified by Getis-Ord-Gi*1 (Figure 6.3) largely over-lapped the hotspots for all species (Figure 6.2). The majority of reported electrocutions occurred along a small proportion of the power grid (Table 6.1).

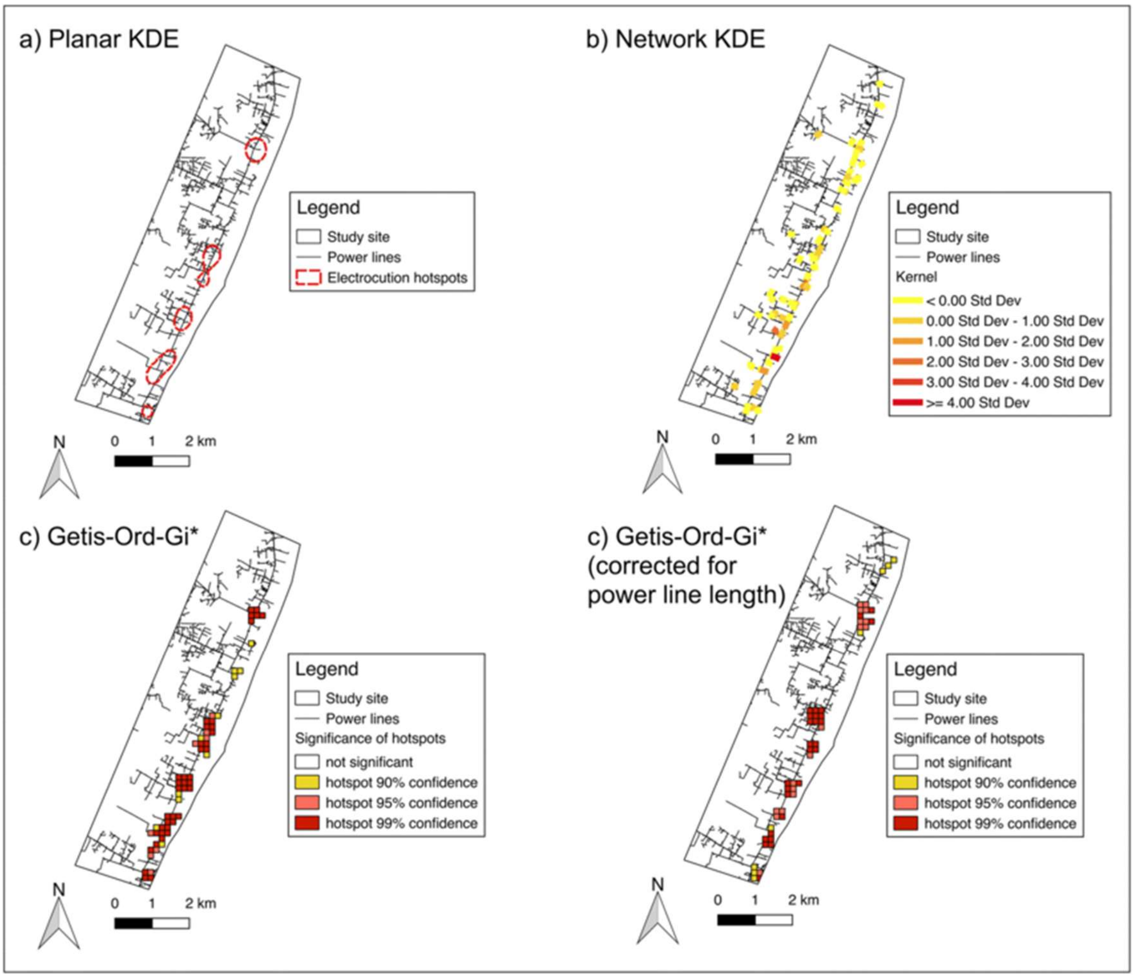

Figure 6.2 Electrocution hotspots identified for primate species in Diani, Kenya, 1998–2016, using four different methods.

6.6.2 Comparison of electrocution hotspots between species

The hotspot overlay map shows high overlap of electrocution hotspots between different species, excluding one Sykes' monkey, one vervet monkey, and two white-tailed small-eared galago hotspots that are isolated (Figure 6.3). The most northerly hotspot shows high overlap between all species except southern yellow baboons. Pearson's coefficients showed small to medium similarity for most species' hotspots (Table 6.2).

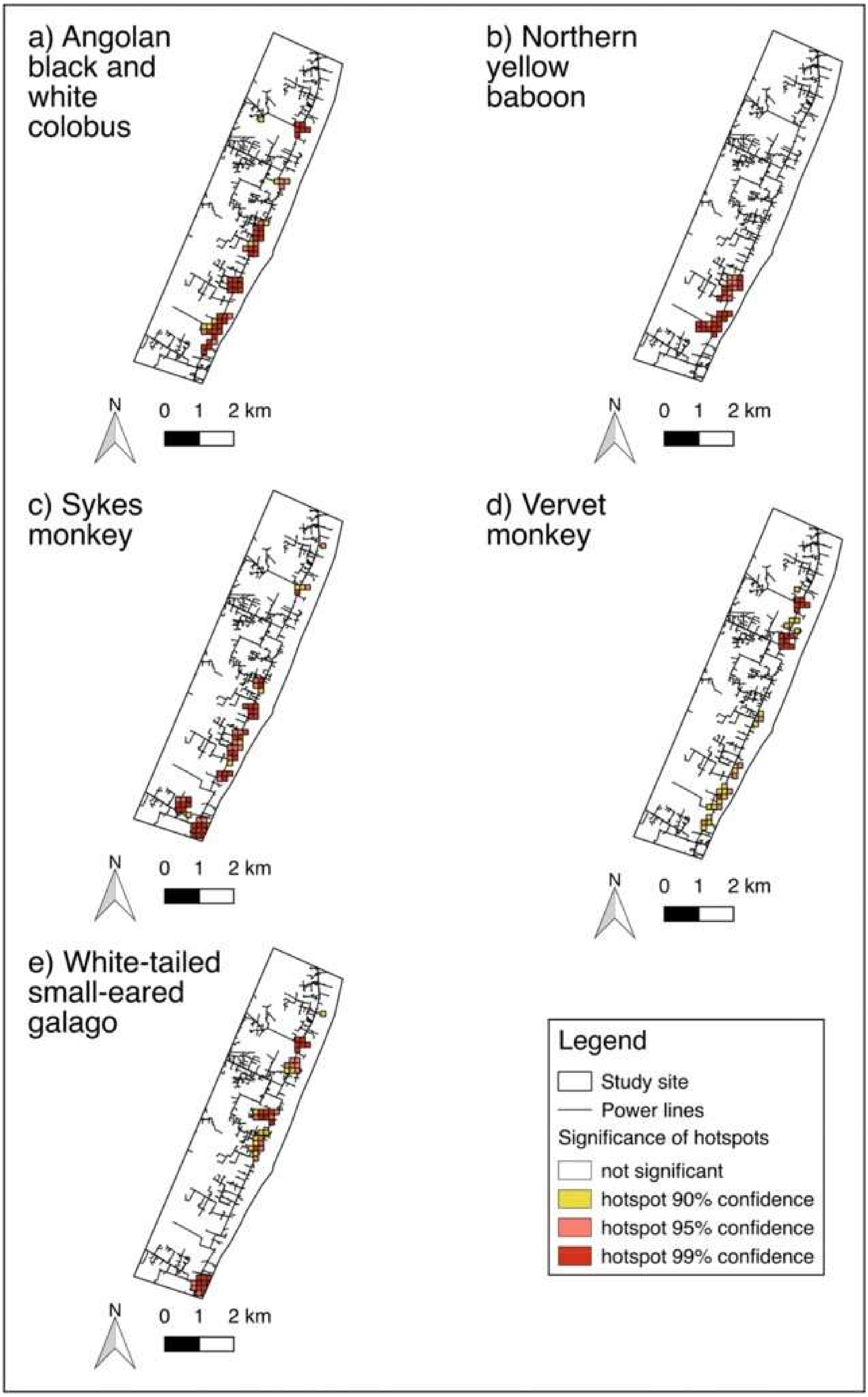

Figure 6.3 Electrocution hotspots identified by Getis-Ord-Gi*1 for five primate species in Diani, Kenya, 1998–2016. Getis-Ord-Gi*1 does not account for power line length.

Table 6.1 Hotspots of primate electrocutions reported in Diani, Kenya between January 1998 and December 2016.

Group	Number of electrocutions	Percentage of total electrocutions for each species	Getis-Ord-Gi*1(95%) hotspots		Number of hotspots	Planar kernel density estimation hotspots	
			Percentage of electrocutions occurring in hotspots	Percentage of power grid in hotspots		Percentage of electrocutions occurring in hotspots	Percentage of power grid in hotspots
All species	329	100	56	10	5	51	10
Southern yellow baboon *Papio cynocephalus cynocephalus*	7	2	100	6	1	57	1
Angolan black and white colobus *Colobus angolensis palliatus*	232	71	58	9	4	63	13
Sykes' monkey *Cercopithecus mitis albogularis*	47	14	73	11	8	60	6
White-tailed small-eared galago *Otolemur garnettii lasiotis*	31	9	53	9	5	68	9
Vervet monkey *Chlorocebus pygerythrus hilgerti*	12	4	50	4	2	42	1

6.6.3 Comparison of seasonal electrocution hotspots

We observed electrocutions at a rate of 2.22 per month during the short dry season, 1.46 per month during the long rains, 1.96 per month during the long dry season, and 1.44 per month during the short rains. Seasonal hotspots showed high overlap between seasons (Figure 6.4). Pearson's coefficients showed high similarity between hotspots for the short dry season and long dry season, long rains and short dry season, and long rains and long dry season (Table 6.3). Similarity was low between hotspots

Table 6.2 Results of Pearson's correlation between hotspots of primate electrocutions reported for five primate species in Diani, Kenya, 1998–2016.

	Angolan black and white colobus	White-tailed small-eared galago	Sykes' monkey	Vervet monkey
Southern yellow baboon	$r = 0.50$ $p < 0.001$	$r = 0.07$ $p = 0.103$	$r = 0.25$ $p < 0.001$	$r = 0.21$ $p < 0.001$
Angolan black and white colobus	–	$r = 0.01$ $p = 0.901$	$r = 0.27$ $p < 0.001$	$r = 0.33$ $p < 0.001$
White-tailed small-eared galago	–	–	$r = 0.26$ $p < 0.001$	$r = 0.04$ $p = 0.316$
Sykes' monkey	–	–	–	$r = 0.24$ $p < 0.001$

Table 6.3 Results of Pearson's correlations between season-specific hotspots of reported primate electrocutions in Diani, Kenya, 1998–2016.

	Long rains	Short dry season	Short rains
Long dry season	$r = 0.51$ $p < 0.001$	$r = 0.73$ $p < 0.001$	$r = 0.04$ $p = 0.409$
Long rains	–	$r = 0.58$ $p < 0.001$	$r = 0.109$ $p = 0.011$
Short dry season	–	–	$r = 0.29$ $p < 0.001$

for short rains and short dry season, and there was no relationship between hotspots for the short rains and long rains (Table 6.3). Pearson's coefficients indicated no significant correlation between short rain and long rain hotspots (Table 6.3).

6.6.4 Changes over time

Electrocutions occurred at a mean rate of 20.45 per year. OLS regression showed no statistically significant relationship in yearly rate (coefficient = 0.36, R^2 = 0.078, df = 18, p = 0.1). OLS of electrocutions year^{-1} population^{-1} for Angolan black-and-white colobus, Sykes' monkeys, vervet monkeys, and southern yellow baboons also showed no trend (Angolan black-and-white colobus: coefficient = 0.0014, R^2 = 0.099, df = 9, p = 0.4, Sykes' monkey: coefficient = 0.00020, R^2 = 0.20, df = 8, p = 0.2, vervet monkey: coefficient = −0.00011, R^2 = 0.0052, df = 8, p = 0.8, southern yellow baboon: coefficient = −0.00013, R^2 = 0.048, df = 9, p = 0.5). The hotspot overlay map (Figure 6.4) showed relatively consistent overlap of hotspots since 1998. One hotspot from 1998 to 2003 has disappeared, one has increased in area, and between 2010 and 2016 two new hotspots appeared.

6.6.5 Association of electrocution hotspots with primate population density and power line density

For Angolan black-and-white colobus and Sykes' monkeys, spatially weighted regression models indicated a positive association between primate density and electrocution density, and power line density and electrocution density (Table 6.4). Overlay of electrocution hotspots onto primate density KDE showed that hotspots generally coincide with areas of high primate density (Figure 6.5). However, some areas of high primate density coincide with power lines and are not associated with electrocution hotspots.

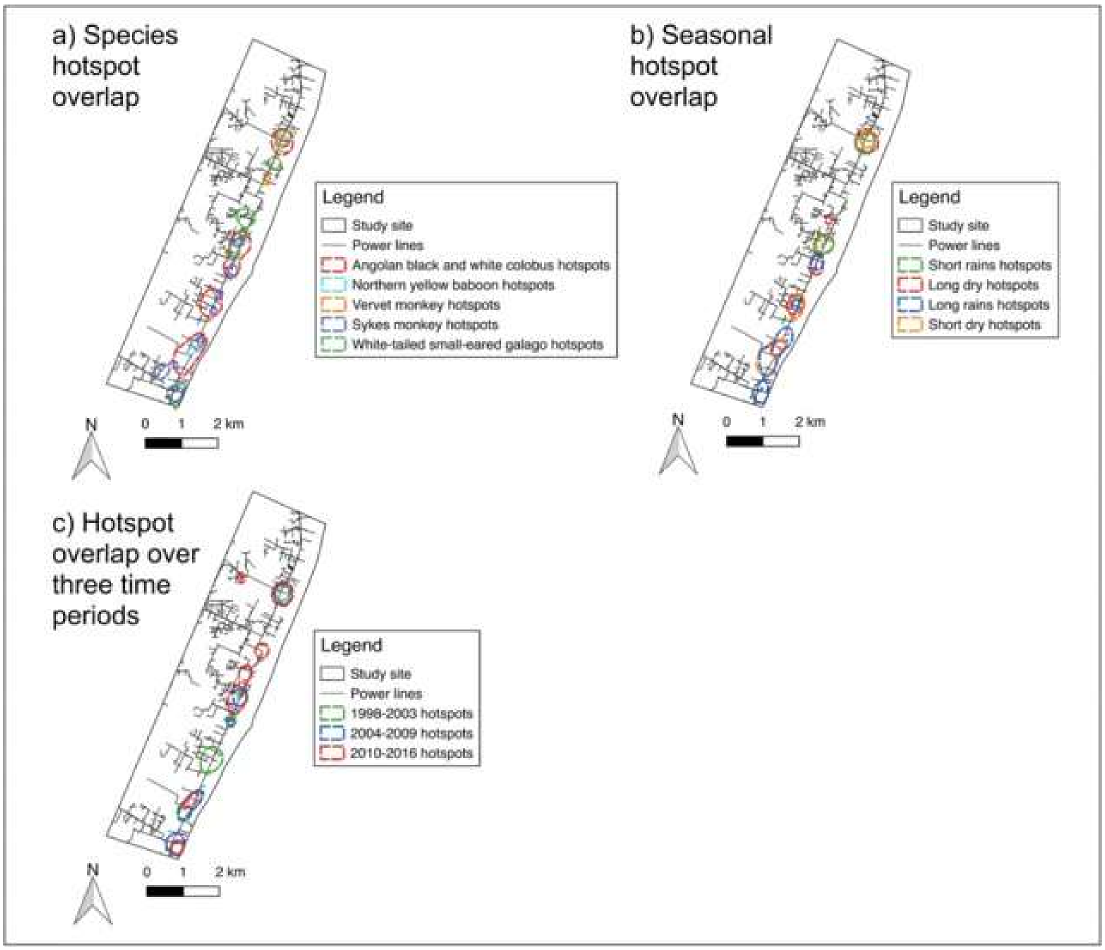

Figure 6.4 Maps showing overlay of primate electrocution hotspots identified by planar kernel density estimation for species, seasons, and over time, in Diani, Kenya between 1998 and 2016.

Table 6.4 Spatially Weighted Regression coefficients for electrocutions reported in Diani, Kenya, 1998-2016. Species included are Angolan black and white colobus (*Colobus angolensis palliatus*), Sykes' monkey (*Cercopithecus mitis albogularis*), and vervet monkey (*Chlorocebus pygerythrus hilgerti*) with mean density of electrocutions per cell as the dependent variable and mean density of individuals per cell and power line density per cell as the explanatory variables.

Species	Angolan black and white colobus	Sykes' monkey	Vervet monkey
Regression model:	Spatial lag	Spatial lag	Spatial error
Covariate:			
Mean density of individuals per cell	0.013	0.0017	0.00064
	$p = < 0.001$	$p < 0.001$	$p = 0.1$
Power line density	6.44e-05	1.31e-05	2.72e-06
	$p = 0.002$	$p = 0.007$	$p = 0.3$
R^2	0.086	0.086	0.0078
Degrees of freedom	545	545	545

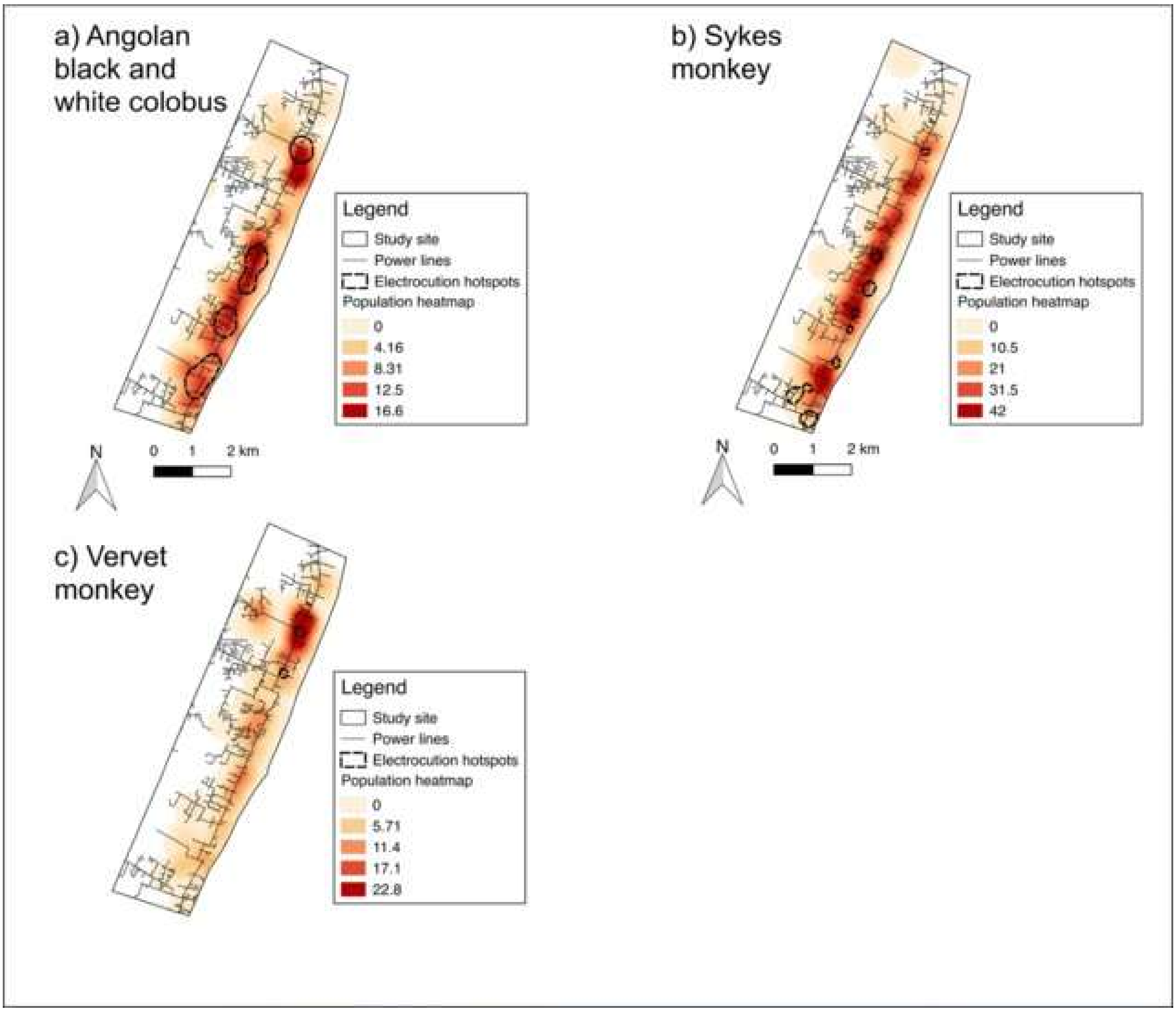

Figure 6.5 Map showing overlay of electrocution hotspots and mean density of individuals calculated by planar kernel density estimation for three species of primate in Diani, Kenya, 1998–2016.

6.7 Discussion

Primate electrocutions are not randomly distributed across the landscape in Diani. Electrocutions occur in hotspots that show little variation in location between species and seasons. Yearly electrocution rate is stable, but the location of hotspots has changed over time. Primate density and power line density are associated with hotspots, but the low R^2 values suggest the presence of additional risk factors, such as power line structure and environmental factors.

Hotspots identified in this study show that most primate electrocutions occurred on a small proportion of the power grid. This pattern is similar to that reported for Hanuman langurs in India, where a high incidence of electrocutions occurred in one location at the same power pole (Ram et al., 2015) and is commonly observed in avian studies (Dwyer et al. 2014; Guil et al. 2011; Mañosa 2001; Tintó et al. 2010).

We found that planar KDE and Getis-Ord-Gi*1 were the most practical methods to test for the presence of hotspots in our study. The output from network KDE identified specific sections of power line with high electrocution density, whereas the planar KDE identified broader, discrete areas of high electrocution density in Diani. Although applying planar KDE to a network-based dataset may produce biased estimates (Okabe et al., 2009), we found that hotspots from the planar KDE showed high overlap with hotspots from the Getis-Ord-Gi*, which did account for the network nature of the dataset. For Getis-Ord-Gi*, we found that accounting for power line length within each cell resulted in areas of high electrocution density with high power line density being omitted from the hotspot map, suggesting that electrocution risk is greater in areas with high power line density. Identifying only hotspots in areas with low power line density is not practical for our purpose, as areas where high electrocution density coincides with high power line density should also be prioritised for mitigation.

Understanding how species hotspots relate to each other is important to ascertain whether species-specific mitigation strategies are required (Teixeira et al., 2017). The Pearson's correlation suggested small to medium similarity between most species-specific hotspots but overlay of planar KDE hotspots showed substantial overlap for most species. The Pearson's correlation may have identified lower similarity between hotspots, as this method examines the association of hotspots between each pair of species, whereas the planar KDE examines the overlap between all the species.

Consequently, the planar KDE demonstrated a higher degree of overlap, as a high proportion of species-specific hotspots fall within the Angolan black-and-white colobus hotspots, as this species has the most extensive electrocution hotspots. Similarity between species hotspots is unsurprising as the primate species in Diani have overlapping ranges (Moreno-Black, 1977), and many of them have been documented to interact with each other (de Jong & Butynski, 2010; Moreno-Black, 1977). Frequent association and overlapping ranges are likely to lead to similarities in location of electrocutions between the species.

The species-specific hotspots generally fall within the planar KDE hotspots created for all species. This suggests a general, non–species-specific approach would be beneficial for most primates in Diani, but a species-specific approach may be needed to further reduce Sykes' monkey, vervet monkey, and white-tailed small-eared galago electrocutions.

Electrocution rate increased during the dry seasons, but the locations of electrocution hotspots showed minimal variation between the seasons. This suggests variations in seasonal risk do not usually need to be factored into prioritisation of areas for mitigation interventions in Diani. In contrast to our results, higher risk of electrocution is typically associated with wet seasons, as shown for raptors (Olendorff et al., 1981), Asian elephants (*Elephas maximus*: Palei et al., 2014), and rhesus macaques (*Macaca mulatta*: (Kumar and Kumar 2015). A proposed explanation for elevated risk during the dry season in Diani is increased vegetation growth toward the start of the long dry season, resulting in increased contact between trees and power lines (Slade, 2016). An alternative explanation is seasonal use of power lines by monkeys, possibly linked to the availability of food resources (Lokschin et al., 2007).

Since 1998 yearly electrocution rates have remained stable, but the location of hotspots has varied. Changes in location of hotspots may be due to the rapid development of Diani, which has resulted in the construction of new power infrastructure and ultimately in changes to food resource distribution. Alternatively, these changes may be associated with variable detection rates in some areas owing to the movement of people or urbanisation. For instance, a hotspot from 1998 to 2003 that has disappeared is associated with an abandoned hotel that burnt down in 1998 (Colobus Conservation, pers. comm. 2017); therefore, electrocutions are unlikely to be reported. Owing to these confounding factors it is important to include all available data from the whole study period to make an informed decision on mitigation strategies (Eberhardt et al., 2013).

Electrocution hotspots are associated with primate density and power line density for Sykes' monkeys and Angolan black-and-white colobus. Additional risk factors that were not included in our study may be associated with power line structure and environmental factors such as vegetation cover and food abundance, as shown in avian studies (Dwyer et al., 2014; Guil et al., 2011; Mañosa, 1997; Tintó et al., 2010). It is important to identify these risk factors to identify high-risk areas before electrocutions occur and target these areas for mitigation (Dwyer et al., 2014; Shaw et al., 2010).

In addition, we showed that there are specific areas where high primate density coincides with power line infrastructure, yet not associated with electrocution hotspots, suggesting that there may be protective factors at these sites. It may be helpful to assess potential protective factors in these locations, which could include a behavioural change of primates (avoidance), or fewer environmental and structural risk factors.

Limitations of this study primarily relate to data collection techniques. As Colobus Conservation relies on reports from community members, incidents in inaccessible areas are likely to go underreported, while incidents close to the main road are more likely to be reported. Furthermore, the movement of wounded animals may affect data collection (Bevanger, 1999). The dataset is composed of all known electrocution and electric shock cases, including incidents that were directly observed, where the primate was found attached to the power line, and those found away from power lines, dead or alive. We do not know how far primates who have electric shock injuries travel, but we assume that the location of individuals that survive the initial injury provides a good indication of the area that they were electrocuted. Despite these limitations, this study benefits from a dataset spanning 18 years, which increases the reliability of using hotspots to guide mitigation strategies.

Electrocution is an issue for many threatened primate species, yet the development of effective evidence-based mitigation strategies is limited. This study provides a framework for systematic spatial prioritisation of high-risk areas that will contribute to more effective mitigation planning. This framework can be used across the world to understand and reduce primate electrocutions. Future studies should aim to objectively evaluate and compare current mitigation measures, especially comparing fatalities before and after. Furthermore, electrocution hotspots should be profiled to identify risk factors such as habitat and high-risk power line components, to guide a proactive mitigation approach that aims to reduce the risk before mortality has occurred.

6.8 Acknowledgements

We thank Kenya Wildlife Service and the National Commission for Science, Technology, and Innovation for permission to conduct this research. We also express our appreciation to Colobus Conservation for providing the dataset for analysis and the Diani community for years of contributions to animal welfare care. Thank you to Kenya Power for providing the GIS power infrastructure map that made this analysis possible. Thank you to Kelly-Marie Martin of Colobus Conservation for providing logistical support during the research period and Khalfani Mwitu for invaluable help in data collection. We would like to thank Stuart E. Hamilton for his valuable input on the manuscript's methods. Thanks to the editor and two anonymous reviewers for their comments and suggestions on previous versions of this article.

Chapter 7. Discussion

With the United Nations' Sustainable Development Goals promoting the expansion of roads (United Nations, 2015b) and power lines (United Nations, 2015a), and the global economy as a primary driver of urbanisation (Chen et al., 2014), addressing the impact of linear infrastructure on biodiversity within towns and cities becomes increasingly crucial. In the town of Diani, southeastern Kenya, the wide taxonomic range of six sympatric primates (colobus, Sykes' monkey, vervet, baboon, two species of galago) provided this study with a unique opportunity to unravel conservation challenges stemming from its main road and power lines. By discerning the impact from these two types of linear infrastructure, and implementing and evaluating mitigation measures, this thesis has the main aim of improving urban co-existence between people and primates.

Diani's community reports approximately 250 primate welfare incidents annually to Colobus Conservation, the local primate conservation organisation (Colobus Conservation, unpubl. database). Chapters 2 & 5 of this thesis show that of these reports, almost half are attributed to injuries and deaths caused by Beach Road and the town's power lines (37% and 16%, respectively), together surpassing those caused by illness, intraspecific fighting and infanticide, dog attacks, unwanted 'pest' behaviour, poaching, and human cruelty combined. While the incident rate from the road was higher for colobus and Sykes' monkeys (3% of the population annually) than for the vervets (2%) and baboons (1.8%), for the power lines, overwhelmingly the colobus was most affected (80% of the electrocution reports). In both cases, species' that are more arboreal, were at higher risk than those more terrestrial. However, for electrocutions, among the arboreal species, individuals with larger body mass were found to be at greater risk.

For Diani's colobus, the cumulative population percentage lost each year because of incidents attributed to Beach Road and the power lines is 8% (Chapters 2 & 5), which is unsustainable (Hart, 2007; Robinson & Bodmer, 1999). As Diani's colobus is a source population for maintaining Kenya's metapopulation (Anderson, 2005a), this may well have a negative knock-on effect on the global population in terms of increased population fragmentation and reduced genetic variability (Cunneyworth et al., 2020; McDonald et al., 2022).

This thesis also found that the cumulative population percentage injured and killed annually by Beach Road and the power lines for Sykes' monkeys is 3.3%, for vervets is 2.0%, and for baboons is 1.8% (Chapters 2 & 5), which are likely sustainable losses for the local populations. However, while these species are considered Least Concern on the IUCN Red List, they represent more than 1000 individuals injured or killed over the past 25 years. This thesis, therefore, highlights the need for addressing the issue of individual well-being separate from the population or species-level concerns (Chapter 5).

To address the risks from Diani's Beach Road, this thesis found that canopy bridges can successfully mitigate both the road barrier effect (Chapter 3) and monkey-vehicle collisions (Chapter 4), though some caveats remain such as where canopy bridges should best be installed to reduce risks (Chapter 4) and that not all species will use them (Chapter 3). Yet, the cost-effectiveness calculation of bridge use found that in 2020, for the quarter of a million estimated annual crossings on 29 bridges, each crossing costs only 4 US₵. This was based on bridge capital, installation, maintenance and replacement costs (Chapter 3), making this a highly economical mitigation. To address the risks from Diani's power lines, this thesis found that of the six species of primates, the main risk is to colobus (Chapter 5 & 6). Because colobus electrocution hotspots occur on only 9% of the town's power lines, spatially mapping the incidents (Chapter 6) then targeting those areas for mitigations such as trimming vegetation around the power lines and insulating electricity cables (Chapter 5), can be cost effective.

Together, the cumulative results of this thesis provide sufficient understanding to examine two methodological challenges in the literature outlined in Section 7.1 of this thesis below. It also offers practical recommendations when developing mitigation measures addressing the impacts from roads and power lines on primates. This is presented in Section 7.2. Typical of the scientific process, I outline several research avenues building on the work here in Section 7.3. Lastly, in Appendix II, I describe how the insights gained from these analyses have been used to inform on local, national, and international conservation issues related to primates and linear infrastructure.

7.1 Methodological challenges in the literature

The results of this thesis highlight two methodological challenges in the literature. 1) Many studies estimate the varying risks of wildlife-vehicle collisions and electrocutions across species by conducting carcass surveys. In Section 7.1.1 below, the reasons why this may not be a sufficient method to accurately determine the risks to wildlife are discussed in light of the results of Chapters 2, 5, & 6. 2) In the literature for roads, the barrier effect and primate-vehicle collisions are presented as two types of impact even though a few authors suggest that theoretically, they should be considered related impacts. I outline in Section 7.1.2 why these few authors are likely correct given the results of Chapter 4 of this thesis.

7.1.1 Do carcass surveys estimate the varying risks of wildlife-vehicle collisions and electrocutions across species?

In Diani, Colobus Conservation compiles community reports of primate welfare incidents. When the team responds to callouts, they record carcasses and those injured, where the team searches for the individual when the individual has moved away from the incident site. Of the total incidents recorded, injured individuals accounted for 31% of vehicle collisions (Chapter 2) and 51% of electrocutions (Chapter 5).

This is likely a common phenomenon across sites. For example, of community reports to the authorities of urban marmosets (*Callithrix penicillata*) in Belo Horizonte, Minas Gerais, Brazil, 36.7% were of injured individuals across the various incident types (Goulart et al., 2010). Other studies also indicate considerable number of surviving individuals. For Rhesus macaques (*Macaca mulatta*) in the Shivalik hills area in northern India, of the 73 cases of electrocution injuries, 73% survived (Kumar and Kumar 2015). For toque macaques (*Macaca sinica*) in Sri Lanka, 22% of the electrocution cases were injured individuals. A study of Chacma baboons (*Papio ursinus*) in Cape Town, South Africa, also indicates that individuals survived electrocutions (Beamish, 2009; Beamish & O'Riain, 2014).

Where there are no long-term studies, central authority, or organisations that respond to community callouts, researchers rely on carcass surveys to quantify vehicle collisions and electrocutions with wildlife (Abra et al., 2021; Franceschi et al., 2022; Uddin et al., 2021). These surveys estimate the relative species-specific risks associated with that infrastructure type. However, because these surveys count carcasses, they overlook individuals who survive the incident, either with a permanent disability (Beamish, 2009) or those that die away from the road or roadside (Campbell et al., 2016) or the power lines (Bevanger, 1999; Dwyer, 2006; Kadlecova et al., 2022).

Adjusting these carcass counts for detection bias has received considerable attention, especially regarding carcass removal by predators (Huso, 2011; Santos et al., 2011). However, injury bias has only gained recent interest. A mammal study in Canada compared carcass detection during driving and walking surveys (Lee et al., 2021). While the driving survey restricted their counts to carcasses on the road, the walking surveys included carcasses along the road verges. The authors considered those carcasses to be individuals injured and dying after a collision with a vehicle. To address this injury bias, they suggested introducing a sizeable correction factor of 2.8 to surveys of carcasses found directly on roads when calculating the cost-benefit analysis for mitigation implementation.

Birds of prey injured by power lines also constitute a considerable proportion of the incidents, unrecorded in power line carcass surveys. Across wildlife rehabilitation centres in the Czech Republic, 20% of the diurnal raptors were admitted due to injuries caused by power infrastructure (Kadlecova et al., 2022) and in Arizona, 16% of the 85 Harris's hawks trapped had confirmed or suspected electric shock injuries (Dwyer, 2006).

The implications of this thesis together with those of other studies, challenges the assumption in the literature that wildlife carcass surveys reflect the varying vehicle collision and electrocution risks that different species face from these types of linear infrastructure. Consequently, when individuals surviving the event are not included in descriptions of the actual impact on wildlife, that estimate is severely under reported. This thesis found that if only carcass surveys were used in Diani to assess the number of incidents of monkey-vehicle collisions and electrocutions, correction factors of 1.5 and 2.15, respectively, would need to be applied to provide a more accurate estimate of the impact.

7.1.2 Are the road barrier effects and wildlife-vehicle collisions related impacts on wildlife?

Chapter 4 of this thesis examined whether canopy bridges reduced vehicle collisions on Diani's Beach Road by comparing collision hotspots before and after installation. We limited the analysis to three years either side of the bridge installation year to reduce variability in the road effect zone due to changes in the urban environment (Forman et al., 1997; Forman & Alexander, 1998; Forman & Deblinger, 2000). Contrary to expectations, almost 20% of the bridges either developed a collision hotspot where there was no hotspot before bridge installation, or where there was a hotspot, that hotspot remained after installation.

This suggests that at these bridge locations, there was a strong barrier effect before bridge installation. With bridge installation, that barrier effect reduced, and road crossings were facilitated. But, for all three species of monkeys that use the bridges (colobus, Sykes' monkey, vervet), during the same crossing event, often, some members of a group cross the road on the ground while others cross on the bridge. Because of this association of bridge crossings with ground crossings, there is an increased vehicle collision risk with bridge installation.

To understand why this happens challenges our common assumption that species showing fewer vehicle collisions are less affected by roads than those more frequently involved (Abra et al., 2021; Baskaran & Boominathan, 2010; Caires et al., 2019). Given this assumption, studies tend to analyse separately, mitigation effectiveness for the road barrier effect (Soanes et al., 2024) and wildlife-vehicle collisions (Rytwinski et al., 2016). For primates, the extent to which canopy bridges reduce the road barrier effect is measured by crossing frequency (Birot et al., 2020; Chan et al., 2020; Das et al., 2009; Flatt et al., 2022; Hernández-Pérez, 2015; Kumar et al., 2013). In contrast, the extent to which canopy bridges reduce vehicle collisions is measured by comparing the number of incidents before and after bridge installation (Maria et al., 2022; Monticelli et al., 2022; Rojas & Gregory, 2022; Yap et al., 2022).

Fahrig and Rytwinski (2009) implied that the road barrier effect and wildlife-vehicle collisions are two related categories influenced by a species' road avoidance behaviour and their ability to avoid oncoming vehicles if they cross the road. Ten years later, Ascensão et al. (2019) explicitly presented that relationship in a simple scenario: If individuals do not cross a road due to a strong barrier effect, fewer vehicle collisions will occur compared to those species exhibiting a weaker road barrier effect. In other words, the strength of the barrier effect for some species can have an inverse relationship to the frequency of vehicle collisions, as long as the proportion of successful to unsuccessful crossings remains constant. The results of this thesis support that hypothesis indicating that there is a strong relationship between these two types of impact. Therefore, the road barrier effect and vehicle collisions should be considered related impacts.

Currently, monitoring of mitigation measures is most often conducted using camera traps mounted on canopy bridges (Fan and Lindshield 2022; Monticelli et al. 2022; Moore et al. 2021; Yap et al. 2022). Data are rarely collected on road crossings on the ground (Gregory et al., 2017) and recommendations for camera trap use to monitor bridge crossings entirely omit discussing ground crossings (Gregory et al. 2013; Gregory et al. 2022). To better understand the relationship between the road barrier effect and vehicle collisions, this thesis recommends that ground crossings should be integrated as a standard component of the before-and-after mitigation monitoring.

7.2 Practical recommendations drawn from this study

The results of this thesis provide an opportunity to discuss two recommendations when mitigation projects are considered for roads and power lines. While a practical guide for installing canopy bridges already exists for those placed in rights-of-way for pipelines (Gregory et al., 2013), roads and power lines have additional considerations that need attention. 1) Certain road features may increase primate-vehicle collisions, necessitating the installation of canopy bridges at those locations. This is discussed in Section 7.2.1. below. 2) Power lines within road reserves add complexity to decision-making concerning canopy bridge installation. How it does so is presented in Section 7.2.2.

7.2.1 The role of road features on monkey-vehicle collisions

Chapter 4 of this thesis identified two road features associated with monkey-vehicle collision hotspots that should be considered when implementing mitigation projects. 1) At S-curves, especially where vegetation grows near the roadside, vehicle collisions may increase because presumably, drivers cannot see monkeys on the road or roadside, and monkeys cannot see oncoming vehicles. A similar suggestion that roadside vegetation creates collision hotspots for ungulate-vehicle collisions has been made (Keken et al., 2019). 2) At T-intersections, where complex streams of vehicles occur, primates may get confused when attempting to cross the road and mistime their crossings, leading to vehicle collisions.

Some primates have routine road crossing locations (e.g. *Pan troglodytes verus*: Hockings et al., 2006) and in those cases, mitigations can be very targeted. However, in general, limiting canopy bridge installation to known locations of primate crossings or collision hotspots might miss key mitigation opportunities. Conservation managers should consider bridges along road sections with a strong barrier effect, where crossings, and therefore collisions, are infrequent (Ascensão et al., 2019). Installing bridges in these areas could reduce the barrier effect, encourage crossings, and enhance resource access and gene flow between populations on opposite sides of a road (Soanes et al., 2018). To do so, identifying primate home ranges that are close to the road, but where individuals and groups do not cross, are possible locations for future bridges (Eberhardt et al., 2013).

7.2.2 Power lines in road reserves

A road reserve is the legal designation of land set aside for the construction, maintenance, and expansion of a road and its associated infrastructure and, therefore, provide for the safety and functionality of the road infrastructure (Kenya Roads Regulations, 2023). Road verges, as part of the road reserve, function as a buffer zone between vehicles and adjacent properties or natural features and provide for the installation of other linear infrastructure such as water pipes, sewer lines, internet cables, and power lines. For these purposes, vegetation management of road reserves is critical (Milton et al., 2015). Where power lines are installed, there are stipulations on vegetation clearance distances to reduce damage to the poles and cables (Kenya Power, undated). These clearance distances, technically called trace maintenance, are shorter at ground level and widen upwards, creating a funnel shape. Power lines installed in a road verge can exacerbate the impact on wildlife more than either road or power lines individually, because of the increased habitat gap created when there is active vegetation management.

The gap created by the road reserve, that is the width of the road plus the verge on either side of the road, has been documented as creating collision hotspots (Keken et al., 2019; Rea, 2003). Similarly, Chapter 4 of this thesis analysed a segment along Diani's Beach Road cleared of woody vegetation for a power line, creating a 30-meter gap between trees on opposite sides of the road reserve. This road segment has become a colobus collision hotspot. The wide gap caused by the vegetation removal for the power lines prevents the installation of canopy bridges. Colobus monkeys are motivated to cross the road at that location but unlike more terrestrial species such as vervets and baboons (Amick, 2018), they do not time their crossing to avoid vehicles. The wide gap between the tree lines on either side of the road appears to complicate crossing events. However, a study is needed to understand colobus and other relevant species behaviour that contributes to collision hotspots under these conditions.

Given the risks associated with wide road reserves where vegetation is managed, when conservation managers begin planning mitigation projects addressing wildlife-vehicle collisions and electrocutions, they should consider the road and its road verges as one category instead of two. For planning, projects should consider reviewing legislation to understand if it allows canopy bridges to be installed in the road reserve. Without this allowance, future government infrastructure projects could require the removal or relocation of the bridges, as it has happened in Diani. It is also advisable to avoid using trees as supports for canopy bridges near power lines, especially if they are closer than the required mandated clearance distance (3 meters on each side of the power pole at ground level in Kenya). Trees leaning toward power lines or with branches within the designated funnel area (9 meters on each side of the cable at cable height in Kenya) should also be avoided, as future vegetation management could require cutting of those trees or branches, rendering the bridges ineffective.

7.3 Recommendations for future avenues of research

The scientific literature describing the impacts and mitigations of roads and power lines on wildlife is growing. Yet, there are many gaps in our knowledge, especially because of the range of morphological, behavioural, and ecological attributes of the target species and the equally wide range of linear infrastructure features. While this thesis has contributed to filling some knowledge gaps, the results have generated further questions. Below, are three areas for future research highlighted by this thesis.

7.3.1 Can estimates of species use of canopy bridges be predicted?

A few studies indicate that canopy bridge use rates are based, in part, on species' attributes. The common perception is that arboreal species use bridges more often than those that are more terrestrial (Gregory et al. 2017, 2022). To test this assumption, Chapter 3 calculated the bridge crossing rate for each of Diani's four species of monkeys. The analysis indicated that indeed, substrate preference predicted well the bridge crossing rate with species that are more arboreal having higher crossing rates than those more terrestrial. While body mass also was an explanatory variable, with smaller species of monkeys more likely to use the bridges. Other variables certainly are at play but to the extent that they do so is not clear. For example, while most primates have an opposable thumb, the thumb is absence in the African colobines (Frost et al., 2015) and the horizontal ladder style canopy bridge was chosen to account for that morphological attribute. Interestingly, the South and Central American spider monkey (*Ateles* sp.) shares some similarities with Diani's colobus. Both are arboreal, have a similar body mass, and lack a thumb. However, the spider monkey also has a prehensile tail, a characteristic common among Platyrrhine monkeys. Evidence suggests that canopy bridges are not used by this genus (Aureli et al., 2022). It may be that to accommodate the complex of traits of spider monkeys, developing a specialized bridge design could work to mitigate its road and power line impacts.

Given the wide range of species’ attributes that affect road crossing rates, it is likely that natural canopy bridges, consisting of tree canopies overlapping across a road, best promote crossings across a wide species range (Gregory et al., 2013, 2017). At the other extreme, unusual bridges such as gliding poles targeting sugar gliders, are expected to have little benefit for nontarget species (Soanes et al., 2013, 2018). Yet, the use pattern of a particular bridge design is expected to differ between target and nontarget species because of variations in species’ attributes. Even though colobus is the target species in Diani and the design chosen was specific to their morphological attributes, they had lower bridge use rates than the non-target species, Sykes’ monkeys. Therefore, developing a predictive model using a wide range of wildlife taxa which incorporates the morphological, behavioural, and ecological attributes that may contribute to bridge crossing rates, would provide greater confidence of predicting outcomes during feasibility studies when conservation managers consider installing bridges. Additionally, since colobus, Sykes' monkeys, and vervets often cross roads both on the ground and on bridges during the same crossing event, exploring new bridge designs or a combination of mitigation measures—such as speed bumps and bridges—may reveal a cumulative impact on reducing the road barrier effect and vehicle collisions.

In addition, the canopy bridge analysis in this thesis identified crossings based on species identification only. This is because the study was conducted across 9 km of road section and encompassed a population of approximately 1500 monkeys so that individual identification or even identifying age or sex was not possible. We know that among chimpanzees, there is a division of roles in road crossing progression order based on age and sex class (Hockings, 2011) suggesting that there may be patterns to the ground versus bridge crossings. Therefore, conducting behavioural studies on individual groups known to cross the road on bridges would provide an opportunity to predict this pattern based on individuals of specific age or sex classes.

7.3.2 Are mitigations to wildlife electrocutions effective?

Chapter 5 of this thesis indicates that because the annual number of electrocutions did not increase between 1998 and 2019 that this was due to the mitigations employed jointly by Colobus Conservation and the local power distribution company. These mitigation measures include an intensive project of trimming vegetation around the power lines, poles, and transformers, insulating power lines, and moving transformers implicated in primate electrocutions. However, a spatiotemporal analysis before and after study of these mitigations has not yet been done in Diani.

At other sites, the mitigation measures used addressing primate electrocutions are trimming vegetation around power infrastructure (Lindshield, 2016), installing power pole shields (Dittus, 2020), power line barriers (Lindshield, 2016), and insulation (Aggimarangsee et al., 2022; Lindshield, 2016; Lokschin et al., 2007) and installing canopy bridges, either above (Lindshield, 2016; Maria et al., 2022) or below (Buss et al., 2022) the power lines. Some of these studies provide a preliminary assessment of electrocutions before and after mitigation implementation and found that these mitigation measures were effective. However, their findings were limited to single locations, and to temporal analyses (before and after) but not incorporating the spatial variable into the analysis of where the electrocutions occurred. While two studies (Dittus, 2020; Lokschin et al., 2007) included both injured and dead cases, the remaining studies reported dead individuals only, introducing an injury bias in the dataset as discussed in Section 7.1.1. above. Therefore, further research should be encouraged to test the effectiveness of electrocution mitigations more extensively, to ascertain their wider applicability.

7.3.3 What about road and power line impacts on small nocturnal primates?

In Diani, there are two types of strepsirrhine primates, both of which are galagos. Of these, only Chapter 6 includes the greater galago in the analyses, highlighting a considerable gap in this study. This is because of the limitations of conducting surveys on nocturnal species in an urban area. Safety of the teams during the night-time censuses restricted the methods to noting presence-absence (sightings and vocalisations) conducted from vehicles. This data collection method resulted in the lack of population size estimates for comparing the number of injuries and deaths reported by the community to Colobus Conservation. The smaller galago is not included in any chapters, as people in Diani have not reported this species of galago injured or killed on the road or power lines over the past 25 years. One report of an injured individual on a road came from outside the study area. People may not report these welfare incidents because they do not recognize the species as a primate, as adult males weigh only 150g and superficially resemble a mouse.

Globally, the understanding of the impact of roads and power lines on the strepsirrhines is limited to three species of galagidae: *Galagoides demidovii* (Cibot et al., 2015), *Otolemur garnettii* (this thesis; Olgun et al., 2021), *Paragalago cocos* (this thesis), and four species of lorisidae: *Perodicticus potto*; (Cibot et al., 2015), *Loris lydekkerianus* (Kumara et al., 2006), *Nycticebus bengalensis* (Al-Razi et al., 2019; Radhakrishna et al., 2006), *Nycticebus coucang* (Leen et al., 2019; Moore et al., 2014; Saptorini et al., 2021; Yap et al., 2022). Each of these studies reports one or a few individuals, or the number of incidents is unstated. There is one notable exception. Recent work recorded 2786 electrocutions in one Sumatran province in one year of the Endangered greater slow loris, *Nycticebus coucang* (International Animal Rescue, 2024; Saptorini et al., 2021). The only species of small, nocturnal primates for which we have extensive data shows clearly that electrocution is a significant threat. This suggests that strepsirrhines warrant further study as it is a significant gap in understanding linear infrastructure impact on this wildlife guild.

7.4 Concluding Remarks

The recognition that linear infrastructure significantly impacts wildlife has now prevailed for more than a century (Schreiber & Graves, 1977; Simmons, 1938). Our understanding of these impacts and how to mitigate them is growing but remains limited in many regards. This thesis fills some of these gaps and given the taxonomic range of the six sympatric species of primate living in Diani, provides an understanding of how to reduce human-primate conflict in an urban setting. Until more research and studies on the effectiveness of different mitigation measures and designs are produced across a wider range of primate species, the results of this thesis can be highly informative to conservation managers. Indeed, they can select one of Diani's species with similar characteristics as their target species or those species that exist in their area, such as substrate preference, body mass, diet, or group structure, and use the results of this study as a guide to assess potential impacts of linear infrastructure and possible outcomes of specific mitigation measures.

Since Wallace (1863) identified the linear biogeographical feature, the Wallace Line, between Asian and Australian fauna, other geographic barriers such as rivers and mountains have been recognised as important drivers of subspeciation and speciation (Sobel et al., 2010). Whereas natural linear features provide opportunities for enriching biodiversity, those that are anthropogenically created are constricting wildlife ranges enhancing local wildlife extinction, and consequently are thought to contribute to ecosystem collapse (Trombulak & Frissell, 2000). Because carcass studies likely grossly underestimate the environmental impact of roads and power lines on wildlife, the continued momentum of this line of research and especially advocacy for reforms is essential for ensuring that future infrastructure projects through sensitive wildlife areas implement best practices.

Chapter 8. References

Abra, F. D., Huijser, M. P., Magioli, M., Bovo, A. A. A., & Ferraz, K. M. P. M. de B. (2021). An estimate of wild mammal roadkill in São Paulo state, Brazil. *Heliyon*, *7*(1), e06015. https://doi.org/10.1016/j.heliyon.2021.e06015

Abuodha, P. (2003). Geomorphology of the Kenyan coast: Not as a result of sea-level change alone. *Buletim Geologico*, *43*, 2–7.

Aggimarangsee, N., Tiansawat, P., & Brockelman, W. Y. (2022). Can electrical wires serve as canopy bridges? A case study of the dusky langur (*Trachypithecus obscurus*) in Thailand. *Folia Primatologica*, *40*(6), 1–10. https://doi.org/10.1163/14219980-20211205

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723.

Al-Razi, H., Maria, M., & Muzaffar, S. B. (2019). Mortality of primates due to roads and power lines in two forest patches in Bangladesh. *Zoologia*, *36*, 1–6. https://doi.org/10.3897/zoologia.36.e33540

Altmann, J., Hausfater, G., & Altmann, S. A. (1985). Demography of Amboseli baboons. *American Journal of Primatology*, *8*, 113–125. https://doi.org/10.1002/ajp.1350080204

Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P., & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. *American Journal of Primatology*, *30*(2), 149–161. https://doi.org/10.1002/ajp.1350300207

Amick, D. (2018). *Road crossing behaviour of four wild primate species in Diani, Kenya* [Masters thesis]. University of Roehampton, UK.

Ampuero, F., & Sá Lilian, R. M. (2012). Electrocution lesions in wild brown howler monkeys *Alouatta guariba clamitans* from São Paulo city: Importance for conservation of wild populations. *Journal of Comparative Pathology*, *146*(1), 88. https://doi.org/10.1016/J.JCPA.2011.11.174

Ampumuza, C., & Kaburu, S. S. K. (2023). Benefits of primate tourism. In S. Waters, M. F. Hansen, J. M. Setchell, S. M. Cheyne, C. Ampumuza, K. T. Hanson, K. J. Hockings, K. Ilham, S. S. K. Kaburu, L. Maréchal, C. R. Ruiz Miranda, & J. Wallis (Eds.), *Responsible primate-watching for primate tourism professionals*. IUCN SSC Primate Specialist Group Section on Human-Primate Interactions.

Anderson, J. (2005). *Habitat fragmentation and metapopulation dynamics of the Angola black-and-white colobus (*Colobus angolensis palliatus*) in coastal Kenya* [PhD thesis]. University of London, UK.

Anderson, J. R. (1986). Encounters between domestic dogs and free-ranging non-human primates. *Applied Animal Behaviour Science*, *15*, 71–96. https://doi.org/10.1016/0168-1591(86)90024-9

Anderson, J., Rowcliffe, J. M., & Cowlishaw, G. (2007). The Angola black-and-white colobus (*Colobus angolensis palliatus*) in Kenya: Historical range contraction and current conservation status. *American Journal of Primatology*, *69*, 664–680. https://doi.org/10.1002/ajp.20377

Anderson, T. K. (2009). Kernel density estimation and K-means clustering to profile road accident hotspots. *Accident Analysis and Prevention*, *41*, 359–364. https://doi.org/10.1016/j.aap.2008.12.014

Andrasi, B., Jaeger, J. A. G., Heinicke, S., Metcalfe, K., & Hockings, K. J. (2021). Quantifying the road-effect zone for a critically endangered primate. *Conservation Letters*, *14*(6). https://doi.org/10.1111/conl.12839

Anselin, L., Syabri, I., & Kho, Y. (2006). GeoDa: An introduction to spatial data analysis. *Geographical Analysis*. https://doi.org/10.1111/j.0016-7363.2005.00671.x

APLIC. (2006). Suggested practices for avian protection on power lines: The state of the art in 2006. In *Edison Electric Institute and Sacramento, CA: APLIC and the California Energy Commission*. https://www.aplic.org/documents

Arenas, J. M., Escudero, A., Mola, I., & Casado, M. A. (2017). Roadsides: An opportunity for biodiversity conservation. *Applied Vegetation Science*, *20*(4), 527–537. https://doi.org/10.1111/avsc.12328

Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation*, *123*(1), 37–44. https://doi.org/10.1016/j.biocon.2004.10.006

Aronson, M. F. J., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., Nilon, C. H., & Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. In *Frontiers in Ecology and the Environment* (Vol. 15, Issue 4). https://doi.org/10.1002/fee.1480

Arroyo-Rodríguez, V., & Fahrig, L. (2014). Why is a landscape perspective important in studies of primates? *American Journal of Primatology*, *76*(10), 901–909. https://doi.org/10.1002/ajp.22282

Ascensão, F., D'Amico, M., & Barrientos, R. (2022). No planet for apes? Assessing global priority areas and species affected by linear infrastructures. *International Journal of Primatology*, *43*(1), 57–73. https://doi.org/10.1007/s10764-021-00207-5

Ascensão, F., Kindel, A., Teixeira, F. Z., Barrientos, R., D'Amico, M., Borda-de-Água, L., & Pereira, H. M. (2019). Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. *Global Ecology and Conservation*, *19*, 1–14. https://doi.org/10.1016/j.gecco.2019.e00661

Ascensão, F., Yogui, D. R., Alves, M. H., Alves, A. C., Abra, F., & Desbiez, A. L. J. (2021). Preventing wildlife roadkill can offset mitigation investments in short-medium term. *Biological Conservation*, *253*, 108902. https://doi.org/10.1016/j.biocon.2020.108902

Aureli, F., Hutschenreiter, A., Araya, D., Arévalo-huezo, E., Avila, T., Boiledieu, C., González, A., Lindshield, S., Narváez, G. M., Rufray, V., Thurber, M., Spaan, D., José, S., Rica, C., Latina, U., Rica, D. C., & Rica, C. (2022). Do spider monkeys use artificial canopy bridges to cross linear infrastructure? *Folia Primatologica*, *0*, 1–10. https://doi.org/10.1163/14219980-20211204

Bai, X., McPhearson, T., Cleugh, H., Nagendra, H., Tong, X., Zhu, T., & Zhu, Y. G. (2017). Linking urbanization and the environment: Conceptual and empirical advances. *Annual Review of Environment and Resources*, *42*, 215–240. https://doi.org/10.1146/annurev-environ-102016-061128

Baoping, R., Ming, L., Yongcheng, L., & Fuwen, W. (2009). Influence of day length, ambient temperature, and seasonality on daily travel distance in the Yunnan snub-nosed monkey at Jinsichang, Yunnan, China. *American Journal of Primatology*, *71*(3), 233–241. https://doi.org/10.1002/ajp.20641

Barrico, L., & Castro, P. (2016). Urban biodiversity and cities' sustainable development. In *World Sustainability Series*. https://doi.org/10.1007/978-3-319-32318-3_3

Barrientos, R., & Bolonio, L. (2009). The presence of rabbits adjacent to roads increases polecat road mortality. *Biodiversity and Conservation*, *18*(2), 405–418. https://doi.org/10.1007/s10531-008-9499-9

Bartonička, T., Andrášik, R., Duľa, M., Sedoník, J., & Bíl, M. (2018). Identification of local factors causing clustering of animal-vehicle collisions. *Journal of Wildlife Management*, *82*(5), 940–947. https://doi.org/10.1002/jwmg.21467

Baskaran, N., & Boominathan, D. (2010). Road kill of animals by highway traffic in the tropical forests of Mudumalai Tiger Reserve, southern India. *Journal of Threatened Taxa*, *2*(3), 753–759. https://doi.org/10.11609/jott.o2101.753-9

Beamish, E. K. (2009). *Causes and consequences of mortality and mutilation in the Cape Peninsula baboon population, South Africa* [Masters thesis]. University of Cape Town, South Africa.

Beamish, E. K., & O'Riain, M. J. (2014). The effects of permanent injury on the behavior and diet of commensal chacma baboons (*Papio ursinus*) in the Cape Peninsula, South Africa. *International Journal of Primatology*, *35*(5), 1004–1020. https://doi.org/10.1007/s10764-014-9779-z

Behnisch, M., Krüger, T., & Jaeger, J. A. G. (2022). Rapid rise in urban sprawl: Global hotspots and trends since 1990. *PLOS Sustainability and Transformation*, *1*(11). https://doi.org/10.1371/journal.pstr.0000034

Benítez-López, A., Alkemade, R., & Verweij, P. A. (2010). The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation*, *143*(6), 1307–1316. https://doi.org/10.1016/j.biocon.2010.02.009

Bennett, G., Gallant, M., & ten Kate, K. (2017). *State of biodiversity mitigation 2017: Markets and compensation for global infrastructure development.* Forest Trends Ecosystem Marketplace, Washington, DC.

Bennett, V. J. (2017). Effects of road density and pattern on the conservation of species and biodiversity. *Current Landscape Ecology Reports*, *2*(1), 1–11. https://doi.org/10.1007/s40823-017-0020-6

Berg, C., Deichmann, U., & Selod, H. (2015, December 8). *How roads support development*. World Bank Blogs. https://blogs.worldbank.org/en/developmenttalk/how-roads-support-development

Bevanger, K. (1998). Biological and conservation aspects of bird mortality caused by electricity power lines: A review. *Biological Conservation*, *86*(1), 67–76. https://doi.org/10.1016/S0006-3207(97)00176-6

Bevanger, K. (1999). Estimating bird mortality caused by collision and electrocution with power lines: A review of methodology. In G. F. Janss & M. Ferrer (Eds.), *Birds and power lines: Collision, electrocution and breeding* (pp. 29–56). Madrid: Quercus.

Biasotto, L. D., Moreira, F., Bencke, G. A., D'Amico, M., Kindel, A., & Ascensão, F. (2022). Risk of bird electrocution in power lines: A framework for prioritizing species and areas for conservation and impact mitigation. *Animal Conservation*, *25*(2), 285–296. https://doi.org/10.1111/acv.12736

Bicca-Marques, J. C., & Calegaro-Marques, C. (1995). Locomotion of black howlers in a habitat with discontinuous canopy. *Folia Primatologica*, *64*(1–2), 55–61. https://doi.org/10.1159/000156833

Bíl, M., Andrášik, R., & Janoška, Z. (2013). Identification of hazardous road locations of traffic accidents by means of kernel density estimation and cluster significance evaluation. *Accident Analysis and Prevention*, *55*, 265–273. https://doi.org/10.1016/j.aap.2013.03.003

Bíl, M., Andrášik, R., & Sedoník, J. (2019). A detailed spatiotemporal analysis of traffic crash hotspots. *Applied Geography*, *107*, 82–90. https://doi.org/10.1016/j.apgeog.2019.04.008

Bíl, M., Andrášik, R., Svoboda, T., & Sedoník, J. (2016). The KDE+ software: A tool for effective identification and ranking of animal-vehicle collision hotspots along networks. *Landscape Ecology*, *31*(2), 231–237. https://doi.org/10.1007/s10980-015-0265-6

Bíl, M., Kubeček, J., & Andrášik, R. (2020). Ungulate-vehicle collision risk and traffic volume on roads. *European Journal of Wildlife Research*, *66*(4), 1–9. https://doi.org/10.1007/s10344-020-01397-8

Birot, H., Campera, M., Imron, M. A., & Nekaris, K. A. I. (2020). Artificial canopy bridges improve connectivity in fragmented landscapes: The case of Javan slow lorises in an agroforest environment. *American Journal of Primatology*, *82*(4), 1–10. https://doi.org/10.1002/ajp.23076

Boardman, A. E., Greenberg, D. H., Vining, A. R., & Weimer, D. L. (2018). Cost-effectiveness analysis and cost-utility analysis. In A. E. Boardman, D. H. Greenberg, A. R. Vining, & D. L. Weimer (Eds.), *Cost-Benefit Analysis: Concepts and Practice* (5th ed., pp. 511–536). Cambridge University Press.

Boinski, S., Jack, K., Lamarsh, C., & Coltrane, J. A. (1998). Squirrel monkeys in Costa Rica: Drifting to extinction. *Oryx*, *32*(1), 45–58. https://doi.org/10.1046/j.1365-3008.1998.00017.x

Botting, I., Ascensão, F., Navarro, L. M., Paniw, M., Tablado, Z., Román, J., Revilla, E., & D'Amico, M. (2023). The road to success and the fences to be crossed: Considering multiple infrastructure in landscape connectivity modelling. *Wildlife Biology*, *e01187*. https://doi.org/10.1002/wlb3.01187

Bouchard, J., Ford, A. T., Eigenbrod, F. E., & Fahrig, L. (2009). Behavioral responses of northern leopard frogs (*Rana pipiens*) to roads and traffic: Implications for population persistence. *Ecology and Society*, *14*(2), 23. https://www.jstor.org/stable/26268308?seq=1&cid=pdf-

Brehme, C. S., Tracey, J. A., Mcclenaghan, L. R., & Fisher, R. N. (2013). Permeability of roads to movement of scrubland lizards and small mammals. *Conservation Biology*, *27*(4), 710–720. https://doi.org/10.1111/cobi.12081

Bronikowski, A. M., Cords, M., Alberts, S. C., Altmann, J., Brockman, D. K., Fedigan, L. M., Pusey, A., Stoinski, T., Strier, K. B., & Morris, W. F. (2016). Female and male life tables for seven wild primate species. *Scientific Data*, 1–8. https://doi.org/10.1038/sdata.2016.6

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Buss, G., Ludwig, G., Beltrão-Mendes, R., Valenca-Montenegro, M. M., Martins, A. B., & Alonso, A. C. (2022). Installation and monitoring of a canopy bridge connecting Atlantic Forest fragments containing endangered species in northeastern Brazil. *Folia Primatologica*, *7*(12), 1–13. https://doi.org/10.1163/14219980-20211207

Butynski, T. M., & de Jong, Y. A. (2019). *Paragalago cocos. The IUCN Red List of Threatened Species 2019:* e.T136212A17963050. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T136212A17963050.en

Butynski, T. M., & de Jong, Y. A. (2020). *Otolemur garnettii* ssp. *lasiotis. The IUCN Red List of Threatened Species 2020:* e.T136900A176831791.en. https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T136900A176831791.en

Butynski, T. M., & de Jong, Y. A. (2021). *Cercopithecus mitis. The IUCN Red List of Threatened Species 2019:* e.T4221A268070453. https://doi.org/10.2305/IUCN.UK.2019-3.RLTS.T4221A196007901.en

Butynski, T. M., & de Jong, Y. A. (2022). *Cercopithecus mitis* ssp. *albogularis (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2022:* e. T40645A210337748. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T40645A210337748.en

Butynski, T. M., & De Jong, Y. A. (2022a). *Chlorocebus pygerythrus* ssp. *hilgerti. The IUCN Red List of Threatened Species 2022:* e.T92252725A205896205. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T92252725A205896205.en

Butynski, T. M., & De Jong, Y. A. (2022b). *Chlorocebus pygerythrus. The IUCN Red List of Threatened Species 2022:* e.T136271A205998680. https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T136271A205998680.en

Caceres, N. C. (2011). Biological characteristics influence mammal road kill in an Atlantic Forest-Cerrado interface in south-western Brazil. *Italian Journal of Zoology*, *78*(3), 379–389. https://doi.org/10.1080/11250003.2011.566226

Caires, H. S., Souza, C. R., Lobato, D. N. C., Fernandes, M. N. S., & Damasceno, J. S. (2019). Roadkilled mammals in the northern amazon region and comparisons with roadways in other regions of Brazil. *Iheringia - Serie Zoologia*, *109*, 1–9. https://doi.org/10.1590/1678-4766e2019036

Campbell, L. A. D., Tkaczynski, P. J., Mouna, M., Qarro, M., Waterman, J., & Majolo, B. (2016). Behavioral responses to injury and death in wild Barbary macaques (*Macaca sylvanus*). *Primates*, *57*(3), 309–315. https://doi.org/10.1007/s10329-016-0540-4

Canellys, B. (2016). *Non-natural foraging practices of yellow baboons (*Papio cynocephalus*) in Diani, Kenya: The effects of tourism on behavior in a human-dominated environment* [Masters thesis]. Oxford Brookes University, UK.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30). https://doi.org/10.1073/pnas.1704949114

Chan, B. P. L., Lo, Y. F. P., Hong, X. J., Mak, C. F., & Ma, Z. (2020). First use of artificial canopy bridge by the world's most critically endangered primate the Hainan gibbon *Nomascus hainanus*. *Scientific Reports*, *10*(1), 15176. https://doi.org/10.1038/s41598-020-72641-z

Chapman, C. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, *29*(2), 177–194. https://doi.org/10.1007/BF02381121

Chardonnet, P., Des Clers, B., Fischer, J., Gerhold, R., Jori, F., & Lamarque, F. (2002). The value of wildlife. *OIE Revue Scientifique et Technique*, *21*(1), 15–51. https://doi.org/10.20506/rst.21.1.1323

Chaves, Ó. M., Stoner, K. E., Arroyo-Rodríguez, V., & Estrada, A. (2011). Effectiveness of spider monkeys (*Ateles geoffroyi vellerosus*) as seed dispersers in continuous and fragmented rain forests in southern Mexico. *International Journal of Primatology*, *32*(1), 177–192. https://doi.org/10.1007/s10764-010-9460-0

Chen, H. L., & Koprowski, J. (2019). Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis. *Hystrix, Italian Journal of Mammalogy*, *29*. https://doi.org/10.4404/hystrix-00185-2018

Chen, M., Zhang, H., Liu, W., & Zhang, W. (2014). The global pattern of urbanization and economic growth: Evidence from the last three decades. *PLoS ONE*, *9*(8), e103799. https://doi.org/10.1371/journal.pone.0103799

Cheney, D. L., Seyfarth, R, M., Andelman, S, J., & Lee, P. C. (1988). Reproductive success in vervet monkeys. In H. Clutton-Brock, T (Ed.), *Reproductive success: studies of individual variation in contrasting breeding systems* (pp. 384–402). University of Chicago.

Cheng, W., & Washington, S. (2005). Experimental evaluation of hotspot identification methods. *Accident Analysis and Prevention*, *37*, 870–881. https://doi.org/10.1016/j.aap.2005.04.015

Cibot, M., Bortolamiol, S., Seguya, A., & Krief, S. (2015). Chimpanzees facing a dangerous situation: A high-traffic asphalted road in the Sebitoli area of Kibale National Park, Uganda. *American Journal of Primatology*, *77*(8), 890–900. https://doi.org/10.1002/ajp.22417

Coffin, A. W. (2007). From roadkill to road ecology: A review of the ecological effects of roads. *Journal of Transport Geography*, *15*(5), 396–406. https://doi.org/10.1016/J.JTRANGEO.2006.11.006

Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173. https://doi.org/10.1016/j.anbehav.2013.11.027

Colino-Rabanal, V. J., Langen, T. A., Peris, S. J., & Lizana, M. (2018). Ungulate-vehicle collision rates are associated with the phase of the moon. *Biodiversity and Conservation*, *27*(3), 681–694. https://doi.org/10.1007/s10531-017-1458-x

Conservation International. (2024). *Coastal Forests of Eastern Africa*. Critical Ecosystem Partnership Fund. https://www.cepf.net/our-work/biodiversity-hotspots/coastal-forests-eastern-africa

Convention on Biological Diversity. (2022). *Decision adopted by the Conference of Parties to the Convention on Biological Diversity: 15/4. Kunming-Montreal Global Biodiversity Framework*.

Cords, M., & Chowdhury, S. (2010). Life history of *Cercopithecus mitis stuhlmanni* in the Kakamega Forest, Kenya. *International Journal of Primatology*, *31*, 433–455. https://doi.org/10.1007/s10764-010-9405-7

Corrêa, F. M., Chaves, Ó. M., Printes, R. C., & Romanowski, H. P. (2018). Surviving in the urban–rural interface: Feeding and ranging behavior of brown howlers (*Alouatta guariba clamitans*) in an urban fragment in southern Brazil. *American Journal of Primatology*, *80*(6). https://doi.org/10.1002/ajp.22865

Crutzen, P. J., & Stoermer, E. F. (2021). The ‘Anthropocene’ (2000). In S. Brenner, G. Lax, P. J. Crutzen, U. Pöschl, J. Lelieveld, & H. G. Brauch (Eds.), *The Anthropocene: Politik—Economics—Society—Science* (Vol. 1, pp. 19–21). Springer, Cham. https://doi.org/10.1007/978-3-030-82202-6_2

Cuarón, A. D. (1995). Pole bridges to avoid primate kills: A sequel to Valladares-Padua et al. *Neotropical Primates*, *3*(3), 74–75. https://doi.org/10.62015/np.1995.v3.279

Cunneyworth, P. M. K. (2015). Power grid electrocution: A risk to primates in rural suburban and urban environments. In H. Rainer, A. White, & A. Lanjouw (Eds.), *State of the Apes: Infrastructure Development and Ape Conservation* (1st ed., pp. 264–265). University Printing House.

Cunneyworth, P. M. K. (2023). *Guidelines for the ethical management of Diani’s baboon population*. Colobus Conservation, Diani, Kenya.

Cunneyworth, P. M. K., de Jong, Y. A., Butynski, T. M., & Perkin, A. (2020). *Colobus angolensis* ssp. *palliatus. The IUCN Red List of Threatened Species 2020:* e.T5148A17983413. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5148A17983413.en

Cunneyworth, P. M. K., Donaldson, A., & Onyancha, F. (2022). Canopy bridges are an economical mitigation reducing the road barrier effect for three of four species of monkeys in Diani, Kenya. *Folia Primatologica*, *15*(1), 1–18. https://doi.org/10.1163/14219980-bja10002

Cunneyworth, P. M. K., & Duke, J. (2020). Vehicle collisions among four species of monkeys between 2000 and 2018 on a suburban road in Diani, Kenya. *International Journal of Primatology*, *41*, 45–60. https://doi.org/10.1007/s10764-020-00135-w

Dániel-Ferreira, J., Bommarco, R., Wissman, J., & Öckinger, E. (2020). Linear infrastructure habitats increase landscape-scale diversity of plants but not of flower-visiting insects. *Scientific Reports*, *10*(1). https://doi.org/10.1038/s41598-020-78090-y

Das, J., Biswas, J., Bhattacherjee, P. C., & Rao, S. S. (2009). Canopy bridges: An effective conservation tactic for supporting gibbon populations in forest fragments. In D. Whittaker & S. Lappan (Eds.), *The Gibbons. Developments in Primatology: Progress and Prospects* (pp. 6–22). Springer, New York, NY.

de Jong, Y. A., & Butynski, T. M. (2010). Three Sykes's monkey *Cercopithecus mitis* × vervet monkey *Chlorocebus pygerythrus* hybrids in Kenya. *Primate Conservation*, *25*(1), 43–56. https://doi.org/10.1896/052.025.0109

de Jong, Y. A., Cunneyworth, P., Butynski, T. M., Maisels, F., Hart, J. A., & Rovero, F. (2020). *Colobus angolensis. The IUCN Red List of Threatened Species 2020:* e.T5142A17945007. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5142A17945007.en

de Jonge, M. M. J., Gallego-Zamorano, J., Huijbregts, M. A. J., Schipper, A. M., & Benítez-López, A. (2022). The impacts of linear infrastructure on terrestrial vertebrate populations: A trait-based approach. *Global Change Biology*, *24*, 7217–7233. https://doi.org/10.1111/gcb.16450

De La Ossa-Nadjar, O., & De La Ossa, J. V. (2015). Vehicle collisions with wild fauna on the two roads that pass through the Montes De María, Sucre, Colombia. *Revista U.D.C.A Actualidad & Divulgación Científica*, *18*(2), 503–511.

de Oliveira, P. R. R., Alberts, C. C., & Francisco, M. R. (2011). Impact of road clearings on the movements of three understory insectivorous bird species in the Brazilian Atlantic Forest. *Biotropica*, *43*(5), 628–632. https://doi.org/10.1111/j.1744-7429.2010.00744.x

Diaz-Varela, E. R., Vazquez-Gonzalez, I., Marey-Pérez, M. F., & Álvarez-López, C. J. (2011). Assessing methods of mitigating wildlife-vehicle collisions by accident characterization and spatial analysis. *Transportation Research Part D: Transport and Environment*, *16*(4), 281–287. https://doi.org/10.1016/j.trd.2011.01.002

Dittus, W. P. J. (2020). Shields on electric posts prevent primate deaths: A case study at Polonnaruwa, Sri Lanka. *Folia Primatologica*, *91*(6), 643–653. https://doi.org/10.1159/000510176

Djoghlaf, A. (2009). *Statement by Ahmed Djoghlaf Executive Secretary of the Convention on Biological Diversity.* Opening of the exert workshop on the development of the city biodiversity index, Singapore 10-12 February 2009.

do Vale, C. A., Sant'Anna, A. C., Júnior, J. G. C., & Prezoto, F. (2020). Reflections on potential risk factors of Callitrichidae run over in an urban area: A case report of marmoset deaths. *Journal of Applied Animal Welfare Science*, 1–8. https://doi.org/10.1080/10888705.2020.1785883

Dodd, N. L., Gagnon, J. W., Boe, S., & Schweinsbury, R. E. (2005). Characteristics of elk-vehicle collisions and comparison to GPS-determined highway crossing patterns. In *ICOET Proceedings* (pp. 461–477). UC Davis: Road Ecology Center. https://escholarship.org/uc/item/5r37r5bm

Donaldson, A. (2017). *Rehabilitation release of vervet monkeys (*Chlorocebus pygerythrus hilgerti*) in south coast Kenya: A scientific approach* [PhD thesis]. Durham University, UK.

Donaldson, A., & Cunneyworth, P. (2015). Case study: Canopy bridges for primate conservation. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 341–343). John Wiley & Sons Ltd. https://doi.org/10.1002/9781118568170.ch41

Dreiss, A. N., Cote, J., Richard, M., Federici, P., & Clobert, J. (2010). Age-and sex-specific response to population density and sex ratio. *Behavioral Ecology*, *21*(2), 356–364. https://doi.org/10.1093/beheco/arp198

Drews, C. (1995). Road kills of animals by public traffic in Mikumi National Park, Tanzania, with notes on baboon mortality. *African Journal of Ecology*, *33*(2), 89–100. https://doi.org/10.1111/j.1365-2028.1995.tb00785.x

Dunham, N. T. (2015). Ontogeny of positional behavior and support use among *Colobus angolensis palliatus* of the Diani Forest, Kenya. *Primates*, *56*(2), 183–192. https://doi.org/10.1007/s10329-015-0457-3

Dunham, N. T. (2017). *Feeding ecology of black and white colobus monkeys from south coastal Kenya: The influence of spatial availability, nutritional composition, and mechanical properties of food items* [PhD thesis]. The Ohio State University, US.

Dunham, N. T., & McGraw, W. S. (2014). Positional behavior and habitat use of Peters' Angola black and white colobus monkey (*Colobus angolensis palliatus*). *African Primates*, *14*, 1–14.

Dwyer, J. F. (2006). Electric shock injuries in a Harris's hawk population. *Journal of Raptor Research*, *40*(3), 193–199. https://doi.org/10.3356/0892-1016(2006)40[193:ESIIAH]2.0.CO;2

Dwyer, J. F., Harness, R. E., & Donohue, K. (2014). Predictive model of avian electrocution risk on overhead power lines. *Conservation Biology*, *28*(1), 159–168. https://doi.org/10.1111/cobi.12145

Eberhardt, E., Mitchell, S., & Fahrig, L. (2013). Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. *Journal of Wildlife Management*, *77*(7), 1353–1359. https://doi.org/10.1002/jwmg.592

Elder, M., & Olsen, S. H. (2019). The design of environmental priorities in the SDGs. *Global Policy*, *10*(S1), 70–82. https://doi.org/10.1111/1758-5899.12596

Eley, R., & Kahumbu, P. (1998). *Diani's Monkeys*. The Regal Press, Kenya.

Elvik, R. (2008). A survey of operational definitions of hazardous road locations in some European countries. *Accident Analysis and Prevention*, *40*, 1830–1835. https://doi.org/10.1016/j.aap.2008.08.001

Estevadeordal, A., Frantz, B., & Taylor, A. M. (2003). The rise and fall of world trade, 1870-1939. *The Quarterly Journal of Economics, President and Fellows of Harvard College*, *118*(2), 359–407. https://doi.org/RePEc:oup:qjecon:v:118:y:2003:i:2:p:359-407

Estrada, A., & Garber, P. A. (2022). Principal drivers and conservation solutions to the impending primate extinction crisis: Introduction to the Special Issue. *International Journal of Primatology*, *43*(1), 1–14. https://doi.org/10.1007/s10764-022-00283-1

Estrada, A., Garber, P. A., & Chaudhary, A. (2020). Current and future trends in socio-economic, demographic and governance factors affecting global primate conservation. *PeerJ*, *8*, e.9816. https://doi.org/10.7717/peerj.9816

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Fiore, A. Di, Anne-Isola Nekaris, K., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M., Gouveia, S., Dobrovolski, R., … Li, B. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1). https://doi.org/10.1126/sciadv.1600946

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: An empirical review and synthesis. *Ecology and Society*, *14*(1), 21. https://doi.org/10.5751/ES-02815-140121

Fan, Y., Cunneyworth, P. M. K., Waters, S., Gregory, T., Oram, F., Abra, F., Spaan, D., Georgiev, A. V., Olgun, H., Aureli, F., & Gnanaolivu, S. D. (2025). *Recommendations for the construction and maintenance of canopy bridges for primates in human–modified landscapes. IUCN SSC Primate Specialist Group Section on Human-Primate Interactions*.

Fan, Y., & Lindshield, S. (2022). Exploring human factors of wildlife conservation along a forest gap using a participatory design-build canopy bridge. *Folia Primatologica*, *0*, 1–16. https://doi.org/10.1163/14219980-20211114

Favilli, F., Bíl, M., Sedoník, J., Andrášik, R., Kasal, P., Agreiter, A., & Streifeneder, T. (2018). Application of KDE+ software to identify collective risk hotspots of ungulate-vehicle collisions in South Tyrol, Northern Italy. *European Journal of Wildlife Research*, *64*(5). https://doi.org/10.1007/s10344-018-1214-x

Fernández, D., Kerhoas, D., Dempsey, A., Billany, J., McCabe, G., & Argirova, E. (2022). The current status of the world's primates: Mapping threats to understand priorities for primate conservation. *International Journal of Primatology*, *43*(1), 15–39. https://doi.org/10.1007/s10764-021-00242-2

Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A., & Carlson, S. M. (2015). Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proceedings of the National Academy of Sciences*, *112*(4), 1083–1088. https://doi.org/10.1073/pnas.1414894112

Filazzola, A., Shrestha, N., & MacIvor, J. S. (2019). The contribution of constructed green infrastructure to urban biodiversity: A synthesis and meta-analysis. In *Journal of Applied Ecology* (Vol. 56, Issue 9). https://doi.org/10.1111/1365-2664.13475

Fish, R. M., & Geddes, L. a. (2009). Conduction of electrical current to and through the human body: A review. *Eplasty*, *9*, e44.

Fitch, G., & Vaidya, C. (2021). Roads pose a significant barrier to bee movement, mediated by road size, traffic and bee identity. *Journal of Applied Ecology*, *58*(6), 1177–1186. https://doi.org/10.1111/1365-2664.13884

Flatt, E., Basto, A., Pinto, C., Ortiz, J., Navarro, K., Reed, N., Brumberg, H., Chaverri, M. H., & Whitworth, A. (2022). Arboreal wildlife bridges in the tropical rainforest of Costa Rica's Osa Peninsula. *Folia Primatologica*, *93*(3–6), 419–435. https://doi.org/10.1163/14219980-20211109

Forman, R. T. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, *29*(1), 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Forman, R. T. T., & Deblinger, R. D. (2000). The ecological road-effect zone of a Massachusetts (U.S.A.) suburban highway. *Conservation Biology*, *14*(1), 36–46. https://doi.org/10.1046/j.1523-1739.2000.99088.x

Forman, R. T. T., Friedman, D. S., Fitzhenry, D., Martin, J. D., Chen, A. S., & Alexander, L. E. (1997). Ecological effects of roads: Toward three summary indices and an overview for North America. In K. Canters (Ed.), *Habitat fragmentation and infrastructure* (pp. 40–54). Ministry of Transport, Public Works and Water Management, Delft, The Netherlands.

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale V.H., Fahrig, L., France, R., C.R., G., Heanue, K., Jones, J. A., Swanson, F. J., Turrentine, T., & Winter, T. C. (2003). *Road Ecology: Science and Solutions*. Island Press.

Franceschi, I. C., Dasoler, B. T., Menger, T., Kindel, A., Almeida Da Silva, F., Cezar, J., Leonardo, G., Braga, R. M., & Zimmermann Teixeira, F. (2022). Monitoring the use of a canopy bridge and underpasses by arboreal mammals on a Brazilian coastal road. *Folia Primatologica*, *0*, 1–12. https://doi.org/10.1163/14219980-20211202

Franquesa-Soler, M., Spaan, D., Hernández-Jaramillo, A., & Andresen, E. (2023). Citizen's perceptions of urban black howler monkeys (*Alouatta pigra*) in the city of Palenque (Mexico): A case study to aid policy decisions. *International Journal of Primatology*, *44*(2), 357–376. https://doi.org/10.1007/s10764-022-00339-2

Frost, S. R., Gilbert, C. C., Pugh, K. D., Guthrie, E. H., & Delson, E. (2015). The hand of *Cercopithecoides williamsi* (mammalia, primates): Earliest evidence for thumb reduction among colobine monkeys. *PLoS ONE*, *10*(5), 1–17. https://doi.org/10.1371/journal.pone.0125030

Gaillard, J. M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, *13*(2), 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8

Galea, B., & Humle, T. (2022). Identifying and mitigating the impacts on primates of transportation and service corridors. *Conservation Biology*, *36*(1), 1–14. https://doi.org/10.1111/cobi.13836

Garcia, C. A., Savilaakso, S., Verburg, R. W., Gutierrez, V., Wilson, S. J., Krug, C. B., Sassen, M., Robinson, B. E., Moersberger, H., Naimi, B., Rhemtulla, J. M., Pietsch, S. A., Bastin, J.-F. O., Dray, A., Araú, M. B., Ghazoul, J., & Waeber, P. O. (2020). The global forest transition as a human affair. *One Earth*, *2*, 417–428. https://doi.org/10.1016/j.oneear.2020.05.002

Garcia, F. de O., Culot, L., de Carvalho, R. E. W. F., & Rocha, V. J. (2022). Functionality of two canopy bridge designs: Successful trials for the endangered black lion tamarin and other arboreal species. *European Journal of Wildlife Research*, *68*(2). https://doi.org/10.1007/s10344-022-01569-8

Garland, T., & Bradley, W. G. (1984). Effects of a highway on Mojave Desert rodent populations. *American Midland Naturalist*, *111*, 47–56.

Getis, A., & Ord, J. K. (1992). The analysis of spatial association by use of distance statistics. *Geographical Analysis*, *24*(3), 189–206. https://doi.org/10.1111/j.1538-4632.1992.tb00261.x

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. *Landscape and Urban Planning*, *91*(1), 1–7. https://doi.org/10.1016/j.landurbplan.2008.11.001

Global Monitoring Report 2013. (2013). Rural-urban dynamics and the Millennium Development Goals Sub-Saharan Africa global monitoring report 2013. In *World Statistics*. https://documents.worldbank.org/en/publication/documents-reports/documentdetail/720451468171242999/global-monitoring-report-2013-rural-urban-dynamics-and-the-millennium-development-goals

González-Suárez, M., Zanchetta Ferreira, F., & Grilo, C. (2018). Spatial and species-level predictions of road mortality risk using trait data. *Global Ecology and Biogeography*, *27*(9), 1093–1105. https://doi.org/10.1111/geb.12769

Goulart, V. D. L. R., Teixeira, C. P., & Young, R. J. (2010). Analysis of callouts made in relation to wild urban marmosets (*Callithrix penicillata*) and their implications for urban species management. *European Journal of Wildlife Research*, *56*(4), 641–649. https://doi.org/10.1007/s10344-009-0362-4

GRASS Development Team. (2017). *Geographic Resources Analysis Support System (GRASS) software, version 7.2.* Open Source Geospatial Foundation. http://grass.osgeo.org

GRASS Development Team. (2018). *GRASS GIS 7.2.3svn reference manual*. Open Source Geospatial Foundation. https://grass.osgeo.org/download/

Gregory, T., Abra, F., Linden, B., Nekaris, K. A. I., Soanes, K., & Teixeira, F. Z. (2022). A new window into canopy bridges as a mitigation strategy for arboreal mammals. *Folia Primatologica*, *93*(3–6), 197–203. https://doi.org/10.1163/14219980-930306IN

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., Costa Faura, M., Dallmeier, F., & Alonso, A. (2013). Methods to establish canopy bridges to increase natural connectivity in linear infrastructure development. *SPE Latin American and Caribbean Health / Safety / Environment / Social Responsibility Conference 2013: Sustainable Solutions for Challenging HSSE Environments in Latin America and the Caribbean*, *December*, 119–128. https://doi.org/10.2118/165598-ms

Gregory, T., Carrasco-Rueda, F., Alonso, A., Kolowski, J., & Deichmann, J. L. (2017). Natural canopy bridges effectively mitigate tropical forest fragmentation for arboreal mammals. *Scientific Reports*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-04112-x

Guil, F., Fernández-Olalla, M., Moreno-Opo, R., Mosqueda, I., Gómez, M. E., Aranda, A., Arredondo, Á., Guzmán, J., Oria, J., González, L. M., & Margalida, A. (2011). Minimising mortality in endangered raptors due to power lines: The importance of spatial aggregation to optimize the application of mitigation measures. *PLoS ONE*, *6*(11). https://doi.org/10.1371/journal.pone.0028212

Gunson, K. E., Clevenger, A. P., Ford, A. T., Bissonette, J. A., & Hardy, A. (2009). A comparison of data sets varying in spatial accuracy used to predict the occurrence of wildlife-vehicle collisions. *Environmental Management*, *44*(2), 268–277. https://doi.org/10.1007/s00267-009-9303-y

Harcourt, C. S. (1984). *The behaviour and ecology of galagos in Kenya coastal forest* [PhD thesis]. University of Cambridge, UK.

Harness, R. E., & Wilson, K. R. (2001). Electric-utility structures associated with raptor electrocutions in rural areas. *Wildlife Society Bulletin*, *29*(2), 612–623.

Hart, D. (2007). Predation on primates: A biogeographical analysis. *Primate Anti-Predator Strategies*, 27–59. https://doi.org/10.1007/978-0-387-34810-0_2

Harvey, P. H., Martin, R. D., & Clutton-Brock, T. H. (1987). Life histories in comparative perspective. In B. Smuts, D. L. Cheney, R. Seyfarth, R. Wrangham, & T. T. Struhsaker (Eds.), *Primate Societies* (pp. 181–196). University of Chicago, Chicago.

Hatter, I. W., & Janz, D. W. (1994). Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. *Canadian Journal of Zoology*, *72*(5), 878–884. https://doi.org/10.1139/z94-119

Heigl, F., Horvath, K., Laaha, G., & Zaller, J. G. (2017). Amphibian and reptile road-kills on tertiary roads in relation to landscape structure: Using a citizen science approach with open-access land cover data. *BMC Ecology*, *17*(1), 1–11. https://doi.org/10.1186/s12898-017-0134-z

Hernández-Matías, A., Real, J., Parés, F., & Pradel, R. (2015). Electrocution threatens the viability of populations of the endangered Bonelli's eagle (*Aquila fasciata*) in Southern Europe. *Biological Conservation*, *191*, 110–116. https://doi.org/10.1016/J.BIOCON.2015.06.028

Hernández-Pérez, E. (2015). Rope bridges: A strategy for enhancing habitat connectivity of the black howler monkey (*Alouatta pigra*). *Neotropical Primates*, *22*(2), 94–96. https://doi.org/10.62015/np.2015.v22.142

Hetman, M., Kubicka, A. M., Sparks, T. H., & Tryjanowski, P. (2019). Road kills of non-human primates: A global view using a different type of data. *Mammal Review*, 1–8. https://doi.org/10.1111/mam.12158

Hewavithana, D. K., Weerakoon, D. K., & Roy, S. Sen. (2023). Assessing the extent and impacts of linear infrastructure on Sri Lanka's natural and protected areas: Implications for future development planning. *Environmental Monitoring and Assessment*, *195*(11). https://doi.org/10.1007/s10661-023-11865-8

Hidalgo-Mihart, M. G., González-Gallina, A., Iglesias-Hernández, J. A., Mendoza-Cárdenas, N., Pérez-Garduza, F., Ita, A. O. De, Chacón-Hernández, A., & Vázquez-Zúñiga, O. (2022). Mammal use of canopy bridges along the Nuevo Xcan-Playa del Carmen highway, Quintana Roo, Mexico. *Folia Primatologica*, *32*(4), 1–11. https://doi.org/10.1163/14219980-20210902

Hill, C. M., & Webber, A. D. (2010). Perceptions of nonhuman primates in human–wildlife conflict scenarios. *American Journal of Primatology*, *72*, 919–924. https://doi.org/10.1002/ajp.20845

Hockings, K. J. (2011). Behavioral flexibility and division of roles in chimpanzee road-crossing. In T. Matsuzawa, T. Humle, & Y. Sugiyama (Eds.), *The chimpanzees of Bossou and Nimba* (pp. 221–229). Primatology Monographs. Springer, Tokyo. https://doi.org/10.1007/978-4-431-53921-6_24

Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: A risky business. *Current Biology*, *16*(17), R668–R670. https://doi.org/10.1016/j.cub.2006.08.019

Holderegger, R., & Di Giulio, M. (2010). The genetic effects of roads: A review of empirical evidence. *Basic and Applied Ecology*, *11*(6), 522–531. https://doi.org/10.1016/j.baae.2010.06.006

Huijser, M. P., Abra, F. D., & Duffield, J. W. (2013). Mammal road mortality and cost-benefit analyses of mitigation measures aimed at reducing collisions with capybara (*Hydrochoerus hydrochaeris*) in São Paulo State, Brazil. *Oecologia Australis*, *17*(1), 129–146. https://doi.org/10.4257/oeco.2013.1701.11

Huijser, M. P., Duffield, J. W., Clevenger, A. P., Ament, R. J., & McGowen, P. T. (2009). Cost justification and examples of cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada. *Proceedings of the 2009 International Conference on Ecology and Transportation*, *14*(2), 625–639.

Huijser, M. P., Mosler-Berger, C., Olsson, M., & Strein, M. (2015). Wildlife warning signs and animal detection systems aimed at reducing wildlife-vehicle collisions. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 198–212). John Wiley & Sons Ltd, UK. https://doi.org/10.1002/9781118568170.ch24

Hulme-Beaman, A., Dobney, K., Cucchi, T., & Searle, J. B. (2016). An ecological and evolutionary framework for commensalism in anthropogenic environments. *Trends in Ecology and Evolution*, *31*(8), 633–645. https://doi.org/10.1016/j.tree.2016.05.001

Huso, M. M. P. (2011). An estimator of wildlife fatality from observed carcasses. *Environmetrics*, *22*(3), 318–329. https://doi.org/10.1002/ENV.1052

International Animal Rescue. (2024). *Slow lorises face a new threat*. https://www.internationalanimalrescue.org/appeal/slowloriselectrocutions

International Energy Agency. (2013, January). *Global Land Transport Infrastructure Requirements*. Global Land Transport Infrastructure Requirements.

Isbell, L. A., Young, T. P., Jaffe, K. E., Carlson, A. A., & Chancellor, R. L. (2009). Demography and life histories of sympatric patas monkeys, *Erythrocebus patas*, and vervets, *Cercopithecus aethiops*, in

Laikipia, Kenya. *International Journal of Primatology*, *30*(1), 103–124. https://doi.org/10.1007/s10764-009-9332-7

IUCN Red List of Threatened Species. (2024). *Summary Statistics*. IUCN Red List of Threatened Species. https://www.iucnredlist.org/resources/summary-statistics

Jackson, N. D., & Fahrig, L. (2011). Relative effects of road mortality and decreased connectivity on population genetic diversity. *Biological Conservation*, *144*(12), 3143–3148. https://doi.org/10.1016/j.biocon.2011.09.010

Jacobs, A. (2015). *Factors affecting the prevalence of road and canopy bridge crossings by primates in Diani Beach, Kenya* [Masters thesis]. University of Kent, UK.

Jacobson, S. L., Bliss-Ketchum, L. L., De Rivera, C. E., & Smith, W. P. (2016). A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. *Ecosphere*, *7*(4), 1–15. https://doi.org/10.1002/ecs2.1345

Jaeger, J. A. G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., & Von Toschanowitz, K. T. (2005). Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling*, *185*(2–4), 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

Jaeger, J. A. G., & Fahrig, L. (2004). Effects of road fencing on population persistence. *Conservation Biology*, *18*(6), 1651–1657. https://doi.org/10.1111/j.1523-1739.2004.00304.x

Janss, G. F. E., & Ferrer, M. (2001). Avian electrocution mortality in relation to pole design and adjacent habitat in Spain. *Bird Conservation International*, *11*(1), 3–12. https://doi.org/10.1017/S0959270901001022

Jedwab, R., Christiaensen, L., & Gindelsky, M. (2017). Demography, urbanization and development: Rural push, urban pull and … urban push? *Journal of Urban Economics*, *98*. https://doi.org/10.1016/j.jue.2015.09.002

Jenkins, A. R., Smallie, J. J., & Diamond, M. (2010). Avian collisions with power lines: A global review of causes and mitigation with a South African perspective. *Bird Conservation International*, *20*(3), 263–278. https://doi.org/10.1017/S0959270910000122

Jornal Nacional. (2022, April 22). *Passagem de Fauna Evita Extinção do Mico-Leão-Dourado*. https://www.youtube.com/watch?v=7pHKP_teweQ

Kadlecova, G., Voslarova, E., & Vecerek, V. (2022). Diurnal raptors at rescue centres in the Czech Republic: Reasons for admission, outcomes, and length of stay. *PLOS ONE*, *17*(12), e0279501. https://doi.org/10.1371/journal.pone.0279501

Kanga, E. M., & Heidi, C. M. (1999). Survey of the Angolan black-and-white colobus monkey, *Colobus angolensis palliatus*, in the Diani Forests, Kenya. *African Primates*, *4*(1–2), 50–54.

Katsis, L., Cunneyworth, P. M. K., Turner, K. M. E., & Presotto, A. (2018). Spatial patterns of primate electrocutions in Diani, Kenya. *International Journal of Primatology*, *39*(4), 493–510. https://doi.org/10.1007/s10764-018-0046-6

Keken, Z., Sedoník, J., Kušta, T., Andrášik, R., & Bíl, M. (2019). Roadside vegetation influences clustering of ungulate vehicle collisions. *Transportation Research Part D: Transport and Environment*, *73*. https://doi.org/10.1016/j.trd.2019.07.013

Kelly, C., Diggins, C., & Lawrence, A. (2013). Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier. *Wildlife Society Bulletin*, *37*. https://doi.org/10.1002/wsb.249

Kiffner, C., Kioko, J., Butynski, T. M., De Jong, Y. A., & Zinner, D. (2022). Population dynamics of the Manyara monkey (*Cercopithecus mitis manyaraensis*) and vervet monkey (*Chlorocebus pygerythrus*) in Lake Manyara National Park, Tanzania. *Primate Biology*, *9*(2), 33–43. https://doi.org/10.5194/pb-9-33-2022

Kioko, J., Kiffner, C., Phillips, P., Patterson-Abrolat, C., & Katers, S. (2015). Driver knowledge and attitudes on vehicle collisions in northern Tanzania. *Tropical Conservation Science*, *8*(2), 352–366. https://doi.org/10.1177/194008291500800206

Kitegile, A. (2016). *The influence of age, size and sex on feeding in yellow baboons: Sexual segregation but not as we know it* [PhD thesis]. Anglia Ruskin University, UK.

Kitegile, A., Hassan, S. N., & Norton, G. W. (2022). A road traversing a protected area has little effect on feeding and foraging behaviour of yellow baboons. *Ecology and Evolution*, *12*(12), 1–11. https://doi.org/10.1002/ece3.9405

Klöcker, U., Croft, D. B., & Ramp, D. (2006). Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. *Wildlife Research*, *33*(1), 5–15. https://doi.org/10.1071/WR04066

Koumbourlis, A. C. (2002). Electrical injuries. *Critical Care Medicine*, *30*(11), 424–430.

Kronprasert, N., Boontan, K., & Kanha, P. (2021). Crash prediction models for horizontal curve segments on two-lane rural roads in Thailand. *Sustainability*, *13*, 1–18. https://doi.org/10.3390/su13169011

Kruuse, M., Enno, S. E., & Oja, T. (2016). Temporal patterns of wild boar-vehicle collisions in Estonia, at the northern limit of its range. *European Journal of Wildlife Research*, *62*(6), 787–791. https://doi.org/10.1007/s10344-016-1042-9

Kumar, A., Devi, A., Gupta, A. K., & Sarma, K. (2013). Population, behavioural ecology and conservation of hoolock gibbon in northeast India. *Rare Animals of India*, 242–266. https://doi.org/10.2174/9781608054855113010014

Kumar, V., & Kumar, V. (2015). Seasonal electrocution fatalities in free-range rhesus macaques (*Macaca mulatta*) of Shivalik hills area in northern India. *Journal of Medical Primatology*, *44*(3), 137–142. https://doi.org/10.1111/jmp.12168

Kumara, H. N., Singh, M., & Kumar, S. (2006). Distribution, habitat correlates, and conservation of *Loris lydekkerianus* in Karnataka, India. *International Journal of Primatology*, *27*(4), 941–969. https://doi.org/10.1007/s10764-006-9054-z

Kütt, L., Lõhmus, K., Rammi, I. J., Paal, T., Paal, J., & Liira, J. (2016). The quality of flower-based ecosystem services in field margins and road verges from human and insect pollinator perspectives. *Ecological Indicators*, *70*. https://doi.org/10.1016/j.ecolind.2016.06.009

Laidlaw, K., Broadbent, E., & Eby, S. (2021). Effectiveness of aerial wildlife crossings: Do wildlife use rope bridges more than hazardous structures to cross roads? *Revista de Biologia Tropical*, *69*(3), 1138–1148. https://doi.org/10.15517/rbt.v69i3.47098

Langur Project Penang. (2022). *Road Ecology & Canopy Bridge*. https://langurprojectpenang.com/road-ecology/

Laurance, W. F., Clements, G. R., Sloan, S., O'Connell, C. S., Mueller, N. D., Goosem, M., Venter, O., Edwards, D. P., Phalan, B., Balmford, A., Van Der Ree, R., & Arrea, I. B. (2014). A global strategy for road building. *Nature*, *513*(7517), 229–232. https://doi.org/10.1038/nature13717

Laurance, W. F., Croes, B. M., Tchignoumba, L., Lahm, S. A., Alonso, A., Lee, M. E., Campbell, P., & Ondzeano, C. (2006). Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, *20*(4), 1251–1261. https://doi.org/10.1111/j.1523-1739.2006.00420.x

Laurance, W. F., Goosem, M., & Laurance, S. G. W. (2009). Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution*, *24*(12), 659–669. https://doi.org/10.1016/j.tree.2009.06.009

Lee, E. S. (1966). A theory of migration. *Demography*, *3*(1). https://doi.org/10.2307/2060063

Lee, T. S., Rondeau, K., Schaufele, R., Clevenger, A. P., & Duke, D. (2021). Developing a correction factor to apply to animal-vehicle collision data for improved road mitigation measures. *Wildlife Research*, *48*(6), 501–510. https://doi.org/10.1071/WR20090

Lerch, M. (2017). International migration and city growth. *United Nations Population Division, Technical Paper No. 10*.

Ligtermoet, E., Ramalho, C. E., Foellmer, J., & Pauli, N. (2022). Greening urban road verges highlights diverse views of multiple stakeholders on ecosystem service provision, challenges and preferred form. *Urban Forestry and Urban Greening*, *74*. https://doi.org/10.1016/j.ufug.2022.127625

Linden, B., Foord, S., Horta-Lacueva, Q. J. B., & Taylor, P. J. (2020). Bridging the gap: How to design canopy bridges for arboreal guenons to mitigate road collisions. *Biological Conservation*, *246*, 108560. https://doi.org/10.1016/j.biocon.2020.108560

Linder, J. M., & Oates, J. F. (2011). Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation*, *144*(2), 738–745. https://doi.org/10.1016/j.biocon.2010.10.023

Lindshield, S. M. (2016). Protecting nonhuman primates in peri-urban environments: A case study of neotropical monkeys, corridor ecology, and coastal economy in the Caribe Sur of Costa Rica. *Ethnoprimatology: Primate Conservation in the 21st Century*, 351–369.

Little, S. J., Harcourt, R. G., & Clevenger, A. P. (2002). Do wildlife passages act as prey-traps? *Biological Conservation*, *107*(2), 135–145. https://doi.org/10.1016/S0006-3207(02)00059-9

Liu, Z., He, C., Zhou, Y., & Wu, J. (2014). How much of the world's land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecology*, *29*(5), 763–771. https://doi.org/10.1007/s10980-014-0034-y

Lokschin, L. X., Rodrigo, C. P., Hallal Cabral, J. N., & Buss, G. (2007). Power lines and howler monkey conservation in Porto Alegre, Rio Grande do Sul, Brazil. *Neotropical Primates*, *14*(2), 76–80. https://doi.org/10.1896/044.014.0206

Macmillan, B. (2018). *An assessment of effectiveness of mitigation strategies used by hotels for 'pest' primates in Diani Beach, Kenya* [Masters thesis]. Oxford Brookes University, UK.

Maibeche, Y., Moali, A., Yahi, N., & Menard, N. (2015). Is diet flexibility an adaptive life trait for relictual and peri-urban populations of the endangered primate *Macaca sylvanus*? *PLoS ONE*, *10*(2), 1–22. https://doi.org/10.1371/journal.pone.0118596

Malo, J. E., Suárez, F., & Díez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? *Journal of Applied Ecology*, *41*(4), 701–710. https://doi.org/10.1111/j.0021-8901.2004.00929.x

Mañosa, S. (1997). Strategies to identify dangerous electricity pylons for birds. In *Biodiversity and Conservation* (Vol. 10).

Maria, M., Al-Razi, H., Akbar, A., Muzaffar, S. Bin, & Nekaris, K. A. I. (2022). Artificial canopy bridge use by primates and other arboreal mammals in a fragmented tropical forest of northeast Bangladesh. *Folia Primatologica*, *36*(1), 1–12. https://doi.org/10.1163/14219980-20211201

Martín, J. M., Rafael, J., López, G., Sousa, H. C., & Barrios, V. (2022). *Wildlife and power lines: Guidelines for preventing and mitigating wildlife mortality associated with electricity distribution networks*. www.iucn.org/mediterranean

Martín, M. P. (2012). *Evaluacíon del uso de puentes para monos según la percepción de la comunidad de Manuel Antonio, Quepos, Costa Rica en Julio y Agosto del 2012.* Medicina de la Conservación.

Martínez, J., & Wallace, R. B. (2011). First observations of terrestrial travel for Olalla's Titi Monkey (*Callicebus Olallae*). *Neotropical Primates*, *18*(2), 49–52. https://doi.org/10.1896/044.018.0203

Mass, V., Rakotomanga, B., Rakotondratsimba, G., Razafindramisa, S., Andrianaivomahefa, P., Dickinson, S., Berner, P. O., & Cooke, A. (2011). Lemur bridges provide crossing structures over roads within a forested mining concession near Moramanga, Toamasina province, Madagascar. *Conservation Evidence*, *8*, 11–18.

Mata Estacio, C., Bincini, R., Chambers, B., & Malo, J. (2015). Predator-prey interactions at wildlife crossing structures: Between myth and reality. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 190–197). John Wiley & Sons Ltd, UK. https://doi.org/10.1002/9781118568170.ch23

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). Biodiversity: The ravages of guns, nets and bulldozers. *Nature*, *536*(7615), 143–145. https://doi.org/10.1038/536143a

McDonald, M. M., Cunneyworth, P. M. K., Anderson, A. G., & Wroblewski, E. (2022). Mitochondrial genetic diversity and divergence dating of Angolan colobus monkeys (*Colobus angolensis*) in the eastern forests of Kenya and Tanzania: Implications for subspeciation and reconstructing historical biogeography. *American Journal of Primatology*, 1–19. https://doi.org/10.1002/ajp.23384

Mcdonald, R. I., Forman, R. T. T., Kareiva, P., Neugarten, R., Salzer, D., & Fisher, J. (2009). Urban effects, distance, and protected areas in an urbanizing world. *Landscape and Urban Planning*, *93*(1). https://doi.org/10.1016/j.landurbplan.2009.06.002

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, *127*(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McLennan, M. R., & Hockings, K. J. (2016). The aggressive apes? Causes and contexts of great ape attacks on local persons. In *Problematic Wildlife* (pp. 373–394). Springer International Publishing. https://doi.org/10.1007/978-3-319-22246-2_18

Mićić, S., Vujadinović, R., Amidžić, G., Damjanović, M., & Matović, B. (2022). Accident frequency prediction model for flat rural roads in Serbia. *Sustainability*, *14*, 1–14. https://doi.org/10.3390/su14137704

Milton, S. J., Dean, W. R. J., Sielecki, L. E., & van der Ree, R. (2015). The function and management of roadside vegetation. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 373–381). Wiley. https://doi.org/10.1002/9781118568170.ch46

Monticelli, C., Maciel, P. C., & de Oliveira Garcia, F. (2022). Rope bridges provide safe connectivity for the southern brown howler monkey (*Alouatta guariba clamitans* Cabrera, 1940) in an urban Atlantic Forest remnant. *Folia Primatologica*, 1–14. https://doi.org/10.1163/14219980-20211108

Montijo, R. P. (2023). *Electrocution risk to three California bird species: golden eagle, common raven, and turkey vulture* [Masters thesis]. University of Southern California, US.

Montilla, S., Rios-Soto, J. A., Mantilla-Castaño, J. C., Patiño-Siro, D., Bustamante-Manrique, S. Botero-Henao, N., Ruiz, S., Arias-Monsalve, H. F., Link, A., & Ramírez-Chaves, H. E. (2020). Eventos de electrocución de *Aotus lemurinus* (Primates) en los Andes Centrales de Colombia. *Mammalogy Notes*, *6*(2), 183.

Moore, J. F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., Cheyne, S. M., Coutant, O., Forget, P. M., Haysom, J. K., Houlihan, P. R., Olson, E. R., Lindshield, S., Martin, J., Tobler, M., Whitworth, A., & Gregory, T. (2021). The potential and practice of arboreal camera trapping. In *Methods in Ecology and Evolution* (Vol. 12, Issue 10, pp. 1768–1779). British Ecological Society. https://doi.org/10.1111/2041-210X.13666

Moore, R. S., Nekaris, K. A. I., & Eschmann, C. (2010). Habitat use by western purple-faced langurs *Trachypithecus vetulus nestor* (Colobinae) in a fragmented suburban landscape. *Endangered Species Research*, *12*(3), 227–234. https://doi.org/10.3354/esr00307

Moore, R. S., Wihermanto, & Nekaris, K. A. I. (2014). Compassionate conservation, rehabilitation and translocation of Indonesian slow lorises. *Endangered Species Research*, *26*(2), 93–102. https://doi.org/10.3354/esr00620

Moreno-Black, G. S. (1977). Different habitat utilization of four Cercopithecidae in a Kenyan forest. *Folia Primatologica*, *27*, 85–107. https://doi.org/10.1159/000155780

Mugatha, S. M., Ogutu, J. O., Cords, M., & Maitima, J. M. (2007). Dynamics of male residence and female oestrus during a breeding season of blue monkeys in the Kakamega Forest, Kenya. *African Journal of Ecology*, *45*(1), 49–54. https://doi.org/10.1111/j.1365-2028.2006.00674.x

Mullu, D. (2016). A review on the effect of habitat fragmentation on ecosystem. *Journal of Natural Sciences Research*, *6*(15), 1–15.

Murthy, A. C., Fristoe, T. S., & Burger, J. R. (2016). Homogenizing effects of cities on North American winter bird diversity. *Ecosphere*, *7*(1). https://doi.org/10.1002/ecs2.1216

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Mysterud, A. (2004). Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildlife Biology*, *10*(3), 203–211. https://doi.org/10.2981/wlb.2004.026

Napier, J. R., & Napier, P. H. (1985). *The natural history of the primates*. Wallingford: Gem Publishing Company (Oxon).

Narváez Rivera, G. M., & Lindshield, S. M. (2016). An experimental evaluation of artificial wildlife bridges crossing structures for New World monkeys in Costa Rica. Conference Proceedings. *Joint Meeting of the International Primatological Society and the American Society of Primatologists*.

Narváez-Rivera, G. M., & Lindshield, S. M. (2022). Assessing the importance of artificial canopy bridge design for Costa Rican monkeys in an experimental setting. *Folia Primatologica*, *0*, 1–21. https://doi.org/10.1163/14219980-20211104

Nekaris, K. A. I., Handby, V., Campera, M., Birot, H., Hedger, K., Eaton, J., & Imron, M. A. (2020). Implementing and monitoring the use of artificial canopy bridges by mammals and birds in an Indonesian agroforestry environment. *Diversity*, *12*(10), 1–7. https://doi.org/10.3390/d12100399

Nekaris, K. A. I., & Jayewardene, J. (2004). Survey of the slender loris (Primates, Lorisidae Gray, 1821: *Loris tardigradus* Linnaeus, 1758 and *Loris lydekkerianus* Cabrera, 1908) in Sri Lanka. *Journal of Zoology*, *262*(4), 327–338. https://doi.org/10.1017/S0952836903004710

Ng, J. W., Nielsen, C., & St. Clair, C. C. (2008). Landscape and traffic factors influencing deer–vehicle collisions in an urban environment. *Human–Wildlife Conflicts*, *2*(1), 34–47. https://doi.org/10.26077/nxw2-yn81

Nowak, K., Wimberger, K., Richards, S. A., Hill, R. A., & le Roux, A. (2017). Samango monkeys (*Cercopithecus albogularis labiatus*) manage risk in a highly seasonal, human-modified landscape in Amathole Mountains, South Africa. *International Journal of Primatology*, *38*(2), 194–206. https://doi.org/10.1007/s10764-016-9913-1

Oates, J. F. (1994). The natural history of African colobines. In G. Davies & J. Oates (Eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution*. Cambridge University Press.

Oates, J. F., & Davies, A. G. (1994). What are the colobines? In A. G. Davies & J. F. Oates (Eds.), *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (pp. 1–10). Cambridge University Press, Cambridge, UK.

Okabe, A., Satoh, T., & Sugihara, K. (2009). A kernel density estimation method for networks, its computational method and a GIS-based tool. *International Journal of Geographical Information Science*, *23*(1), 7–32. https://doi.org/10.1080/13658810802475491

Olendorff, R. R., Miller, A. D., & Lehman, R. N. (1981). *Suggested practices for raptor protection on powerlines: The State of the Art in 1981.* Raptor Research Report No. 4. Salt Lake City, UT: The Raptor Research Foundation.

Olgun, H., Mohammed, M. K., Mzee, A. J., Green, M. E. L., Davenport, T. R. B., & Georgiev, A. V. (2021). The implications of vehicle collisions for the endangered endemic Zanzibar red colobus *Piliocolobus kirkii*. *Oryx*, 1–9. https://doi.org/10.1017/S0030605320000605

Olson, D. D., Bissonette, J. A., Cramer, P. C., Bunnell, K. D., Coster, D. C., & Jackson, P. J. (2014). Vehicle collisions cause differential age and sex-specific mortality in mule deer. *Advances in Ecology*, 1–10. https://doi.org/10.1155/2014/971809

Omollo, W. O. (2022). Application of planning standards in regulating road reserves (Case study: Kisii town in Kenya). *International Journal of Architecture and Urban Development*, *12*(2), 5–18. https://www.researchgate.net/publication/360384355

O'Sullivan, O. S., Holt, A. R., Warren, P. H., & Evans, K. L. (2017). Optimising UK urban road verge contributions to biodiversity and ecosystem services with cost-effective management. *Journal of Environmental Management*, *191*, 162–171. https://doi.org/10.1016/j.jenvman.2016.12.062

Overbeck, V., Gonzalez, P., Lau, W. M., DesJardins, E., Alesci, M., Wellian, J., Kane, J., Henderson, M., Blood, R., & Smith, R. L. (2022). Activity budgets of black and gold howler monkeys living in urban and natural habitats in southwest Paraguay. *Neotropical Primates*, *28*(1–2), 53–61. https://doi.org/10.62015/np.2022.v28.347

Ow, S., Chan, S., Toh, Y. H., Chan, S. H., Lakshminarayanan, J., Jabbar, S., Ang, A., & Loo, A. (2022). Bridging the gap: Assessing the effectiveness of rope bridges for wildlife in Singapore. *Folia Primatologica*, 1–12. https://doi.org/10.1163/14219980-20211110

Oxoli, D., Zurbarán, M., Shaji, S., & Muthusamy, A. (2016). Hotspot analysis: a first prototype Python plugin enabling exploratory spatial data analysis into QGIS. *Peerj Preprints*, *1973*, 1–6. https://doi.org/10.7287/PEERJ.PREPRINTS.2204V4

Pagany, R. (2020). Wildlife-vehicle collisions - Influencing factors, data collection and research methods. *Biological Conservation*, *251*, 108758. https://doi.org/10.1016/j.biocon.2020.108758

Palei, N. C., Palei, H. S., Rath, B. P., & Kar, C. S. (2014). Mortality of the Endangered Asian elephant *Elephas maximus* by electrocution in Odisha, India. *Oryx*, *48*, 602–604. https://doi.org/10.1017/S003060531400012X

Parker, L., Nijman, V., & Nekaris, K. A. I. (2008). When there is no forest left: Fragmentation, local extinction, and small population sizes in the Sri Lankan western purple-faced langur. *Endangered Species Research*, *5*(1), 29–36. https://doi.org/10.3354/esr00107

Pebsworth, P. A., MacIntosh, A. J. J., Morgan, H. R., & Huffman, M. A. (2012). Factors influencing the ranging behavior of Chacma baboons (*Papio hamadryas ursinus*) living in a human-modified habitat. *International Journal of Primatology*, *33*(4), 872–887. https://doi.org/10.1007/s10764-012-9620-5

Penna, A., Dillon, R., Bearder, S. K., Karlsson, J., Perkin, A., & Pozzi, L. (2022). Phylogeography and evolutionary lineage diversity in the small-eared greater galago, *Otolemur garnettii* (Primates: Galagidae). *Zoological Journal of the Linnean Society*, 1–18. https://doi.org/10.1093/zoolinnean/zlac079

Pereira, A. A. B. G., Dias, B., Castro, S. I., Landi, M. F. A., Melo, C. B., Wilson, T. M., Costa, G. R. T., Passos, P. H. O., Romano, A. P., Szabó, M. P. J., & Castro, M. B. (2020). Electrocutions in free-living black-tufted marmosets (*Callithrix penicillata*) in anthropogenic environments in the Federal District and surrounding areas, Brazil. *Primates*, *61*(2), 321–329. https://doi.org/10.1007/s10329-019-00760-x

Périquet, S., Roxburgh, L., le Roux, A., & Collinson, W. J. (2018). Testing the value of citizen science for roadkill studies: A case study from South Africa. *Frontiers in Ecology and Evolution*, *6*, 1–9. https://doi.org/10.3389/fevo.2018.00015

Phillips, B. B., Bullock, J. M., Osborne, J. L., & Gaston, K. J. (2020). Ecosystem service provision by road verges. *Journal of Applied Ecology*, *57*(3), 488–501. https://doi.org/10.1111/1365-2664.13556

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187). https://doi.org/10.1126/science.1246752

Plumptre, A. J., Sterling, E. J., & Buckland, S. T. (2013). Primate census and survey techniques. In E. J. Sterling, N. Bynum, & M. E. Blair (Eds.), *Primate Ecology and Conservation: A Handbook of Techniques* (First, pp. 10–26). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199659449.003.0002

Polak, T., Rhodes, J. R., Jones, D., & Possingham, H. P. (2014). Optimal planning for mitigating the impacts of roads on wildlife. *Journal of Applied Ecology*, *51*(3), 726–734. https://doi.org/10.1111/1365-2664.12243

Prasetyo, D., Lestari, D. A., Wahyuni, T., & Ismanto, A. D. (2022). The effectiveness of artificial canopy bridges for the diurnal primates within a hydroelectric project in North Sumatra-Indonesia. *Folia Primatologica*, *93*, 271–285. https://doi.org/10.1163/14219980-20211106

Printes, R. C. (1999). The Lami Biological Reserve, Rio Grande do Sul, Brazil and the danger of power lines to howlers in urban reserves. *Neotropical Primates*, *7*(4), 135–136.

Printes, R. C., Buss, G., Jardim, M. M. de A., Fialho, M. de S., Dornelles, S. da S., Perotto, M., Brutto, L. F. G., Girardi, E., Jerusalinsky, L., Liesenfeld, M. V. A., Lokschin, L. X., & Romanowski, H. P. (2010). The Urban Monkeys Program: A survey of *Alouatta clamitans* in the south of Porto Alegre and its influence on land use policy between 1997 and 2007. *Primate Conservation*, *25*(1), 11–19. https://doi.org/10.1896/052.025.0103

Pulliam, H. R. (1988). Sources, sinks, and population regulation. *The American Society of Naturalists*, *132*(5), 652–661.

Radhakrishna, S., Goswami, A. B., & Sinha, A. (2006). Distribution and conservation of *Nycticebus bengalensis* in northeastern India. *International Journal of Primatology*, *27*(4), 971–982. https://doi.org/10.1007/s10764-006-9057-9

Ram, C., Sharma, G., & Rajpurohit, L. S. (2015). Mortality and threats to Hanuman langurs (*Semnopithecus entellus entellus*) in and around Jodhpur (Rajasthan). *Indian Forester*, *141*(19), 1042–1045.

Ramp, D., Caldwell, J., Edwards, K. A., Warton, D., & Croft, D. B. (2005). Modelling of wildlife fatality hotspots along the Snowy Mountain Highway in New South Wales, Australia. *Biological Conservation*, *126*(4), 474–490. https://doi.org/10.1016/j.biocon.2005.07.001

Raño, M., Palazzo, M. C., Soliz, A., Holzer, J. C., Perez, D. A., Sánchez, E. M., Romero, V. L., Sánchez Gavier, F., & Kowalewski, M. M. (2022). Community participatory action to build a canopy bridge for wild black and gold howler monkeys (*Alouatta caraya*) in northern Argentina. *Folia Primatologica*, *49*(6), 1–11. https://doi.org/10.1163/14219980-20211203

Rea, R. V. (2003). Modifying roadside vegetation management practices to reduce vehicular collisions with moose *Alces alces*. In *Wildlife Biology* (Vol. 9, Issue 2). https://doi.org/10.2981/wlb.2003.030

Reed, D. H. (2004). Extinction risk in fragmented habitats. *Animal Conservation*, *7*(2), 181–191. https://doi.org/10.1017/S1367943004001313

Riley, C. M., Koenig, B. L., & Gumert, M. D. (2015). Observation of a fatal dog attack on a juvenile long-tailed macaque in a human-modified environment in Singapore. *Nature in Singapore*, *8*, 57–63.

Ritchie, H. (2018). *How urban is the world?* Https://Ourworldindata.Org/How-Urban-Is-the-World.

Ritchie, H., Samborska, V., & Roser, M. (2024). *Urbanization*. Https://Ourworldindata.Org/Urbanization.

Robinson, J. G., & Bodmer, R. E. (1999). Towards wildlife management in tropical forests. *Journal of Wildlife Management*, *63*(1), 1–13. https://doi.org/10.2307/3802482

Rodrigues, N. N., & Martinez, R. A. (2014). Wildlife in our backyard: interactions between Wied's marmoset *Callithrix kuhlii* (Primates: Callithrichidae) and residents of Ilhéus, Bahia, Brazil. *Wildlife Biology*, *20*(2), 91–96. https://doi.org/10.2981/wlb.13057

Rojas, I. A., & Gregory, T. (2022). Canopy bridges: Preventing and mitigating anthropogenic impacts on mantled howler monkeys (*Alouatta palliata palliata*) in Costa Rica. *Folia Primatologica*, *0*, 1–13. https://doi.org/10.1163/14219980-20211006

Rosa, S., & Bissonette, J. (2007). Roads and desert small mammal communities: positive interaction? In C. L. Irwin, D. Nelson, & K. P. McDermott (Eds.), *Proceedings of the 2007 International Conference on Ecology and Transportation* (pp. 562–566). Center for Transportation and Environment, North Carolina State University, Raleigh, North Carolina, USA.

Roscoe, C. J., De Silva, M. A., Hapuarachchi, N. C., & Krishantha, P. A. R. (2013). A new color morph of the southern purple-faced Langur (*Semnopithecus vetulus vetulus*) from the rainforests of southwestern Sri Lanka. *Primate Conservation*, *26*(1), 115–124. https://doi.org/10.1896/052.026.0110

Rose, M. D. (1979). Positional behavior of natural populations: Some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In M. E. Morbeck, H. Preuschoft, & G. Gomberg (Eds.), *Environment, behavior and morphology: Dynamic interactions in primates* (pp. 75–93).

Rosti, H., Pihlström, H., Bearder, S., Pellikka, P., & Rikkinen, J. (2020). Vocalization Analyses of Nocturnal Arboreal Mammals of the Taita Hills, Kenya. *Diversity*, *12*(473). https://doi.org/10.3390/d12120473

Rytwinski, T., Soanes, K., Jaeger, J. A. G., Fahrig, L., Findlay, C. S., Houlahan, J., Van Ree, R. Der, & Van Der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS ONE*, *11*(11). https://doi.org/10.1371/journal.pone.0166941

Saeki, M., & Macdonald, D. W. (2004). The effects of traffic on the raccoon dog (*Nyctereutes procyonoides viverrinus*) and other mammals in Japan. *Biological Conservation*, *118*(5), 559–571. https://doi.org/10.1016/j.biocon.2003.10.004

Saenz-de-Miera, O., & Rosselló, J. (2012). The responsibility of tourism in traffic congestion and hyper-congestion: A case study from Mallorca, Spain. *Tourism Management*, *33*(2), 466–479. https://doi.org/10.1016/j.tourman.2011.06.015

Santarsieri, I. (2019). *How behavioural, environmental and morphological factors affect the likelihood of electrocutions of colobus monkeys (*Colobus angolensis palliatus*) in an anthropogenic environment* [Masters thesis]. University of Roehampton, UK.

Santos, S. M., Carvalho, F., & Mira, A. (2011). How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. *PLoS ONE*, *6*(9). https://doi.org/10.1371/journal.pone.0025383

Saptorini, I., Priambada, N. P., Prameswari, W., Arifin, I., & Sanchez, K. L. (2021). Electrocution cases in rescued Javan slow lorises (*Nycticebus javanicus*) at IAR Indonesia during January 2019 – April 2020. *The 14th Asian Society of Conservation Medicine, The 27th Japanese Society of Zoo and Wildlife Medicine 2021 Joint Conference, Sapporo, Hokkaido, Japan*.

Saralamba, C., José-Domínguez, J. M., & Asensio, N. (2022). Movement dynamics of gibbons after the construction of canopy bridges over a park road. *Folia Primatologica*, *4*(6), 1–13. https://doi.org/10.1163/14219980-20211211

Saralamba, C., & Menpreeda, W. (2018). Increasing connectivity through artificial canopy bridge for the gibbons: a case study on the activity budget. *The 87th Annual Meeting of the American Association of Physical Anthropologists*.

Scheun, J., Bennett, N. C., Ganswindt, A., & Nowack, J. (2015). The hustle and bustle of city life: monitoring the effects of urbanisation in the African lesser bushbaby. *The Science of Nature*, *102*(9–10), 57. https://doi.org/10.1007/s00114-015-1305-4

Schindler, S., Tuljapurkar, S., Gaillard, J.-M., & Coulson, T. (2012). Linking the population growth rate and the age-at-death distribution. *Theoretical Population Biology*, *82*(4), 244–252. https://doi.org/10.1016/j.tpb.2012.09.003

Schipper, J., & Burgess, N. (2004). Northern Zanzibar–Inhambane Coastal Forest Mosaic. In N. Burgess, J. D. Hales, E. Underwood, E. Dinerstein, D. Olson, I. Itoua, J. Schipper, T. Ricketts, & K. Newman

(Eds.), *Terrestrial ecoregions of Africa and Madagascar: A conservation assessment* (pp. 252–253). World Wildlife Fund, Island Press, Washington.

Schorcht, W., Bontadina, F., & Schaub, M. (2009). Variation of adult survival drives population dynamics in a migrating forest bat. *Journal of Animal Ecology*, *78*(6), 1182–1190. https://doi.org/10.1111/j.1365-2656.2009.01577.x

Schreiber, R. K., & Graves, J. H. (1977). Powerline corridors as possible barriers to the movements of small mammals. *Source: The American Midland Naturalist*, *97*(2), 504–508.

Schulze, C., Peters, M., Baumgärtner, W., & Wohlsein, P. (2016). Electrical injuries in animals: Causes, pathogenesis, and morphological findings. *Veterinary Pathology*, *53*(5), 1018–1029. https://doi.org/10.1177/0300985816643371

Schwab, A. C., & Zandbergen, P. A. (2011). Vehicle-related mortality and road crossing behavior of the Florida panther. *Applied Geography*, *31*(2), 859–870. https://doi.org/10.1016/j.apgeog.2010.10.015

Seidler, R. G., Long, R. A., Berger, J., Bergen, S., & Beckmann, J. P. (2015). Identifying impediments to long-distance mammal migrations. *Conservation Biology*, *29*(1), 99–109. https://doi.org/10.1111/cobi.12376

Seiler, A. (2005). Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology*, *42*(2), 371–382. https://doi.org/10.1111/j.1365-2664.2005.01013.x

Seiler, A. (2006). Mortality in wildlife due to transportation. In J. Davenport & J. L. Davenport (Eds.), *The ecology of transportation: Managing mobility for the environment* (Issue June 2006, pp. 165–189). Springer Netherlands. https://doi.org/10.1007/1-4020-4504-2

Sengupta, A., Gazagne, E., Albert-Daviaud, A., Tsuji, Y., & Radhakrishna, S. (2020). Reliability of macaques as seed dispersers. *American Journal of Primatology*, *82*(5). https://doi.org/10.1002/ajp.23115

Shaw, J. M., Jenkins, A. R., Smallie, J. J., & Ryan, P. G. (2010). Modelling power-line collision risk for the blue crane *Anthropoides paradiseus* in South Africa. *Ibis*, *152*(3), 590–599. https://doi.org/10.1111/j.1474-919X.2010.01039.x

Shilling, F. M., & Waetjen, D. P. (2015). Wildlife-vehicle collision hotspots at US highway extents: Scale and data source effects. *Nature Conservation*, *11*, 41–60. https://doi.org/10.3897/natureconservation.11.4438

Simmons, J. R. (1938). *Feathers and fur on the turnpike*. Christopher Publishing House.

Slade, A. (2016). *Survivorship, demographics and seasonal trends among electrocuted primate species in Diani, Kenya* [Masters thesis]. University of Bristol, UK.

Smiraglia, D., Salvati, L., Egidi, G., Salvia, R., Giménez-Morera, A., & Halbac-Cotoara-zamfir, R. (2021). Toward a new urban cycle? A closer look to sprawl, demographic transitions and the environment in Europe. *Land*, *10*(2), 127. https://doi.org/10.3390/land10020127

Smith, D. J., van der Ree, R., & Rosell, C. (2015). Wildlife crossing structures: An effective strategy to restore or maintain wildlife connectivity across roads. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 172–183). John Wiley & Sons Ltd, UK.

Soanes, K., Lobo, M. C., Vesk, P. A., McCarthy, M. A., Moore, J. L., & van der Ree, R. (2013). Movement re-established but not restored: Inferring the effectiveness of road-crossing mitigation for a gliding mammal by monitoring use. *Biological Conservation*, *159*(December 2021), 434–441. https://doi.org/10.1016/j.biocon.2012.10.016

Soanes, K., Mitchell, B., & van der Ree, R. (2017). Quantifying predation attempts on arboreal marsupials using wildlife crossing structures above a major road. *Australian Mammalogy*, *39*(2), 254–257.

Soanes, K., Rytwinski, T., Fahrig, L., Huijser, M. P., Jaeger, J. A. G., Teixeira, F. Z., van der Ree, R., & van der Grift, E. A. (2024). Do wildlife crossing structures mitigate the barrier effect of roads on animal movement. *Journal of Applied Ecology*, 1–14. https://doi.org/10.1111/1365-2664.14582

Soanes, K., Taylor, A. C., Sunnucks, P., Vesk, P. A., Cesarini, S., & van der Ree, R. (2018). Evaluating the success of wildlife crossing structures using genetic approaches and an experimental design: Lessons from a gliding mammal. *Journal of Applied Ecology*, *55*(1), 129–138. https://doi.org/10.1111/1365-2664.12966

Sobel, J. M., Chen, G. F., Watt, L. R., & Schemske, D. W. (2010). The biology of speciation. *Evolution*, *64*(2), 295–315. https://doi.org/10.1111/j.1558-5646.2009.00877.x

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour*, *85*, 1101–1112. https://doi.org/10.1016/j.anbehav.2013.01.023

Sosa, R., & Schalk, C. M. (2016). Seasonal activity and species habitat guilds influence road-kill patterns of neotropical snakes. *Tropical Conservation Science*, *9*(4). https://doi.org/10.1177/1940082916679662

Spellerberg, I. F. (1998). Ecological effects of roads and traffic: A literature review. *Global Ecology and Biogeography Letters*, *7*(5), 317–333. https://doi.org/10.1046/j.1466-822X.1998.00308.x

Steen, D. A., & Gibbs, J. P. (2004). Effects of roads on the structure of freshwater turtle populations. *Conservation Biology*, *18*(4), 1143–1148. https://doi.org/10.1111/j.1523-1739.2004.00240.x

Strier, K. B., & Ives, A. R. (2024). Protected areas are necessary, but not enough to save endangered primates. *The Bulletin of the Ecological Society of America*. https://doi.org/10.1002/bes2.2214

Struhsaker, T., & Siex, K. S. (1996). The Zanzibar red colobus monkey *Procolobus kirkii* conservation status of an endangered island endemic. *African Primates*, *2*(2), 54–61.

Struhsaker, T. T. (1967). Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli Game Reserve, Kenya. *Ecology*, *48*(6), 891–904.

Strum, S. C. (2010). The development of primate raiding: Implications for management and conservation. *International Journal of Primatology*, *31*(1), 133–156. https://doi.org/10.1007/s10764-009-9387-5

Sunnucks, P., & Balkenhol, N. (2015). Incorporating landscape genetics into road ecology. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 110–118). John Wiley & Sons Ltd, UK. https://doi.org/10.1002/9781118568170.ch14

Sutherland, W. J., Pullin, A. S., Dolman, P. M., & Knight, T. M. (2004). The need for evidence-based conservation. *Trends in Ecology and Evolution*, *19*(6), 305–308. https://doi.org/10.1016/j.tree.2004.03.018

Takahashi, M. Q., Rothman, J. M., Raubenheimer, D., & Cords, M. (2019). Dietary generalists and nutritional specialists: Feeding strategies of adult female blue monkeys (*Cercopithecus mitis*) in the Kakamega Forest, Kenya. *American Journal of Primatology*, *81*(7). https://doi.org/10.1002/ajp.23016

Tate, C., Wang, R., Akaraci, S., Burns, C., Garcia, L., Clarke, M., & Hunter, R. (2024). The contribution of urban green and blue spaces to the United Nation's Sustainable Development Goals: An evidence gap map. *Cities*, *145*. https://doi.org/10.1016/j.cities.2023.104706

Taylor, R. A., Ryan, S. J., Brashares, J. S., & Johnson, L. R. (2016). Hunting, food subsidies, and mesopredator release: The dynamics of crop-raiding baboons in a managed landscape. *Ecology*, *97*(4), 951–960. https://doi.org/10.1890/15-0885.1

Teixeira, F. Z., Da Silva, L. G., Abra, F., Rosa, C., Buss, G., Guerreiro, M., Costa, E. R., De Menezes Medeiros, A. S., Gordo, M., & Secco, H. (2022). A review of the application of canopy bridges in the conservation of primates and other arboreal animals across Brazil. *Folia Primatologica*, *18*(4). https://doi.org/10.1163/14219980-20211210

Teixeira, F. Z., Kindel, A., Hartz, S. M., Mitchell, S., & Fahrig, L. (2017). When road-kill hotspots do not indicate the best sites for road-kill mitigation. *Journal of Applied Ecology*, *54*(5), 1544–1551. https://doi.org/10.1111/1365-2664.12870

Teixeira, F. Z., Printes, R. C., Fagundes, J. C. G., Alonso, A. C., & Kindel, A. (2013). Canopy bridges as road overpasses for wildlife in urban fragmented landscapes. *Biota Neotropica*, *13*(1), 117–123. https://doi.org/10.1590/s1676-06032013000100013

The Human Right to a Clean, Healthy and Sustainable Environment: Resolution Adopted by the General Assembly on 28 July 2022, Pub. L. No. A/RES/76/300 (2022).

The Kenya Roads (Roadside Stations) Regulations, Pub. L. No. 2007 (No 2 of 2007), The Kenya Roads Act (2023).

Thomas, S. C. (1991). Population densities and patterns of habitat use among Anthropoid primates of the Ituri Forest, Zaire. *Biotropica*, *23*(1), 68–83. https://doi.org/10.2307/2388690

Tintó, A., Real, J., & Mañosa, S. (2010). Predicting and Correcting Electrocution of Birds in Mediterranean Areas. *The Journal of Wildlife Management*, *74*(8), 1852–1862. https://doi.org/10.2193/2009-521

Torres-Romero, E. J., Nijman, V., Fernández, D., & Eppley, T. M. (2023). Human-modified landscapes driving the global primate extinction crisis. *Global Change Biology*, *29*(20), 5775–5787. https://doi.org/10.1111/gcb.16902

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities and of aquatic ecological effects of roads on terrestrial communities. *Conservation Biology*, *14*(1), 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Tuttle, D. P., Gülen, G., Hebner, R., King, C. W., Spence, D. B., Andrade, J., Wible, J. A., Baldick, R., & Duncan, R. (2016). *The history and evolution of the U.S. electricity industry*. https://energy.utexas.edu/sites/default/files/UTAustin_FCe_History_2016.pdf

Tye, S. P., Fey, S. B., Gibert, J. P., & Siepielski, A. M. (2024). Predator mass mortality events restructure food webs through trophic decoupling. *Nature*, *626*(7998), 335–340. https://doi.org/10.1038/s41586-023-06931-7

Uddin, M., Dutta, S., Kolipakam, V., Sharma, H., Usmani, F., & Jhala, Y. (2021). High bird mortality due to power lines invokes urgent environmental mitigation in a tropical desert. *Biological Conservation*, *261*, 109262. https://doi.org/10.1016/J.BIOCON.2021.109262

United Nations. (2015a). *Goal 7: Ensure access to affordable, reliable, sustainable and modern energy for all*. Department of Economic and Social Affairs Sustainable Development. https://sdgs.un.org/goals/goal7

United Nations. (2015b). *Goal 9: Build resilient infrastructure, promote sustainable industrialization and foster innovation*. Department of Economic and Social Affairs Sustainable Development. https://sdgs.un.org/goals/goal9

United Nations. (2015c). *Goal 11: Make cities and human settlements inclusive, safe, resilient and sustainable*. Department of Economic and Social Affairs Sustainable Development. https://sdgs.un.org/goals/goal11

United Nations. (2019). *World Urbanization Prospects. The 2018 Revision*. https://digitallibrary.un.org/record/3833745?v=pdf

Vakhlamova, T., Rusterholz, H.-P., Kanibolotskaya, Y., & Baur, B. (2016). Effects of road type and urbanization on the diversity and abundance of alien species in roadside verges in Western Siberia. *Plant Ecology*, *217*(3), 241–252. https://doi.org/10.1007/s11258-016-0565-1

Valladares-Padua, C., & Cullen Jr., L. (1995). A pole bridge to avoid primate road kills. *Neotropical Primates*, *3*(1), 13–15.

van der Grift, E. A., & van der Ree, R. (2015). Guidelines for evaluating use of wildlife crossing structures. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 119–128). Wiley. https://doi.org/10.1002/9781118568170.ch15

van der Grift, E. A., van der Ree, R., Fahrig, L., Findlay, S., Houlahan, J., Jaeger, J. A. G., Klar, N., Madriñan, L. F., & Olson, L. (2013). Evaluating the effectiveness of road mitigation measures. *Biodiversity and Conservation*, *22*(2), 425–448. https://doi.org/10.1007/s10531-012-0421-0

van der Grift, E. A., van der Ree, R., & Jaeger, J. A. G. (2015). Guidelines for evaluating the effectiveness of road mitigation measures. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook for Road Ecology* (pp. 129–137). John Wiley & Sons Ltd, UK.

van der Ree, R., Gagnon, J. W., & Smith, D. J. (2015). Fencing: A valuable tool for reducing wildlife-vehicle collisions and funnelling fauna to crossing structures. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 159–171). John Wiley & Sons Ltd, UK. 10.1002/9781118568170

van der Ree, R., Jaeger, J. A. G. R., Rytwinski, T., & van der Grift, E. A. (2015). Good science and experimentation are needed in road ecology. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology*. John Wiley & Sons Ltd, UK.

van der Ree, R., van der Grift, E., Gulle, N., Holland, K., Mata, C., & Suarez, F. (2007). Overcoming the barrier effect of roads: How effective are mitigation strategies? An international review of the use and effectiveness of underpasses and overpasses designed to increase the permeability of roads for wildlife. *Proceedings of the 2007 International Conference on Ecology and Transportation*, 423–431.

van Doorn, A. C., & O'Riain, M. J. (2020). Nonlethal management of baboons on the urban edge of a large metropole. *American Journal of Primatology*, *82*(8). https://doi.org/10.1002/ajp.23164

Vaughan, A. (2020, September 15). "Massive failure": The world has missed all its biodiversity targets. *New Scientist*. https://www.newscientist.com/article/2254460-massive-failure-the-world-has-missed-all-its-biodiversity-targets/

Wallace, A. R. (1863). On the physical geography of the Malay Archipelago. *Proceedings of the Royal Geographical Society of London*, *33*, 217–234. https://doi.org/10.2307/1799061

Wallis, J. (2020). *Papio cynocephalus* ssp. *cynocephalus*. *The IUCN Red List of Threatened Species 2020:* eT136898A92251027. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T136898A92251027.en

Waters, S., El Harrad, A., Chetuan, M., Bell, S., & Setchell, J. (2017). Dogs disrupting wildlife: Domestic dogs harass and kill Barbary macaques in Bouhachem forest, North Morocco. *African Primates*, *12*, 55–58.

Weeks, S. (2015). Case study: The Mount Kenya elephant corridor and underpass. In R. van der Ree, D. J. Smith, & C. Grilo (Eds.), *Handbook of Road Ecology* (pp. 353–356). John Wiley & Sons Ltd, UK.

Weston, N., Goosem, M., Marsh, H., Cohen, M., & Wilson, R. (2011). Using canopy bridges to link habitat for arboreal mammals: Successful trials in the Wet Tropics of Queensland. *Australian Mammalogy*, *33*(1), 93–105. https://doi.org/10.1071/AM11003

White, F. (1983). *Vegetation of Africa: A descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa.* UNESCO.

Wijtten, Z., Hankinson, E., Pellissier, T., & Lemarkat, R. (2012). Activity Budgets of Peters' Angola Black-and-White colobus (*Colobus angolensis palliatus*) in an east African coastal forest. *African Primates*, *7*(2), 203–210.

Wikimedia. (2024). *Monkey warning road signs*. https://commons.wikimedia.org/wiki/Category:Monkey_warning_road_signs

WWF. (2022). Living Planet Report 2022 - Building a nature-positive society. In R. E. A. Almond, M. Grooten, D. Juffe Bignoli, & T. Petersen (Eds.), *In collaboration with the Zoological Society of London*. WWF Gland, Switzerland.

Xing, J., Wang, H., Zhang, Y., Ray, D. A., Tosi, A. J., Disotell, T. R., & Batzer, M. A. (2007). A mobile element-based evolutionary history of guenons (tribe Cercopithecini). *BMC Biology*, *5*, 1–10. https://doi.org/10.1186/1741-7007-5-5

Yap, J. L., Rosely, N. F. N., Mahadzir, M., Benedict, M. L., Muniandy, V., & Ruppert, N. (2022). "Ah Lai's Crossing" – Malaysia's first artificial road canopy bridge to facilitate safer arboreal wildlife crossings. *Folia Primatologica*, *0*, 1–15. https://doi.org/10.1163/14219980-20211105

Yap, J. L., Ruppert, N., & Rosely, N. F. N. (2019). Activities, habitat use and diet of wild dusky langurs, *Trachypithecus obscurus* in different types of habitat in Penang, Malaysia. *Journal of Sustainability Science and Management*, *14*(4), 58–72.

Yeo, J.-H., & Neo, H. (2010). Monkey business: human–animal conflicts in urban Singapore. *Social & Cultural Geography*, *11*(7), 681–699. https://doi.org/10.1080/14649365.2010.508565

Zuberogoitia, I., Del Real, J., Torres, J. J., Rodríguez, L., Alonso, M., & Zabala, J. (2014). Ungulate vehicle collisions in a peri-urban environment: Consequences of transportation infrastructures planned assuming the absence of ungulates. *PLoS ONE*, *9*(9). https://doi.org/10.1371/journal.pone.0107713

Þórhallsdóttir, G., & Ólafsson, R. (2017). A method to analyse seasonality in the distribution of tourists in Iceland. *Journal of Outdoor Recreation and Tourism*, *19*, 17–24. https://doi.org/10.1016/j.jort.2017.05.001

Appendix I Co-authored publications and reports

Chapter 6 was the first of the analytical chapters published for this PhD thesis. That was in 2018. Since then, I have authored an additional seven related articles, of which one is general biodiversity conservation, and one is on the global impact of roads on primates. The remaining five are focussed on colobus (*Colobus angolensis*). Below I provide citations and abstracts for these publications and reports.

Praill, L.C. et al., 2023. Road Infrastructure and Primate Conservation: Introducing the Global Primate Roadkill Database. Animals, 13(10), 1692. https://www.10.3390/ani13101692.

Cunneyworth, P.M.K.: 4 of 19 authors.

Abstract

As road infrastructure networks rapidly expand globally, especially in the tropics, previously continuous habitats are being fragmented, resulting in more frequent wildlife–vehicle collisions (WVC). Primates are widespread throughout many sub-/tropical countries, and as their habitats are fragmented, they are increasingly at risk of WVC. We created the Global Primate Roadkill Database (GPRD), the largest available standardized database of primate roadkill incidents. We obtained data from published papers, un-published and citizen science databases, anecdotal reports, news reports, and social media posts. Here, we describe the collection methods for the GPRD and present the most up-to-date version of the database in full. For each primate roadkill incident, we recorded the species killed, the exact location, and the year and month the roadkill was observed. At the time of publication, the GPRD includes 2862 individual primate roadkill records from 41 countries. As primates range in more than twice as many countries, the absence of data from these countries is not necessarily indicative of a lack of primate vehicular collisions. Given the value of these data for addressing both local and global research questions, we encourage conservationists and citizen scientists to contribute to the GPRD so that, together, we can better understand the impact road infrastructure has on primates and evaluate measures which may help mitigate risk-prone areas or species.

Clements, H.S., Do Linh San, E., Hempson, G. *et al.* The bii4africa dataset of faunal and floral population intactness estimates across Africa's major land uses. *Sci Data* **11**, 191 (2024). https://doi.org/10.1038/s41597-023-02832-6

(**Cunneyworth, P.M.K.**: 51 of 209 authors. My contribution was as a biodiversity expert with input on the writing of the draft and approving the manuscript.

Abstract

Sub-Saharan Africa is under-represented in global biodiversity datasets, particularly regarding the impact of land use on species' population abundances. Drawing on recent advances in expert elicitation to ensure data consistency, 200 experts were convened using a modified-Delphi process to estimate 'intactness scores': the remaining proportion of an 'intact' reference population of a species group in a particular land use, on a scale from 0 (no remaining individuals) to 1 (same abundance as the reference) and, in rare cases, to 2 (populations that thrive in human-modified landscapes). The resulting bii4africa dataset contains intactness scores representing terrestrial vertebrates (tetrapods: ±5,400 amphibians, reptiles, birds, mammals) and vascular plants (±45,000 forbs, graminoids, trees, shrubs) in sub-Saharan Africa across the region's major land uses (urban, cropland, rangeland, plantation, protected, etc.) and intensities (e.g., large-scale vs smallholder cropland). This dataset was co-produced as part of the Biodiversity Intactness Index for Africa Project. Additional uses include assessing ecosystem condition; rectifying geographic/taxonomic biases in global biodiversity indicators and maps; and informing the Red List of Ecosystems.

IUCN Red List of Threatened Species: Assessments

de Jong, Y.A., **Cunneyworth, P.**, Butynski, T.M., Maisels, F., Hart, J.A. & Rovero, F. 2020. *Colobus angolensis*. *The IUCN Red List of Threatened Species 2020*: e.T5142A17945007. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5142A17945007.en

Abstract

Colobus angolensis is listed as Vulnerable. Despite a very large geographic range, the species is threatened in most parts of its range by habitat loss, degradation and fragmentation caused mainly by collection of timber and fuelwood, conversion of forest to farmland, the expansion of human settlements and encroachment due to a fast growing human population (Bocian and Anderson 2013, McDonald et al.2023).

Cunneyworth, P., de Jong, Y.A., Butynski, T.M. & Perkin, A. 2020. *Colobus angolensis* ssp. *palliatus*. The IUCN Red List of Threatened Species 2020: e.T5148A17983413. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T5148A17983413.en

Abstract

Colobus angolensis palliatus is listed as Vulnerable due to a suspected population reduction throughout its range and a suspected future population reduction primarily due to deforestation as a result of land conversion to agriculture. Hunting is also a threat. These threats have not ceased. The forest habitat across the range is severely fragmented, limiting gene flow among populations. Recent extirpations of C. a. palliatus have been documented and additional extirpations inferred. It is likely that the rate of decline in the population will remain at 30% over the next three generations.

McDonald, M.M., Johnson, S.M., Henry, E.R., **Cunneyworth, P.M.K**., 2019. Differences between ecological niches in northern and southern populations of Angolan black and white colobus monkeys (*Colobus angolensis palliatus* and *Colobus angolensis sharpei*) throughout Kenya and Tanzania. Am J Primatol., e22975. https://doi.org/10.1002/ajp.22975.

Abstract

Ecological niche models can be useful for clarifying relationships between environmental factors and a species' geographic distribution. In this study, we use presence-only data and environmental layers to create an ecological niche model to better understand the distribution of the East African Angolan black and white colobus monkey, *Colobus angolensis palliatus*, and to assess whether the model supports considering the population as two separate subspecies, *Colobus angolensis sharpei* and *C. a. palliatus*. We found the range of the predicted distribution for suitable habitat of *C. a. palliatus* as currently classified to be only 12.4% of that shown in the International Union for Conservation of Nature Red List range map and to be fragmented. As *C. angolensis* is considered a "Least Concern" species, this difference suggests that generalized maps may lead to understating the species' extinction risk. When presence points were divided into two previously proposed subspecies—*C. a. palliatus* (Kenya and Northern Tanzania) and *C. a. sharpei* (Southern Tanzania)—we found significant environmental differences between the distributions. The most important ecological variable for *C. a. palliatus* was predominantly precipitation of the driest month (69.1%) whereas for *C. a. sharpei* annual precipitation (44.8%) and land cover (normalized difference vegetation index, 16.4%) were the most important. When comparing suitable ranges for the separate distributions, we found only a 1.2% geographical overlap. These differences are consistent with previous subspecies delineations of *C. a. palliatus* and *C. a. sharpei* based upon morphology, pelage, and genetics. Our study suggests that extirpation of *C. a. palliatus* in suitable habitat areas and occurrence of this subspecies in anthropogenic environments, warrant further consideration for conservation actions.

McDonald, M.M.*, **Cunneyworth, P.M.K.***, Anderson, A.G., Wroblewski, E. 2021. Mitochondrial genetic diversity and divergence dating of Angolan colobus monkeys (*Colobus angolensis*) in the eastern forests of Kenya and Tanzania: Implications for subspeciation and reconstructing historical biogeography. Am J Primatol. 2022. e23384. https://doi.org/10.1002/ajp.23384

* denotes joint first authors

Abstract

Whether the *Colobus angolensis* that reside in the fragmented forests in eastern Kenya and Tanzania represent one subspecies or two has been debated for 50 years. Morphological and more recent genetic and ecological studies suggest that these populations represent two subspecies, *C. a. palliatus* and *C. a. sharpei*. However, their distribution of mitochondrial variation remains unresolved since the genetic study only characterized four populations at the range ends. Therefore, we characterized five populations in the area of the hypothesized subspecies divide. We identified eight new haplotypes which, combined with those previously identified, provided 26 haplotypes from nine populations for analysis. Haplotypes found south of the Rufiji River cluster together but separately from northern haplotypes. The largest sequence differences within cytochrome b occur between population pairs representing opposite sides of the river; their mean difference (1.5%) is more than that of other primate subspecies. Analysis of molecular variance attributes most of the variation to that north versus south of the river. These results support the previous subspecies distinction between *C. a. palliatus* (northern) and *C. a. sharpei* (southern), divided by the Rufiji River. The estimated time of the most recent common ancestor of all haplotypes indicates that the subspecies have been isolated from each other for approximately 550,000 years. The common ancestor of northern and southern haplogroups was 370,000 and 290,000 years ago, respectively. Nevertheless, the correlation between genetic and geographic distances suggests that isolation-by-distance contributed to population structuring. Significant variation among populations, with only three haplotypes shared between populations, also indicates that an extended period of isolation drove population distinctiveness. Considering these results, we evaluate hypotheses about the founding and differentiation of these subspecies during Pleistocene climatic fluctuations and propose a novel, more direct migration route from Central Africa to their current range navigating Lake Tanganyika, the central Tanzanian corridor, and Rufiji River.

McDonald, M.M.*, **Cunneyworth, P.M.K.***, Anderson, A.G., Wroblewski, E. 2021. Wild origins and mitochondrial genetic diversity of Angolan Colobus monkeys (*Colobus angolensis*) in AZA-accredited zoos and its implications for ex situ population management. Zoo Biology. 2023;1–7. https://onlinelibrary.wiley.com/doi/10.1002/zoo.21775.

* denotes joint first authors

Abstract

Across zoo's accredited by the Association of Zoos and Aquariums (AZA), species are typically managed as a single population to retain 90% of the founding members' gene diversity. Often, little is known about the specific geographic origins of the founders or how representative the ex situ population's genetic diversity is of the wild population. This study uses mitochondrial DNA (mtDNA) sequencing to investigate haplotype diversity and geographic female founder origin of the AZA-managed Angolan colobus (*Colobus angolensis*) monkey population. We obtained fecal samples from individuals closely related to founder animals at five zoos and found four haplotypes among 23 individuals. Analyzed together with wild *C. angolensis* haplotypes, we found two haplotypes identical to those found in Tanzanian populations: one haplotype, possessed by 13 individuals (descended from three founders), matched an East Usambara Mountains haplotype, while the other, possessed by seven individuals (from four founders), matched a haplotype found in both the South Pare Mountains and Rufiji River. Two haplotypes were not detected in wild populations but were closely related to haplotypes found in the Rufiji River (one individual descended from one founder) and Shimoni, Kenya (two individuals descended from one founder) populations, suggesting nearby origins. Thus, the AZA-managed population of Angolan colobus likely originated from several localities, but all have mtDNA lineages associated with the subspecies C. a. palliatus, a Vulnerable subspecies. Examining founders' mtDNA haplotypes may be a useful addition to the zoo population management toolkit to help improve breeding recommendations by identifying individuals with rare haplotypes and revealing likely kinship among founders.

Appendix II Conservation impact of this thesis

Local conservation actions

Roads

Colobus Conservation conducted a fundraising campaign in 2024 that highlighted Chapters 2, 3 & 4 results. That campaign secured a donation of materials for 100 canopy bridges. These bridges are currently being installed across various locations, including private properties, beach access points, and over roads extending southward along the Kenya coastline. The choice of road locations for bridge placement is guided by the monkey-vehicle hotspot mapping in Chapter 4. The anticipated outcome is a significant reduction in the road barrier effect and vehicle collisions. These bridges will also improve aerial connectivity in other areas across the town offering greater protection from snares, dog attacks, and other ground-based threats, further supporting the conservation of the local colobus population, and the other primates.

Power Lines

In 2014, I began liaising with Kenya Power, the parastatal overseeing power distribution in the country. After raising issues of primate electrocutions with the company's Integrity and Ethics Department and the Department of Safety, Heath, and Environment, I secured a project to protect Diani's colobus. In January 2017, Kenya Power replaced 12 km of bare cables with Aerial Bundled Conductors and moved three transformers that were known as primate electrocution hotspots. The locations targeted for this work was guided by the hotspot mapping of Chapter 6.

In addition, Colobus Conservation developed a local insulation method for low voltage power lines, involving cutting plastic electrical conduit tubes laterally and clipping over the cables. In 2024, we successfully raised US$ 30,000 in cash and materials based on the results of Chapters 5 & 6 for an insulation project using our local method. The insulation project is now in progress, in collaboration with Kenya Power.

National conservation actions

Roads

Given the publication of Chapters 2–4, the East African Wildlife Society reached out to me to attend a meeting March 2022 to provide input on the Environmental Impact Assessment for the proposed road project of a 223-km, four-lane dual carriageway, from Mai Mahiu to Mau Summit, Kenya. The project proposed eleven new and upgraded crossing points. During that meeting, I stressed the importance of integrating canopy bridges or trees on the wildlife overpasses. This design would support the safe passage specifically of arboreal animals, minimising the road's disruptions to their natural behaviours and habitats. That project has yet to be finalised so whether these recommendations have been incorporated is, at present, unknown.

Power lines

In collaboration with the Peregrine Fund, we have conducted two meetings (Soysambu: 26 April 2024; Liakipia: 29 January 2025) (Appendix Figure 1) with Kenya Power, other players in the country's power distribution section, Kenya Wildlife Service, and local conservation organisations, to discuss wildlife electrocutions, their patterns, and mitigations to the impacts. At those meetings, I presented the results of Chapters 5 & 6. These meetings are the first big step bringing Kenya's main players together in one room to discuss achievable solutions to reduce the impacts of electrocution on primates and other wildlife across the country.

Appendix Figure 1 Participants of the wildlife electrocution meeting 26 April 2024, Soysambu, Kenya. Photo courtesy of The Peregrine Fund.

International conservation actions

Roads

I presented the results of Chapters 2–4 at the 2018 International Primatological Society (IPS) conference, as well as at the 2020 and 2023 African Conference for Linear Infrastructure and Ecology (ACLIE). These presentations, it is hoped, contributed to the broader scientific understanding of primate conservation in the context of linear infrastructure. To enhance my presentation at the 2018 IPS conference, I brought a section of the horizontal ladder canopy bridge that is used in Diani. That presentation led to Kenya's Institute of Primate Research contacting me requesting a more detailed presentation to their staff on how to implement a canopy bridge program for a road and power line in a forest on the outskirts of Nairobi. I gave that presentation on 22 May 2024.

Currently, I am contributing to two projects related to canopy bridges. The first is with a team led by Dr. Siân Waters to write the IUCN Best Practices for canopy bridge projects of which I am co-first author. The second is with a team led by Dr. Fernanda Abra where we are compiling attributes of species that use canopy bridges to determine their use patterns. A draft of this paper will be presented at the International Conference on Ecology and Transportation, May 2025, in Denver, Colorado.

Power lines

I wrote Annex I for the State of the Apes: Infrastructure Development and Ape Conservation (Cunneyworth, 2015). That article discussed electrocutions in rural, suburban, and urban environments. I also presented Chapters 5 & 6 results at the 2020 and 2023 African Conference for Linear Infrastructure and Ecology (ACLIE). In the 2023 presentation, I combined the information accrued from this thesis to provide guidance on the impact of power lines within road reserves, on the economics of canopy bridges, and how the barrier effect and wildlife-vehicle collisions are related categories.