

Bangor University

MASTERS BY RESEARCH

Mind the Monkeys: Road Ecology of the Zanzibar Red Colobus

Skinner, Harry

Award date:
2023

Awarding institution:
Bangor University

[Link to publication](#)

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Download date: 27. Apr. 2024



PRIFYSGOL
BANGOR
UNIVERSITY

**Mind the Monkeys: Road Ecology of the
Zanzibar Red Colobus**

A thesis submitted to Bangor University by

Harry Olgun - 500414078

In candidature for the degree of

Master of Research in the Biological Sciences

Supervised by

**Dr Alexander V. Georgiev¹, Professor John Healey¹, Dr Graeme Shannon¹
& Dr Tim R.B. Davenport²**

¹School of Natural Sciences, Bangor University

²Re:wild, Arusha, Tanzania

Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. Chapter 1 has been published in *Oryx* (16th March 2021)

(<https://doi.org/10.1017/S0030605320000605>): Olgun, H., Mohammed, M.K., Mzee, A.J., Green, M.L., Davenport, T.R. and Georgiev, A.V., 2022. The implications of vehicle collisions for the endangered endemic Zanzibar red colobus *Piliocolobus kirkii*. *Oryx*, 56(2), pp.268-276.

Abstract

Every taxon on Earth is experiencing negative effects from anthropogenic disturbance and to cope with these significant changes some animals are modifying their behaviours. However, the degree to which these behavioural changes mitigate against the novel risk from humans and the true impact that further infrastructural development, in particular, is to have on wildlife within their habitats is still not fully understood. In this thesis, I studied the risk that a road intersecting the habitat of multiple Zanzibar red colobus (*Piliocolobus kirkii*) groups at Jozani-Chwaka Bay National Park (JCBNP), Zanzibar, poses to individuals and examined whether colobus adopt behaviours that might mitigate the risk of primate-vehicle collisions when crossing the road. In my first chapter, I examined mammalian roadkill recorded over a 4-year period (January 2016 – December 2019) in the vicinity of JCBNP. I found that primates accounted for the majority of dead mammals on the road, and that rainfall did not influence roadkill occurrence. For the Zanzibar red colobus specifically, all age-sex classes were killed in proportion to their availability within the local population (in groups which ranged across or near the road). The rate at which colobus were killed on the road was similar to what other primate populations experience from natural predation. However, because car-induced mortality, unlike natural predation, did not affect predominantly the very young and old individuals, road-related mortality would have a distinct effect on population structure. By comparing mortality rates from the present study to estimates of colobus mortality estimated on the same road in the early 1990s, I also show that colobus roadkill has been significantly reduced by installing several speedbumps near the national park entrance. In the second chapter of this thesis, I examine whether colobus are able to perceive roads as risky, as well as to determine risk variance between two different road types. Specifically, I compared the main tarmac road at the southern edge of JCBNP to a smaller dirt road in the same study area. Using video recordings obtained during two research trips over a one-year period (July-September 2019 and February-March 2020) and opportunistic data, I quantified three behavioural indicators of risk awareness: hesitancy to cross, crossing time and mid-cross sitting occurrence. Analyses of video footage revealed that colobus did not seem to perceive the risk variance associated with the different roads. However, despite age having no effect on wariness when crossing roads, females showed greater wariness than males, and females with clinging infants even more so. Combining these observations with data from chapter 1, I suggest that this wariness by females is not enough to reduce the risk that roads

pose to colobus as we there was no corresponding difference in mortality likelihood of females, by comparison to males in the roadkill dataset.

Acknowledgements

I thank the Department of Forestry of the Revolutionary Government of Zanzibar for permission to conduct this research and their support in the field; the staff at Jozani-Chwaka Bay National Park for their hospitality; and Ali Kassim, Ameir Abdalla and Mwinyi Abdalla for assistance with data collection; K.Madeweya and S.Fakih for logistical advice and assistance; Zoe Melvin, John Healey, Graeme Shannon, Tim Davenport, Landry Green and Carlos Cardenas-Iniguez for their helpful comments. The Zanzibar Red Colobus Project was supported by funding to Alexander Georgiev from the Royal Society and Bangor University. Partial funding to for this research was provided by the School of Natural Sciences, Bangor University. Thank you to Zoe Melvin and Alexander Georgiev to their continued support in the field, experiencing the good and bad days and providing the important emotional and intellectual support that was crucial to my development and research success. A further thankyou to my supervisory team who have supported me and provided me with the much-needed training and advice required for this thesis, as well as the support in not only my academic but personal issues I faced during this degree. In particular, I would like to thank Alexander Georgiev for his continued patience and support during the most difficult time, and I am incredibly grateful to have him as a supervisor, providing weekly pep talks and late-night research discussions, this thesis would not have been possible without him.

Table of contents

Chapter 1: Introduction	6
Chapter 2: The implications of vehicle collisions for the Endangered endemic Zanzibar red colobus <i>Piliocolobus kirkii</i>	9
Abstract.....	9
Introduction.....	10
Methods.....	13
Study site.....	13
Roadkill data	13
Rainfall data	14
Demographic composition of roadside colobus groups	14
Statistical analyses	15
Results	16
Discussion	18
Chapter 3: Zanzibar red colobus monkeys do not show differential risk awareness when crossing roads that differ in likelihood of primate-vehicle collisions	24
Abstract.....	24
Introduction.....	25
Methods.....	29
Study site.....	29
Study subjects	30
Behavioural observations.....	31
Behavioural Variable Construction.....	32
Statistical Analysis.....	32
Results	34
Road-crossing at the group level.....	34
Road-crossing at the individual level.....	35
Discussion	40
Conclusions.....	45
Bibliography	47

Chapter 1: Introduction

Roads can have a multitude of effects on wildlife, from behavioural alterations and population fragmentation to more direct effects, such as roadkill (Jaegar, *et al.*, 2005). Many of the primary effects of roads are negative, such as habitat loss, fragmentation, and degradation (Underhill, 2003). These negative primary effects can be exacerbated by the secondary effects that roads can cause. Increases in vehicle traffic can increase pollution within forests, as well as ease the access to forests for hunters and increase the susceptibility to the introduction and spread of invasive species (Laurance, *et al.*, 2009). Road ecology to date has focused on more temperate environments, larger mammals, and terrestrial species (Holderegger & Di Giulio, 2010; Smith, van der Ree and Rosell, 2015). However, roads are expected to have an even greater impact on wildlife in tropical regions, where biodiversity is higher (van der Ree, Smith & Grilo, 2015). Road ecology research may thus be under-sampling precisely the habitats and regions in which the impact of roads on wildlife may be both widespread and significant from a conservation perspective.

One area in which road ecologists have focused their attention in particular, is designing and evaluating the effectiveness of various mitigation strategies for reducing the effects of roads on populations of wild animals (Rytwinski, *et al.*, 2016). Wildlife bridges for arboreal species which approach the road via the tree canopy (Biro, *et al.*, 2020; Linden, *et al.*, 2020) and underpasses for terrestrial species, even as large as elephants (Okita-Ouma, *et al.*, 2021), are two of the primary mitigation approaches. Both approaches concentrate on offering connectivity and alternative routes across roads, so that animals can avoid crossing roads terrestrially. By contrast, speed bumps place the burden for risk mitigation on vehicle drivers instead of the wildlife and are thus independent from the likelihood of wildlife engaging with mitigation measures they are meant to use. Speed bumps have been shown to reduce roadkill for many species as this mitigation is unlikely to be ignored by drivers (Schutt, 2008; Farmer and Brooks, 2012; Da Silva, De Menezes and Santos, 2022), unlike road signs, which are a cheaper alternative mitigation strategy. Although signage has proven to be effective, this is only true for novel signs and drivers quickly become habituated to signage and eventually ignore it (Collinson, Marneweck and Davies-Mostert 2019).

In addition to studies of roadkill to evaluate the impact of roads on wildlife mortality, behavioural research on how animals respond to roads (avoidance or attraction) and cross roads, when they must, is fundamental to a wholistic understanding of the road ecology of a species. Behavioural studies of road crossings, however, are particularly scarce in the literature, precluding an evaluation of both the way animals may deal with the risks from vehicles and of their adoption of human-made mitigation measures such as canopy bridges or underpasses. The few existing studies on road crossing behaviour do give us an insight that behaviours related to roads may differ between species. In koalas, males and juveniles are more likely to cross roads compared to female and only if their range is within 100 m of roads (Dexter, *et al.* 2017). By contrast, in hedgehogs, demographics did not affect crossing behaviours but locations of roads did: hedgehogs were more likely to cross larger roads when other preferable habitats, such as open fields, were not nearby (Rondinini & Doncaster, 2002). Without this fundamental understanding of animal behaviour at the habitat-road interface, conservation efforts cannot proceed effectively, as mitigation measures that do not reduce road mortality can still be costly and time consuming to implement. Roads have become a fundamental infrastructure to human life, so we must develop our understanding further to aid conservation of at-risk species.

Road ecology research within the field of primatology, by comparison to studies of other taxa in temperate regions, is still in its infancy. Primate road ecology studies often focus on roadkill at an anecdotal level, giving only limited understanding of primate road ecology (Hetman, *et al.*, 2019). In addition to this, even thorough and systematic studies on primate roadkill patterns only describe observed patterns of mortality and seek explanations to the variation in roadkill frequencies when considering factors affecting this, such as habitat types and seasonality (D'Amico, *et al.*, 2015; Kioko, *et al.*, 2015). Studies of behavioural mitigation by primates when crossing roads are still rare (Hockings, *et al.*, 2006; Hockings, 2011; Cibot, *et al.*, 2015). Similarly lacking are quantitative evaluations of the effectiveness of mitigation measures for reducing primate roadkill. For example, despite their potential utility, no papers to date have examined the effectiveness of speed bumps in reducing primate roadkill frequency (Junker, *et al.*, 2017). Yet, primates are expected to be some of the most vulnerable species, in terms of the effects of roadkill mortality on their populations, because their slow life histories (Jones, 2011) and increased generation times limit the rate of population replacement (Van Allen, 2012). The risk roads pose to primate populations is

expected to become even more prevalent over the coming years due to the estimated 60% increase in global road networks (Dulac, 2013). With 60% of primate species threatened with extinction and 75% of primate species having declining populations (Estrada, *et al.*, 2017), the need for further in-depth understanding has never been more crucial.

Although the literature on primate roadkill is beginning to catch up with other roadkill research, through increased literature output as well as tools such as social media aiding in data availability (Hetman, *et al.*, 2019; Schwartz, Shilling and Perkins 2020), we still lack a clear understanding of the effects of roadkill on population persistence as well of the ability of primates to engage in effective behavioural strategies when handling the risks posed by roads. Behavioural studies of primate road crossing behaviours have thus far focused exclusively on chimpanzees (Hockings, *et al.*, 2006; Hockings, 2011; Cibot, *et al.*, 2015), leaving a potentially significant taxonomic variation unexplored.

In this thesis I study the behaviour of the Zanzibar red colobus along a road by Jozani-Chwaka Bay National Park to examine the risks that roads pose to colobus and whether the monkeys are capable of adapting behaviours in order to mitigate this risk. Through a 4-year data set of roadkill, coded video road crossings and demographic data on the roadside groups of the Zanzibar red colobus in the area, I can assess, not only the roadkill frequency that the colobus experience at Jozani, but the potential impact and annual loss per year as well as assess their behaviour for risk-perceptive and risk-reducing adaptations, a combined insight that we are currently missing from the literature. This combined insight gives us a much greater understanding of the risks that roads pose to the colobus, as well as understand how wildlife may be able to incorporate behavioural plasticity to reduce this risk from road, in turn reducing roadkill and increasing population persistence.

Chapter 2: The implications of vehicle collisions for the Endangered endemic Zanzibar red colobus *Piliocolobus kirkii*

This chapter is published as:

Olgun, H., Mohammed, M.K., Mzee, A.J., Green, M.L., Davenport, T.R. and Georgiev, A.V., 2022. The implications of vehicle collisions for the Endangered endemic Zanzibar red colobus *Piliocolobus kirkii*. *Oryx*, 56(2), pp.268-276.

<https://doi.org/10.1017/S0030605320000605>

Abstract

Roads affect wildlife in a variety of negative ways. Road ecology studies have mostly concentrated on areas in the northern hemisphere despite the potentially greater impact of roads on biodiversity in tropical habitats. Here, we examine 4 years (January 2016–December 2019) of opportunistic observations of mammalian roadkill along a road intersecting Jozani-Chwaka Bay National Park, Unguja, Zanzibar. In particular, we assess the impact of collisions on the population of an endemic primate, the Endangered Zanzibar red colobus *Piliocolobus kirkii*. Primates accounted for the majority of roadkill in this dataset. Monthly rainfall was not associated with roadkill frequency for mammals generally, nor for the Zanzibar red colobus. No single age–sex class of colobus was found dead more often than expected given their occurrence in the local population. The overall effect of roadkill on colobus populations in habitats fragmented by roads is unknown given the lack of accurate, long-term life history data for this species. Our findings suggest that mortality from collisions with vehicles in some groups of colobus is within the range of mortality rates other primates experience under natural predation. Unlike natural predators, however, vehicles do not kill selectively, so their impact on populations may differ. Although a comparison with historical accounts suggests that the installation of speedbumps along the road near the Park's entrance has led to a significant decrease in colobus roadkill, further actions to mitigate the impact of the road could bring substantial conservation benefits.

Introduction

One of the many ways in which roads affect wildlife is via increased mortality from collisions with vehicles (Trombulak & Frissell, 2000; Coffin, 2007, Newmark, 2008; Laurance, *et al.*, 2009). Two key aspects need to be considered when examining the potential impact of vehicle collisions on the status of a species. Firstly, the scale of the problem needs to be assessed by determining the frequency of collisions and the factors affecting the frequency and spatial and temporal distribution of roadkill. Secondly, we need to examine the effects of road mortality on population structure and persistence.

Road ecology has made substantial progress in addressing the first issue. Numerous studies have documented patterns of wildlife–vehicle collisions across a variety of biomes (Rytwinski & Fahrig, 2012; van der Ree, *et al.*, 2015; Monge-Nájera, 2018; Krief, *et al.*, 2020). The magnitude of the problem is illustrated in a study of community-reported welfare cases involving primates along a 10-km stretch of road in a coastal resort town in Kenya. Collisions with vehicles were the single most frequent incident cause reported over a 19-year period (37% of all cases, $n = 1,896$), with 83% of collisions being fatal for the monkeys (Cunneyworth & Duke, 2020). Environmental factors such as variation in rainfall can affect roadkill frequency. Some studies have reported more roadkill in wet seasons, whereas others found greater roadkill mortality in dry seasons (Jeganathan, *et al.*, 2018, Njovu, *et al.*, 2019; Cunneyworth & Duke, 2020). Fatal collisions with vehicles are more frequent on roads near and within than outside or further away from protected areas (Garrigia *et al.*, 2012; Kioko, *et al.*, 2015; Akrim, *et al.*, 2019, Njovu, *et al.*, 2019). Road type also has an effect: bigger roads with a better surface, which allow for greater speed and larger vehicles, cause greater mortality (Drews, 1995; Caro, *et al.*, 2014; Epps, *et al.*, 2015; Collinson, *et al.*, 2019a). Species vary in their susceptibility, with larger, longer-lived animals with slower life histories being particularly vulnerable to collisions (Rytwinski & Fahrig, 2012). Amongst primates, the degree of terrestriality can also affect roadkill risk: more arboreal species appear to be killed at greater frequency when crossing roads than species that spend more time on the ground (Cunneyworth & Duke, 2020).

Despite the increasing literature on roadkill (Schwartz, Shilling and Perkins, 2020), few studies have addressed the second issue, assessing the impact of road-induced mortality on

population structure and persistence (e.g. Hells & Buchwald, 2001) Individuals within a population can have different mortality risks. For example, Florida scrub jays *Aphelocoma coerulescens* breeding in territories along a major road were at greater risk of roadkill mortality than those nesting further away from roads. Within the roadside populations, this risk was highest for birds that had immigrated into these areas during the first 2 years in their new territory, whereas for birds that had been living in these areas for longer it was similar to those in non-road territories (Mumme et al., 2000). Similarly, fledgling Florida scrub jays near roads experienced significantly increased mortality in their first months of life but not later. This shows that individuals that are new to anthropogenic landscapes and struggle to navigate them safely are at higher risk (ibid.). Differences in age and experience could also explain roadkill mortality patterns in some mammals. In Mikumi National Park, Tanzania, amongst groups of yellow baboons *Papio cynocephalus* that frequented a road intersecting their habitat, young, presumably less experienced, individuals were killed more frequently than expected based on their representation in groups that visited the road (Drews, 1995). However, the same pattern of vulnerability in different age classes of yellow baboons was not observed at a different site (Cunneyworth & Duke, 2020). Variation in the relative vulnerability of age–sex classes has also been reported amongst the four different monkey species studied (ibid.), suggesting that site- and species-specific assessments are necessary to establish how different populations might be affected by roads. Knowing which age–sex classes are most at risk is important for understanding if and how road mortality will affect the population in the long term. For example, the loss of a young reproductive female is more likely to have adverse effects on the maintenance of a population than the loss of males or sexually immature individuals (Coulson, *et al.*, 2001). For primates, given their slow life histories (Charnov & Berrigan, 2005), high vulnerability to extinction (75% of primate species have declining populations; Estrada, *et al.*, 2017), and the limited literature on primate road ecology (Hetman, *et al.*, 2019), examining the potential long-term demographic impact of wildlife–vehicle collisions is particularly important.

Red colobus *Piliocolobus* spp. are a genus of threatened African primates (Struhsaker, 2005). The Endangered Zanzibar red colobus *Piliocolobus kirkii* is endemic to Unguja Island, Zanzibar, and roadkill may be a particularly prominent source of mortality in at least one locality (Struhsaker & Siex, 1998). The species faces increasing pressure from habitat loss caused by agricultural expansion, human development, and timber logging

(Davenport, 2019). According to the most recent comprehensive census, the population is estimated to be c. 5,800 individuals and appears to be in decline, with a low recruitment rate compared to other red colobus species and primates more broadly (Davenport, *et al.*, 2019). Almost 50% of the Zanzibar red colobus population occur in Jozani-Chwaka Bay National Park, the only national park in Zanzibar (*ibid.*). They are the main attraction for visitors to the Park and provide a crucial source of revenue for the local economy (Saunders, 2011; Carius & Job, 2019). Increased tourist vehicle traffic (in addition to other types of traffic) on the main road intersecting the southern edge of the Park, however, also poses a risk to colobus as multiple groups range on both sides of the road, cross it frequently and occasionally get hit by vehicles. In the absence of natural predators, roadkill incidents may be the most significant source of extrinsic mortality for this subpopulation of *P. kirkii*. Currently, however, there are no accurate data to assess the magnitude of this threat for the species.

Here, we analysed a 4-year dataset on mammalian roadkill at Jozani-Chwaka Bay National Park to examine the frequency and seasonality of reported deaths (carcasses that remained on the road). For the Zanzibar red colobus we also examined the demographics of individuals killed in vehicle collisions. We hypothesized that age–sex classes were killed at rates that were different from their availability in the population, and we tested several predictions. Amongst adults, it could be that (1) adult males are over-represented in the roadkill data, compared to females, because of their potentially greater propensity for risk-taking (i.e. being less cautious). Alternatively, (2) adult females could be over-represented because they may be slower to cross than males, especially when carrying dependent offspring. Regarding age-class differences in road mortality, (3) subadults and juveniles could be over-represented in the roadkill because (a) they may be slower and lacking in learned abilities to avoid oncoming vehicles effectively, and (b) because subadults could be the age class most likely to disperse from their natal group. Alternatively, (4) adults could be over-represented in the roadkill dataset because they may perceive roads as more familiar environments and so be less cautious than immatures when crossing. We discuss our findings in the context of historical accounts for vehicle-related deaths at this study site, to assess the effectiveness of speedbumps as a road mitigation strategy to reduce mortality of the Zanzibar red colobus across its range. According to a systematic review of the literature, there is currently no evidence to evaluate the effectiveness of speedbumps as a mitigation measure for primate

conservation (Junker, *et al.*, 2019), so our case study of the Zanzibar red colobus provides valuable baseline data.

Methods

Study site

Jozani-Chwaka Bay National Park on Unguja Island, Zanzibar (Fig. 1a), is the last stronghold of the endemic Zanzibar red colobus (Siex, 2003; Davenport, *et al.*, 2019). At its southern edge, a major road (c. 5 m wide) intersects the home ranges of multiple colobus groups (Fig. 1b). These groups often cross the road in search of food and sleeping sites, thereby risking collisions and fatalities. There are four speedbumps along a 600-m stretch of this road but colobus also range and cross the road outside this speed buffer zone.

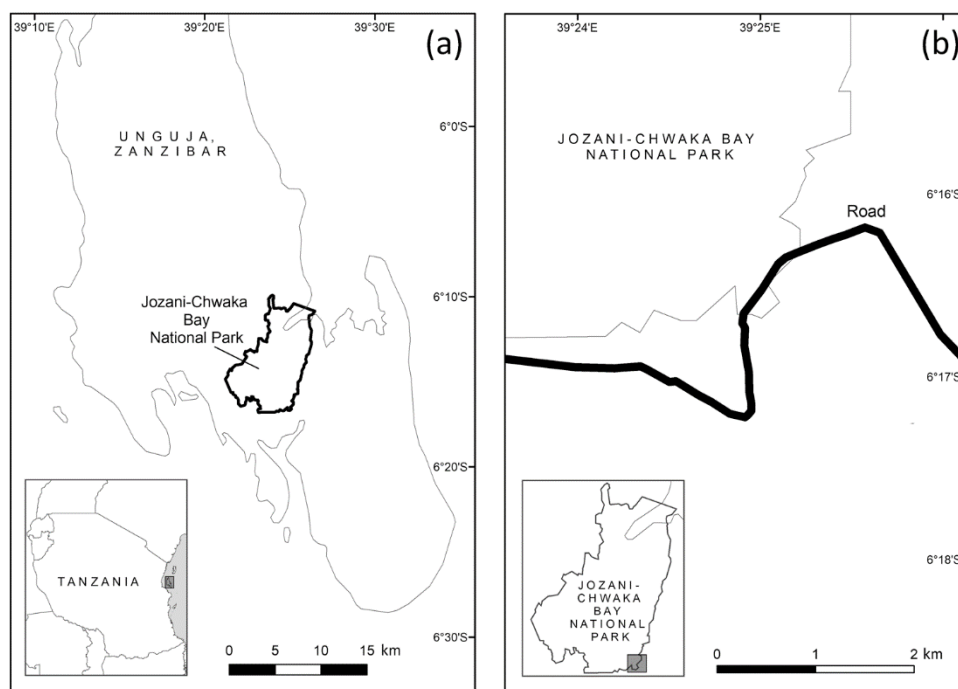


Fig.1 Location of the study site: (a) Jozani-Chwaka Bay National Park, Zanzibar, Tanzania, and (b) the road from which roadkill data were collected.

Roadkill data

Roadkill was recorded opportunistically by Jozani-Chwaka Bay National Park staff along the main road intersecting the Park at its southern edge over 4 years based both on direct

observation and reports from the public (January 2016–December 2019; 43 months of records were available; data from 5 months were missing). Although no systematic road surveys were conducted, all staff members working at Park headquarters commuted from nearby villages into work on a daily basis along the main road, where they could spot roadkill of any species (although they probably paid more attention to colobus). Staff also monitored the road nearest to headquarters repeatedly during the day as they led groups of tourists around the area in search of colobus on both sides of the road. Dead colobus further away from headquarters were reported voluntarily and without reward by members of the public to Park staff. Based on descriptions of approximate locations in the notes, we estimate that roadkill was reported from a 3.40–6.54 km section of the road. Although all mammals were counted if found or reported, we assume that members of the public were more likely to report dead Zanzibar red colobus, rather than smaller mammals. In most cases of dead colobus, in addition to the date and location of the observation, the age class and sex were also noted. Records of individuals who may have been hit by a vehicle but did not die on the road were not available.

Rainfall data

To examine the association between roadkill frequency and monthly rainfall, we used estimates of daily precipitation for Jozani-Chwaka Bay National Park during January 2016–December 2019 (43 months). We obtained precipitation estimates from the NASA Langley Research Center's POWER Project, which uses satellite observations to model rainfall distribution across the world and has been validated in previous studies (White, *et al.*, 2011).

Demographic composition of roadside colobus groups

To examine if colobus of different age–sex classes were equally likely to die on the road as a result of vehicle collision, we compared the representation of these classes in the roadkill dataset to that in a census of groups near the road. Davenport, *et al.*, (2019) collected data on group size and composition during a census in the Park in 2014. Survey teams located colobus via a total sweep census and followed each group for 2–3 days to count all of its members and obtain data on its movement. Trained and experienced observers recorded age–sex classes with a high degree of inter-observer reliability (Davenport, *et al.*, 2019).

Based on the spatial data recorded while following these groups in 2014, and our knowledge of the distribution and movements of groups in the same area in 2018–2019, we selected 18 of the total 151 groups identified in the park by survey teams (Davenport et al., 2019) that met our definition of roadside groups. We considered roadside groups to be those that were observed within a 300 m perpendicular distance from the road on at least one occasion during the period when the group had been followed. Of these 18 groups, six were seen to cross the road and one came within 5 m of the road. For the remaining 11 groups, the mean minimum perpendicular distance to the road at which they were observed was 95 m (range: 17–217 m), and the mean furthest distance was 378 m (range: 221–590 m). Although ranging data for these groups were limited (52 group-follow days; two groups followed for 2 consecutive days; 16 for 3 days), given our knowledge of the area and of the species' ranging ecology, we considered all 18 groups to be roadside groups, with a reasonable likelihood of crossing the road. Groups that were observed further than 300 m from the road, although capable of crossing, are not likely to do so often, given the presence of other groups' home ranges between them and the road. Although Zanzibar red colobus are not strictly territorial and exhibit substantial intergroup home range overlap (Siex, 2003; Struhsaker, 2010), based on observations in eight groups ranging at various distances from the road over a 15-month period (Zanzibar Red Colobus Project, unpubl. data) we are reasonably confident our 300 m cut-off did not exclude any groups that crossed the road frequently. If anything, the 300-m threshold could include groups that were not very likely to cross the road. Thus, in addition to using the 18 groups as the baseline population to estimate vehicle collision mortality rates, we considered two more conservative definitions of roadside groups in our analyses. Firstly, we restricted the comparison to only the 13 groups that were observed within 100 m of the road, and secondly, we restricted the demographic dataset further to only those seven groups that ranged closest to the road (i.e. the six that were seen to cross it and the one that was recorded within 5 m of it).

Statistical analyses

We analysed data in *R* 3.6.1 (R Core Team, 2018). We tested the association between rainfall and roadkill frequencies with the Spearman rank correlation test. We compared the age–sex class composition of roadkill to the demography of the local population of colobus via Fisher's exact test (for sex class) and performed a likelihood ratio test for comparisons across the different age classes, using the *R* package *MASS* (Venables & Ripley, 2002).

Results

Over the 4-year study period (43 months of opportunistic data collection) we recorded seven mammal species as roadkill (Table 1). The majority (66%) of carcasses were of diurnal animals. Primates were recorded as roadkill most often, accounting for 83% of all deaths. Zanzibar red colobus were particularly common in the dataset, with 55% of all carcasses.

Table 1 Roadkill recorded along the main road near Jozani-Chwaka Bay National Park, Zanzibar (January 2016 – December 2019; n = 43 months of recording).

Species	Activity pattern	Total roadkill	Kills/month
Zanzibar red colobus <i>Piliocolobus kirkii</i>	Diurnal	29	0.67
Small-eared greater galago <i>Otolemur garnetti</i>	Nocturnal	13	0.30
Rats (Muridae)	Nocturnal	3	0.07
Bushy-tailed mongoose <i>Bdeogale crassicauda</i>	Nocturnal	2	0.05
Black & rufous elephant shrew <i>Rhynchocyan petersi</i>	Diurnal	2	0.05
White-collared guenon <i>Cercopithecus albogularis</i>	Diurnal	2	0.05
Squirrels (Sciuridae)	Diurnal	2	0.05
<i>Total</i>		53	1.23

On average, 1.23 carcasses were found on the road per month (range: 0–6). Mean monthly rainfall at the study site was 105 mm (range: 5–456 mm). Variance in rainfall, however, was unrelated to all-species roadkill frequency ($r_s = -0.248$, $n = 43$ months, $P = 0.109$; Fig.2).

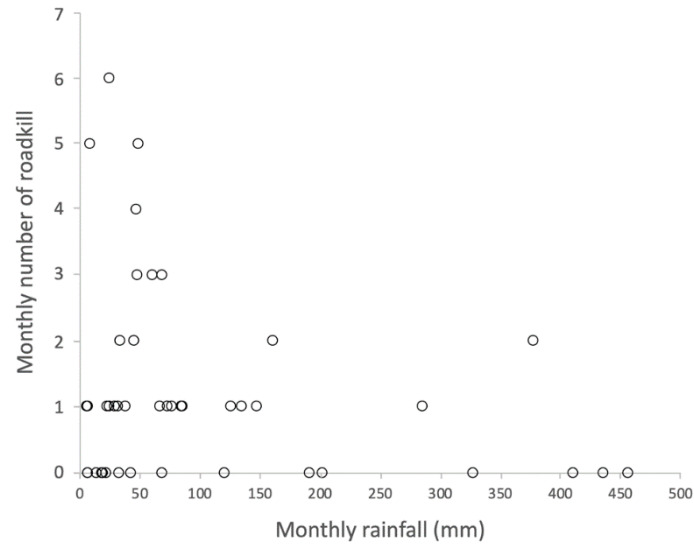


Fig. 2 Relationship between monthly rainfall at Jozani-Chwaka Bay National Park and mammalian roadkill frequency along the Jozani road (n = 43 months).

A mean of 0.67 Zanzibar red colobus carcasses were found on the road per month (range: 0–6). Rainfall was not related to the monthly frequency of colobus roadkill ($r_s = -0.128$, $n = 43$ months, $P = 0.412$). The ratio of adult female:male colobus in the roadkill dataset was 2.75, and in the 18 roadside groups it was 3.54 (Table 2). However, the proportion of males and females that were killed did not differ significantly from their proportion in the 18 roadside groups (Fisher's exact test: odds ratio = 1.287, $P = 0.750$). The proportions of different age classes in the roadkill dataset also did not differ from their expected values based on the demographic composition of the 18 roadside groups (likelihood ratio test: $\chi^2 = 5.302$, $df = 2$, $P = 0.071$; Table 2). Different age–sex classes were therefore equally likely to be found dead on the road, given their distribution in the local population. This result did not change across the different definitions of roadside groups we considered (Table 2).

Table 2 Annual mortality rate (%) of Zanzibar red colobus caused by vehicle collisions on the road intersecting Jozani-Chwaka Bay National Park, for three categories of colobus groups with different risks of collision (see Methods).

Age-sex class		Population estimates for groups observed at various distances from the road			Annual mortality % to vehicle collisions		
		18 groups (300 m from roadside)	13 groups (100 m from roadside)	7 groups (crossing or within 5 m of roadside)	18 groups (300 m from roadside)	13 groups (100 m from roadside)	7 groups (crossing or within 5 m of roadside)
Roadkill observed							
Adults by sex¹							
Adult females	11	209	167	106	1.32	1.65	2.59
Adult males	4	59	48	32	1.69	2.08	3.13
All individuals by age							
All adults	19	268	215	138	1.77	2.21	3.44
Subadult/juvenile	8	61	50	39	3.28	4.00	5.13
Infants	2	80	69	47	0.63	0.72	1.06
Total	29	409	334	224	1.77	2.17	3.24

¹The sum of adult females and adult males does not equal the number of adults in the roadkill data because some of the adults killed were not sexed.

To examine the overall impact of vehicle collisions on population-level mortality, we estimated annual mortality rates using the three subpopulations that we considered at risk (depending on the confidence in our estimation of their likelihood of crossing the road). If only the 7 groups nearest the road are taken into account, their annual loss to collisions is 3.24%. This number is lower (1.77%) if we consider all 18 groups within c. 300 m of the road to be at similar risk of collisions (Table 2).

Discussion

This is the first study to quantify the effects of vehicle collisions on mortality of the Zanzibar red colobus, an Endangered endemic primate. This dataset is an important contribution to the literature on road ecology more broadly, given the relatively low number of roadkill studies in the tropics, compared to the northern hemisphere (van der Ree, *et al.*, 2015; Monge-Nájera, 2018; Collinson, *et al.*, 2019a). Primates, and colobus in particular, were the most common species found as roadkill near Jozani-Chwaka Bay National Park. The number of primate deaths from collisions is likely an underestimate, however, as some individuals do not die on impact but survive long enough to move off the road, and others may be thrown off the road by the impact of the collision. The absolute number of non-colobus deaths is probably also an underestimate. Because the National Park and the tourism industry in the

area are focused on this charismatic primate species, other animals that die on the road may go unreported by members of the public. Our finding that diurnal species were more often killed on the road contradicts previous studies from other sites in Africa that reported a higher number of nocturnal animals amongst roadkill (Kioko, *et al.*, 2015; Njovu, *et al.*, 2019). This could be because of differences in habitats and species diversity but could also reflect methodological differences. Many previous studies have relied exclusively on early-morning road surveys to quantify roadkill, whereas our opportunistic records were not restricted to the early hours of the day. Up to 62% of carcasses on roads can be removed by scavengers in as little as 2 hours (Schwartz, *et al.*, 2018), so animals that die during the day may not remain there until the following morning.

Monthly variation in rainfall was not related to monthly roadkill frequency at Jozani, neither for all mammals nor for colobus. This suggests that, unlike in some other studies (e.g. da Rosa & Bager, 2012; Machado, *et al.*, 2015; Jeganathan, *et al.*, 2018; Njovu, *et al.*, 2019; Cunneyworth & Duke, 2020), precipitation may not influence mammal movements across the road or drivers' behaviour to the same extent here. Alternatively, it may be that our dataset underestimated roadkill frequency during the wet months of the year. As the records of roadkill were collected opportunistically by Park staff and/or reported by members of the public, it is feasible such monitoring was less extensive in wet weather. Future systematic roadkill surveys could address this question.

Contrary to our predictions, male and female Zanzibar red colobus were found dead on the road in similar proportions to their availability within roadside groups. Likewise, adults, subadults/juveniles and infants were observed as roadkill as often as expected. These findings mirror observations from Diani beach, Kenya, where no differences between Angola colobus *Colobus angolensis* age–sex classes involved in vehicle collisions were found (Cunneyworth & Duke, 2020). This suggests that the way Zanzibar red colobus cross the road does not expose any particular age–sex class to a significantly higher risk. Behavioural data on individual rates of crossing and collision risk would allow further tests of this hypothesis. The estimates of group demographics we used to calculate the mortality rates for colobus near the road may be biased in two ways. Firstly, data on group composition were collected in 2014, whereas data on roadkill were from 2016–2019. Secondly, in the demographic data

from 2014 we did not distinguish between subadults and juveniles. A similarly ambiguous classification of immature animals applies to the roadkill records. This is therefore an imperfect but nonetheless valuable preliminary analysis that can serve as a baseline for future, more detailed surveys of roadkill mortality in this species.

We estimated the annual loss of colobus to vehicle collisions to be 1.77–3.24% (depending on the baseline estimate for the population that is at risk; Table 2). To put this figure into context, data on mortality rates from natural predators could be informative. The Zanzibar red colobus experiences very limited natural predation at Jozani. The Zanzibar leopard *Panthera pardus adersi* is probably extinct (Goldman & Walsh, 2002) and there are no crowned eagles *Stephanoaetus coronatus* (Struhsaker, 2010) in Zanzibar. The main predatory threat to the species are therefore feral/village dogs (Georgiev, *et al.*, 2019) and people (Davenport *et al.*, 2019), but reliable data for estimating the magnitude of these sources of mortality are unavailable. Data on natural predation on wild primates are generally difficult to obtain and are available from only a few long-term studies of individually recognized primates. One review of primate predation across species and study sites estimated annual mortality from predation to be 0–15% (Cheney & Wrangham, 1987). More recent studies have shown that under exceptional circumstances predation rates can be higher (e.g. 40–50% of red colobus killed by chimpanzees at Ngogo, Uganda; Teelen, 2008), but mean predation rate across species, populations and habitats has been estimated to be c. 6% (Cheney & Wrangham, 1987). Our highest estimate of 3.24% annual road mortality for the Zanzibar red colobus, therefore, falls within the lower range of mortality rates experienced by different primates from natural predation, and is higher than natural predation mortality for some red colobus populations elsewhere. For example, at Mahale, Tanzania, in some years annual predation loss has been estimated to be as low as 1.1–1.3% (Boesch, *et al.*, 2002). Unlike natural predators, which may predominantly kill animals in poorer condition, vehicles remove individuals from a population without regard to their condition or health (Bujoczek, *et al.*, 2011). In addition, even non-lethal collisions can have a negative impact on animals via increases in glucocorticoid production (Narayan, 2019) and non-lethal injuries. Taken together, the direct and indirect consequences of colobus–vehicle collisions could lead to suboptimal population health that could contribute to reduced persistence of roadside groups.

To assess whether roadkill mortality would contribute to a population decline near the roads and lead to roadside habitats becoming a population sink, we need longitudinal demographic data on birth rates, natural mortality rates and rates of migration between groups. Such high-quality longitudinal data do not currently exist for the Zanzibar red colobus. However, by using estimates of birth rates and interbirth intervals from a previous study of the same population (Siex & Struhsaker, 1999) we can provide a tentative assessment. Siex & Struhsaker (1999) estimated an interbirth interval of 27.9 months in the groups in the study area, which equals a birth rate of 0.43 infants/female/year. Using this estimate, and our demographic data for the three categories of groups at various distances from the road (Table 2) we can calculate an annual population increase via births of 27.32, 27.10 and 25.75% (mean = 26.72%), respectively. Using our group composition data to estimate population increase as the percentage of infants present during a census from the total number of non-infant individuals observed during census (adults and juveniles/subadults), we obtained the following estimates of annual increase for our three categories of roadside groups: 24.32, 24.04 and 26.55% (mean = 25.64%). These estimates are similar to the numbers based on the interbirth interval estimation of Siex & Struhsaker (1999). Despite the inherent uncertainty of estimates produced via such indirect calculations, this does suggest that the current annual roadkill mortality rate of 1.77–3.24% is probably offset by annual population growth, estimated here by two methods to be 24–27%. Longitudinal demographic data are required to produce a more robust assessment of population viability for the Zanzibar red colobus populations living at risk of colliding with vehicles, particularly as there are no data to provide an estimate of annual mortality rates from natural causes.

In line with observations elsewhere (e.g. Drews, 1995), after the Jozani road was tarmacked in 1996, vehicles started travelling at greater speed and roadkill became a more common problem (Struhsaker & Siex, 1998). National Park staff at the time suggested that a colobus may be killed every 2–3 weeks (*ibid.*). Struhsaker & Siex (1998) estimated, based on a population of 150 colobus exposed to the road, that 12–17% were lost to road accidents per year. By comparison, our data show lower mortality in 2016–2019: one colobus fatality occurred nearly every 6 weeks and we estimate an annual mortality loss of 1.77–3.24% (Table 2). Changes in population size and group ranging patterns in the 20 years that separate these estimates may account for the difference in mortality rates. A major factor, however, has been the installation of four speedbumps and colobus-crossing warning signs near the

main entrance of the park. These interventions reportedly achieved an 80% reduction in mortality in the years after they were implemented (T. Struhsaker, pers. comm. in Epps, *et al.*, 2015). Based on a mean estimated annual mortality before the speedbumps were installed of 14.5%, a relative reduction of 80% would have resulted in an estimated annual mortality of 2.9% after the installation of the speedbumps. This figure lies within our mortality estimates of 1.77–3.24% for 2016–2019, showing that in the years since the speed bump installation mortality rates have probably remained stable. As these speedbumps only cover c. 600 m of the road that intersects colobus ranges, extending the speedbump zone along the entirety of the road that lies within the known range of colobus at Jozani (c. 1.8 km) would probably bring further reductions in roadkill.

In estimating the potential mitigation effects on colobus roadkill, a comparison with a different site is helpful. At Jozani, we report 0.67 Zanzibar red colobus deaths per month over a maximum of 6.4 km of road. Angolan colobus at Diani Beach, Kenya, are involved in vehicle collisions at a rate of 0.67 individuals per month. With a reported fatality rate of 83% across the four primate species studied at that site (Cunneyworth & Duke, 2020) a mean of 0.56 colobus die per month along the 10 km road at Diani (i.e. 60% of the colobus deaths per km of road observed at Jozani: 0.1 at Jozani vs 0.06 at Diani). The lower rate of colobus roadkill per km of road at Diani is probably a result of a greater extent of road mitigation measures. Diani has 10 speedbumps and 29 wildlife bridges, whereas Jozani has only four speedbumps and one wildlife bridge. Direct comparison of colobus group crossing rates and frequency of collision per crossing event between these two sites would help establish if the higher fatality rate at Jozani could be further reduced by additional road mitigation measures. One successful strategy for reducing primate roadkill at some sites has been the use of wildlife bridges (Valladares-Padua, *et al.*, 1995; Mass, *et al.*, 2011); Leen, *et al.*, 2019; Linden *et al.*, 2020). Bridges are particularly beneficial for arboreal species within a suitable surrounding environment, where the animals approach roads through the canopy (Birot *et al.*, 2019; Leen *et al.*, 2019). If arboreal primates are moving on the ground, however, they are unlikely to ascend a bridge to cross a road; they tend to continue crossing terrestrially, even if bridges are available (Jacobs, 2015). The roadside environment at Jozani is mostly unsuitable for wildlife bridges suspended between trees, and the colobus often approach roads on the ground from agricultural land or from low-height canopy. Considering this, the colobus at Jozani would probably continue to cross terrestrially even if more wildlife bridges

were built. Speedbumps, which are unlikely to be ignored by drivers (Schutt, 2008) may be the most appropriate solution for sites such as Jozani, similar to recommendations made elsewhere for chimpanzee crossings (McLennan & Asiimwe, 2016). Complementing this approach with additional, less costly, interventions can also be beneficial. Warning signs with photographic images of animals, placed near roadkill hotspots, can lead to additional reductions in roadkill by altering driver behaviour over short distances (Collinson *et al.*, 2019b). Although such mitigation measures can become less effective as drivers habituate to them, they can still be effective for visitors (Huijser, *et al.*, 2015). Updating the roadside signage more frequently with visually captivating images of colobus in their natural habitat may serve the dual purpose of both preventing driver habituation and attracting more tourists to the area by highlighting the ecotourism opportunity. Some colobus groups elsewhere on the island also inhabit areas where roads intersect their home ranges (Davenport, *et al.*, 2019). Identifying roadkill hotspots outside the immediate area of Jozani-Chwaka Bay National Park and implementing road mitigation measure may contribute to efforts to slow the population decline of this primate throughout its range.

Proactive road mitigation measures may be particularly relevant as road networks in Africa are projected to increase by 60% between 2000–2050 (Dulac, 2013). The continued growth of the tourism industry, with its demand for quick, easy and efficient travel (Khadaroo & Seetanah, 2008), will worsen the already serious issue of wildlife–vehicle collisions (Caro *et al.*, 2014). Understanding the impact of roads on animal populations and the most effective way to counteract them will be crucial in achieving a balance between the demands of economic development and wildlife conservation.

Chapter 3: Zanzibar red colobus monkeys do not show differential risk awareness when crossing roads that differ in likelihood of primate-vehicle collisions

Abstract

Behavioural plasticity is an important mechanism for wildlife to mitigate against negative anthropogenic disturbances. Behavioural responses to human activity have been exhibited in most vertebrate taxa, with responses to light and noise pollution as well as hunting being particularly well documented. However, few studies have explored the behavioural response to the risk of crossing roads, despite significant wildlife mortality occurring on roads around the world. Examining whether wild animals are able to adjust their behaviour when dealing with such evolutionarily unfamiliar risks in novel anthropogenic landscapes is important when assessing the ability of populations to persist in rapidly changing landscapes. To assess the ability of a forest-specialised primate to perceive the risk of wildlife-vehicle collisions and adjust its behaviour accordingly, I examined 45 crossing events by two groups of Zanzibar red colobus, *Piliocolobus kirkii*, (comprising 473 individual monkey crossings). I tested if colobus were able to perceive risk variance associated with crossing two roads that differed in traffic speed and frequency and thus their associated risk of primate-vehicle collisions at Jozani-Chwaka Bay National Park, Zanzibar, Tanzania. I quantified three behavioural indicators of risk awareness from video recordings: hesitancy to cross, crossing time, and mid-road sitting occurrence. Analyses of these metrics suggest that colobus did not seem to perceive the difference in risk when crossing a busy tarmac road (where they are sometimes hit and killed by vehicles) versus a quieter dirt road (where no known collisions or deaths have been reported or observed). Experience with roads (age class) did not affect colobus wariness when crossing. Females, in general, however, appeared warier when crossing roads than males, and females with infants were warier than females without. This suggests that females, and those with infants, in particular, are more risk averse, relative to males. Despite this, previous studies at the same location show that Zanzibar red colobus females are killed on the tarmac road as frequently as males, given their availability in the population, suggesting that ‘wariness’ alone is not sufficiently effective in reducing relative female mortality on the road. These findings underline the importance of pro-active risk mitigation by conservationists and wildlife managers. Constructing speed-bumps and erecting warning signs along busy roads that intersect primate habitats, for example, would alleviate some of the risk many species face from fatal collisions with vehicles.

Introduction

Humans are rapidly changing landscapes globally, through infrastructural development, settlements, and agricultural expansion, and almost all organisms reside in environments affected by anthropogenic disturbance (Sih, et al., 2011). An important mechanism that animals use to cope with and adapt to novel anthropogenic conditions is behavioural plasticity (López-Sepulcre & Kokko, 2012) with behavioural adaptations often being the first to occur (Thieltges & Poulin, 2008; Hart, 2011; Blix 2016). The most common behavioural responses to anthropogenic disturbance are changes to habitat choice, movement, foraging, social and reproductive behaviours (Tuomainen & Candolin, 2011). Evidence of the ability of animals to respond to changes in risk due to anthropogenic disturbance have been well document in multiple studies for many species (Bunnefeld, *et al.*, 2006; Lone, *et al.*, 2015; Suscke, *et al.*, 2020).

The degree to which behavioural responses to risk are present and appropriate to the specific context amongst species can be, at least partly, explained by variation in brain size, given that larger brains, relative to body size, are associated with greater problem-solving ability (Benson-Amran, *et al.*, 2016). In support of this idea, mammals with greater relative brain size are more successful at establishing lasting populations when introduced into novel environments (Sol, *et al.*, 2008). Primates have the largest brains relative to body size among mammals (Clutton-Brock & Harvey, 1980; Whiten & Byrne, 1997; Burger, *et al.*, 2019) so would be predicted to be particularly adept at dealing with novel risks in their environments. The fact that over 60% of primates worldwide are threatened with extinction and over 70% have declining populations (Estrada, *et al.*, 2017), however, also shows there are limits to such plasticity.

One particular risk that would require a rapid behavioural response is associated with roads intersecting primate habitats and the risk of primate-vehicle collisions. Studies of roadkill in the tropics suggest that primates could be at a particularly greater risk from negative effects of roads as species with lower reproductive rates, later sexual maturity and longer generation times will not be able to recover from population declines quickly (Rytwinski & Fahrig, 2012, González-Gallina, *et al.*, 2013; Balčiauskas, *et al.*, 2020). Most primate road ecology studies to date have focused on roadkill patterns and explaining the variation in their

frequency and contributing factors (Kioko, *et al.*, 2015; McLennan & Asiimwe, 2016; Cunneyworth & Duke, 2020; Olgun, *et al.*, 2022). By contrast, studies of the possible behavioural mitigation strategies that primates may adopt for avoiding being killed on the roads are still rare. This is an important omission given the growing recognition of the role that anthropogenically modified habitats will have for the long-term survival of species (Bryson-Morrison, *et al.*, 2017; de Almeida-Rocha, *et al.*, 2017). The responses to vehicles vary greatly between taxa. Most manatee species are often seen to be unresponsive to vehicles, however, Florida manatees (*Trichechus manatus*) do use avoidance tactics, such as quicker movement or retreating to lower depths of water, although not related roadkill, boats are still vehicles posing risks to marine life (Miksis-Olds, *et al.*, 2007). Similarly, birds found close to roadsides are seen to avoid and disperse when vehicles approach (Lima, *et al.*, 2015). Amphibians and reptiles are seen to actively increase their risk of vehicle collisions through their behavioural responses, where they freeze in position, likely due to their predators often being motion sensitive (Mazerolle, Huot & Gravel, 2005). These responses suggest that there is limited capability in mitigating against the dangers from vehicles, likely due to the cognitive ability of species where we see species with higher cognitive ability, such as dolphins, showing greater capability in their behavioural plasticity to mitigate against the risk from vehicles (Lima, *et al.*, 2015). Studies of how primates tackle road crossings can offer unique insight into the capacity of species for behavioural plasticity, as well as to allow the design of more effective mitigation strategy aimed at reducing the risk of primate-vehicle collisions.

The existing literature on primate road ecology provides some evidence that primates can exhibit behavioural plasticity to mitigate against anthropogenic risks. For example, in areas where wildlife bridges have been erected, bridge-naïve populations start using them to avoid crossing roads terrestrially (Teixeira, *et al.*, 2013; Birot, *et al.*, 2020; Chan, *et al.*, 2020). Studies of two chimpanzee populations, in Guinea and Uganda provide additional insight (Hockings, *et al.*, 2006; Hockings, 2011; Cibot, *et al.*, 2015). Hockings, *et al.* (2006) found that chimpanzees showed defensive spatial positioning of group members and increased vigilance, and also travelled faster on roads than inside the forest. Cibot, *et al.* (2015) also found evidence of behavioural adaptations to road-crossing: chimpanzees showed increased vigilance when crossing a tarmacked road and healthier individuals led group movement across the road more often than when climbing or descending feeding trees. These

chimpanzee studies, however, are the only ones to date to provide detailed analysis at the individual level demonstrating that primates can and do change their behaviour to mitigate the risk of crossing roads. Whether other primate species, that may lack the cognitive abilities and behavioural plasticity of great apes, employ similar tactics in anthropogenically-altered environments in relation to road-crossing remains to be established.

I studied the Zanzibar red colobus (*Piliocolobus kirkii*) to investigate the degree of behavioural plasticity that may help mitigate increased mortality risk that roads impose on these monkeys. The ecological intelligence hypothesis suggests that specialised folivores such as colobus may lack the cognitive abilities of other primates such as frugivorous chimpanzees (Deaner, *et al.*, 2007; DeCasien, *et al.*, 2017). Behavioural responses of colobus in other contexts support this notion. For example, when red colobus are hunted by chimpanzees, they occasionally stand their ground against these much larger predators (Watts & Mitani, 2015) rather than flee away through the canopy, a strategy that is not always successful, suggesting an inability to optimally resolve this issue. However, few if any studies have tested the intelligence and problem-solving abilities of colobines, which limits the conclusions we can draw from observational studies of predator-prey interactions such as this. In favour of the Zanzibar red colobus being potentially able to adjust to the risks of crossing roads is the observation that unlike other species of red colobus (e.g., Ugandan red colobus: *P. tephrosceles*, Chapman, *et al.* 2013) *P. kirkii* seem to be able to survive in areas of relatively high anthropogenic disturbance even after their native forests have been partially or fully felled (Davenport, *et al.* 2019) with some groups' home ranges encompassing even coastal villages that are highly developed for tourism (Zanzibar Red Colobus Project, unpublished data). Other examples of behavioural plasticity exhibited by this species include their incorporating diverse and exotic plant foods into their diet, depending on local food availability in their respective habitats (Siex & Struhsaker, 1999; Nowak & Lee 2013). In rural agricultural landscapes, they even adopt charcoal-feeding for its putative digestion-enhancing qualities when feeding on exotic tree leaves rich in antifeedants (Struhsaker, *et al.* 1998). Whether such dietary behavioural plasticity translates to other domains and could thus help the colobus mitigate the high-risk situations of road crossing, however, remains an open question.

To examine whether Zanzibar red colobus are engaging in behavioural risk-mitigation when crossing roads, I observed groups of colobus at Jozani-Chwaka Bay National Park (JCBNP), a site with a documented frequencies of colobus road mortality. Early data before speed bumps were constructed on the tarmac road intersecting the colobus habitat suggest that 17% of the roadside population at the time were killed annually (approximately 1 colobus every 3 weeks) (Struhsaker & Siex, 2008). More recent data highlights the effectiveness of the speedbumps in reducing colobus mortality to about 3.2% of the current roadside population per year (approx. 1 colobus every 6 weeks) (Olgun, et al., 2022). The colobus in this area cross two roads which differ in their structural characteristics and traffic flow, thus posing distinct risk levels of primate-vehicle collision. The main tarmac road is where all documented colobus mortalities occur (Olgun, et al., 2022). Despite the presence of speed bumps in some sections, which reduce the speed of vehicles and thus the risk of fatal collisions, colobus also frequently cross in sections of the road without speed-bumps. The dirt road, on the other hand is of such poor quality that the cars that pass along it (almost all tourist vehicles on the way to see a mangrove boardwalk south of JCBNP) travel at low speed and thus pose little threat to any crossing monkeys. If colobus were able to distinguish the different risk levels that crossing the two roads posed, I predicted that they should exhibit different crossing strategies. I examined this question at two levels – group and individual. Specifically, I predicted that at the group level: (P1) groups would cross the tarmac road at a faster rate (colobus/minute) than the dirt road, and that (P2) smaller groups would cross both roads (but especially the tarmac one) at a faster rate than large groups. At the individual level I predicted that individuals crossing the tarmac road vs. the dirt road, would exhibit: (P3) greater hesitancy to cross, (P4) faster speed of crossing (m/sec), and (P5) lower frequency of stopping mid-road.

I first tested these predictions across all individuals (adults and immatures) but to further probe whether age-sex classes may differ in their level of risk-awareness and behavioural adjustment I also tested the following predictions: (P6) females would exhibit greater risk awareness than males, (P7) adults would exhibit greater risk awareness than immatures; and that (P8) females with clinging offspring would exhibit greater risk awareness than females without.

Methods

Study site

I studied colobus road-crossing behaviour at Jozani-Chwaka Bay National Park (JCBNP) on Unguja Island, Zanzibar (Fig. 1). At the southern edge of JCBNP a major road intersects the home ranges of at least 7 groups (Olgun, *et al.*, 2022). This is a busy tarmac road that connects the east-coast tourist areas to the capital and international airport on the west coast. At the entrance to the national park, a smaller dirt road intersects this major road, as well as the home range of several colobus groups. The roads differ in size, with the tarmac road at an average of 6.44 metres in width and the smaller dirt road is an average 4.25 metres in width.

This part of the national park comprises of a mixture of habitats: groundwater and mahogany forest, as part of JCBNP, but also extends outside of this forest (Siex, 2003; Siex & Stuhsaker, 1999). Colobus groups travel into coral rag forest, salt pans, mangroves, agricultural matrixes, low-canopy secondary forest, and agricultural land. Agricultural habitat in this area is intensely used by humans.



Figure 1 Study site location on Unguja Island, Zanzibar, and the approximate home ranges of two main study groups (95% kernel polygon) at Jozani-Chwaka Bay National Park, Zanzibar.

Study subjects

This study focused on two colobus groups that ranged across both the tarmac road and the dirt road within the study area: ‘Baobab Group’ and ‘Camp Group’. The study was conducted during two research trips over a two-year period (July-September 2019 and February-March 22) as part of the Zanzibar Red Colobus Project (<https://www.zanzibarredcolobusproject.org/>). Changes in group size and composition reflected births, deaths via road collisions, or possible immigration/emigration events. (Table 1).

Table 1. Group composition of groups during the study.

	July – September 2019				February – March 2020			
Group	Adult males	Adult females		Immatures	Adult males	Adult females		Immatures
		Total	W/ clinging infant			Total	W/ clinging infant	
Baobab	3	11	1	2	3	7	4	7
Camp	4	22	2	9	4	14	4	13

Both groups were well habituated to human observers, as they are frequently visited by tourists for primate-watching walks at Jozani-Chwaka Bay National Park (Saunders 2011; Warkentin 2019). One of the groups, ‘Baobab Group’, ranged almost entirely in anthropogenically-modified landscapes, whereas ‘Camp Group’ shared its time between disturbed habitats and the core forest of JCBNP.

Behavioural observations

I followed the colobus on 20 observation days, 10 full-day follows with each study group (15th July – 24th September 2019; 4th February – 19th March 2020) within both study periods for a total of 198 hours. Road-crossings were recorded continuously. Observations usually started at or near the colobus sleeping site or wherever they were found in the morning, if their sleeping site was not known from the previous day (median start time = 07:30 h, range 07:00 – 09:30 h), and ended in the afternoon/evening as they settled in their sleeping trees or contact with the group was lost (median end time = 18:07 h, range 14:30 – 18:45 h). During these full-day follows, 35 group road-crossing events were recorded on 11 different days. A further ten crossing events were recorded opportunistically (i.e., were not part of full day follows), bringing the total number of crossing events analysed to 45. Most crossing events were recorded on video, often with supplementary narration for context, resulting in 315 minutes of video footage. All time-based behaviours were scored to the nearest second from video footage. Fifteen crossing events in the dataset were recorded by pen and paper in the field and so yielded less detailed data than those recorded on video. A group crossing event began when the first colobus entered the road and ended once all group members were on the same side of the road. Sometimes individuals crossed multiple times per crossing event. One individual therefore could contribute multiple individual crossing datapoints per group-level

crossing event. The group-level crossing event was only completed after individuals stopped crossing altogether and were on the same roadside.

For each group-level crossing event, I recorded the following variables. Firstly, I recorded the road type (tarmac or dirt) and the group identity (Baobab group or Camp group). I also noted the start and end time of the full group crossing, as well as the number of individuals that crossed to calculate the rate of crossings (colobus/minute), allowing for comparison between groups of different size. At the individual level, I recorded the age and sex class of each crossing monkey as adult male, adult female (with or without clinging infants) or immature (infant or juvenile of unknown sex crossing the road independently) based on size and maturity. Subadults, were classed as 'adults' based on size.

Behavioural Variable Construction

I calculated three behavioural metrics that I interpreted as indicators of risk awareness when crossing roads. First, I quantified the frequency of hesitation to cross at the edge of the road, defined as a pause between the moment an individual approached the road and when the colobus started to cross, without engaging in other behaviours in the meantime. Second, I calculated individual crossing speed in metres/second, accounting for the different widths of the two roads (6.44 metres for the tarmac road and 4.25 metres for the dirt road). I recorded individual crossing time as the time between the first limb making contact and final limb breaking contact with the road (in seconds) and then divided road width by this time to calculate speed. The speed of crossing calculated in this manner incorporates differences resulting from some colobus taking a longer route to cross the road than the perpendicular, shortest path and/or the time they spent sat on the road while crossing it. Third, I specifically quantified mid-road sitting occurrence (presence/absence), defined as the monkey making physical contact of the buttocks with the road and resting on it for any period of time.

Statistical Analysis

All analyses were performed in RStudio version 1.2.5019 (R Core Team, 2020) using the `lmerTest` function from the `lmerTest` package for mixed models (Kuznetsova & Brockhoff,

2017). I tested for differences between groups in crossing rates and in relation to road type with a Mann-Whitney U test.

To test our predictions regarding risk awareness at an individual level, I constructed a series of linear mixed-effects models. Sample size differs for each of the three metrics (hesitancy before crossing, crossing speed, and mid-road crossing occurrence) because not all variables were measurable for all individual crossing events. Each of the three sets of models included road type to test the prediction that when crossing the main tarmac road, monkeys would show greater risk awareness. To examine individual risk awareness variation, I analysed differences between adult and immature monkeys, differences between adult males and adult females, and differences between adult females without dependent offspring and mothers with clinging infants. In total I ran 9 models (3 risk awareness metrics x 3 paired comparisons) due to limitations of sample size and the structure of the dataset. Group-level crossing event identity was included as a random effect in all models. Crossing colobus were not always identifiable as individuals in the field or from video footage, so I could not account statistically for repeated observations of the same individual. Individual crossing speed (m/s) was log-transformed to meet model assumptions for models testing individual crossing speed. Hesitancy occurrence and mid-cross sitting occurrence (both scored as 0/1) were analysed with binomial regression models. The fit of the global models as described above (containing all fixed and random effects) was compared against their null equivalents (only random effect: crossing event ID) with maximum likelihood estimation via the likelihood ratio test. Parameter estimates and significance of predictors in the full models that provided a significantly better fit to the data than the null model were produced with restricted maximum likelihood estimation. Model assumptions were verified by visual inspection of residual plots, residual histograms, QQ plots and PP plots. Variance inflation factors (VIFs) obtained via the vif function of the car package (Weisberg, 2019) confirmed multicollinearity was not an issue in the models (all VIFs <2). It should be noted that within the individual level analysis, due to the difficulty of identifying each individual and therefore this not being possible, there is pseudo-replication within the data which cannot be controlled for when using mixed-models.

Results

I recorded 45 group crossing events, containing a total of 473 individual colobus crossings (Table 2).

Table 2. Number of colobus crossings recorded and analysed for each road type and group considered at both the group (full group crossing events) and individual (individual monkey crossings) levels.

Road Type	Crossing Events		Individual Crossing	
	Camp Group	Baobab Group	Camp Group	Baobab Group
Dirt	2	15	28	120
Tarmac	4	24	94	231
Total	6	39	122	351

Road-crossing at the group level

For analysis on road-crossing at the group level, when comparing the two groups, I only considered tarmac road crossings as the larger group crossed the dirt road very rarely ($N = 2$ for the larger group vs $N = 15$ for the smaller group) and the sample size was not large enough for meaningful analyses. Groups took between 1 minute and 108 minutes 35 seconds to cross the tarmac road fully (mean = 22 minutes and 42 seconds ± 0.19 s). The mean \pm SE crossing rate for each road crossing is one colobus per 70 ± 8.4 s. However, when analysing road-crossing against road type, I grouped both Camp group and Baobab group data to allow a comparison against the two road types. There was no significant difference in group crossing rates between the two road types (tarmac = one colobus per 69 ± 11.4 s vs. dirt = 73 ± 11.4 s; $W = 144$, $N_{\text{tarmac}} = 28$, $N_{\text{dirt}} = 17$, $P = 0.807$). There was no significant difference in crossing rates between the two groups (Camp group = one colobus per 101 ± 18.6 s vs. Baobab group = 61 ± 13.2 s; $W = 16$, $N_{\text{Camp group}} = 4$, $N_{\text{Baobab group}} = 24$, $P = 0.12$). The prediction that colobus groups crossed the riskier tarmac road at a faster rate than the less risky, dirt road was not supported. Neither was the prediction that the smaller (Baobab) group would show a higher crossing rate than the larger (Camp) group.

Road-crossing at the individual level

Hesitancy to cross

Colobus hesitated to cross a road in 22.8% of individual crossing events (N =149 individual crossing events, for which hesitancy occurrence could be established) (Table 3). Hesitancy to cross occurred in 21% of tarmac road crossings and in 23.3% of dirt road crossing. Hesitancy to cross was observed in 28.6% of male crossings and in 20.4% of female crossings. None of these differences were, however, significant as the full model incorporating road type and sex did not provide a significantly better fit to the data than the null model (Model 1: $AIC_{null} = 129.73$, $AIC_{full} = 132.21$, $\chi^2 = 1.516$, $P = 0.469$). There was no significant difference in hesitancy occurrence between age classes either (immatures = 37.5%, adults = 22%). Road type had no significant effect in this analysis either (tarmac = 21.6% and dirt = 24.6%), as the full model incorporating age category and road type did not provide a significantly better fit to the data than the null model (Model 2: $AIC_{null} = 140.3$, $AIC_{full} = 142.54$, $\chi^2 = 1.757$, $P = 0.416$). When considering females, those with clinging infants showed hesitancy before crossing significantly more often than females without infants (females with clinging infants = 32%, females without = 17%; Fig. 3) but effect of road type on hesitancy occurrence in this comparison (tarmac = 18.8% and dirt = 22.5%) was also not significant (Model 3; Table 4). Our predictions that females with clinging offspring would show greater hesitancy occurrence than females without was thus supported, although our predictions about the effects of sex, age and road type were not supported.

Table 3. Total number of observations of hesitancy occurrence before crossing the road for each sex, age and presence of clinging offspring class analysed.

Hesitancy occurrence before road crossing									
Road type	Sex (Model 1)			Age Class (Model 2)			Presence of clinging infant (Model 3)		
	Male	Female	Total	Adult	Immature	Total	AF W/I	AF	Total
Dirt road	11	49	60	60	1	61	7	42	49
Tarmac road	17	64	81	81	7	88	18	46	64
Total	28	113	142	141	8	149	25	88	113

AF W/I = Adult female with clinging infant; AF = Adult female without a clinging infant.

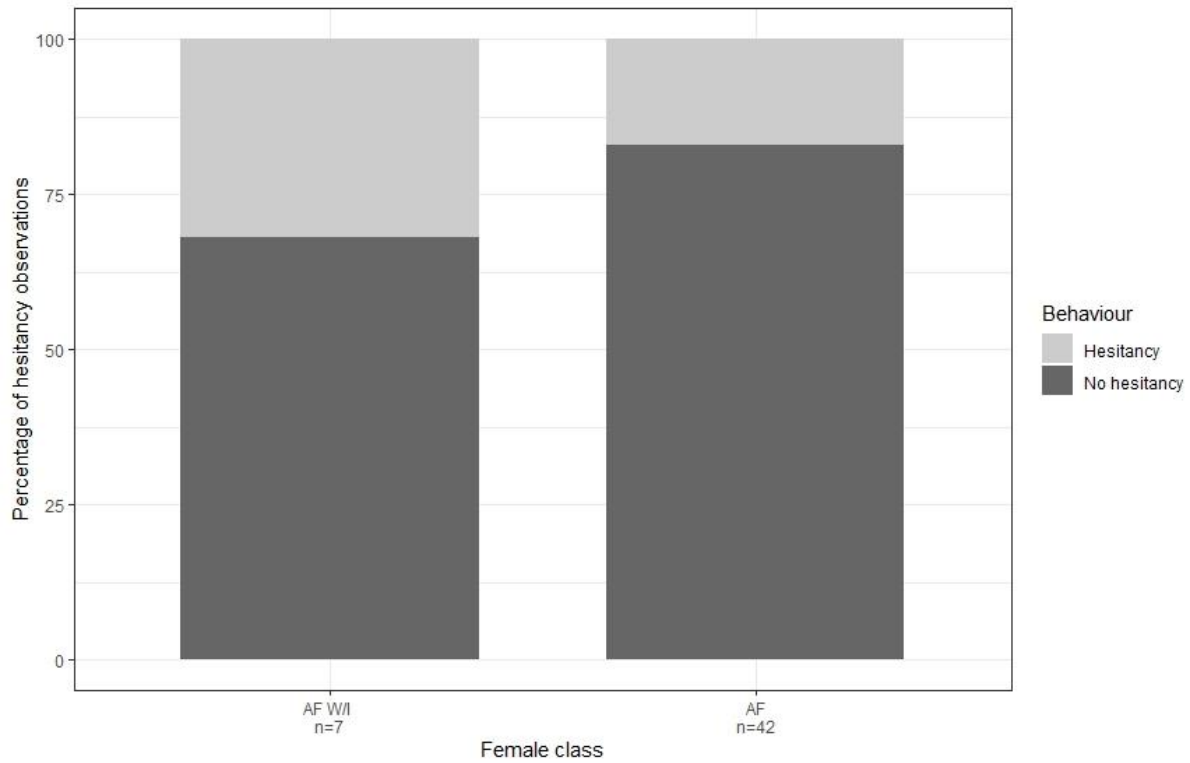


Fig 3. Hesitancy occurrence before road crossing for adult females with infants (AF W/I) and adult females without infants (AF).

Table 4 Linear mixed-effects model output for factors predicting variation in female class hesitancy occurrence.

Model 3: Effect of the presence of clinging offspring on hesitancy occurrence before road crossing				
Likelihood ratio test:				
AIC Null	AIC Full	X ²	p	
93.90	91.52	6.379	0.041	
Full model output:				
	Estimate	Std. error	Z value	P
Intercept	-5.980	3.279	-1.824	0.068
Female class (with infant)	2.756	1.305	2.111	0.035
Road (tarmac)	-2.559	2.052	-1.247	0.212

Crossing speed

Colobus crossed roads with a mean speed of 2.25 ± 0.68 m/s (N = 214 individual crossings for which speed was measurable) (Table 5). Males crossed the road significantly slower than females (males = 1.50 ± 0.18 ; females = 2.43 ± 0.14 m/s; Fig. 4) but effect of road type on crossing speed (tarmac = 2.33 ± 0.17 and dirt = 2.08 ± 0.16 m/s) was not significant (Model 4; Table 6; Figure 4). There was no significant difference in crossing speed between age classes (immatures = 2.61 ± 0.36 m/s, adults = 2.23 ± 0.12 m/s). Road type had no significant

effect in this analysis either (tarmac = 2.33 ± 0.16 and dirt = 2.13 ± 0.16 m/s), as the full model incorporating age category and road type did not provide a significantly better fit to the data than the null model (Model 5: $AIC_{\text{null}} = 611.77$, $AIC_{\text{full}} = 611.45$, $\chi^2 = 4.321$, $P = 0.115$). There was no significant difference in crossing speeds between females with clinging infants and females without (with infant = 2.70 ± 0.33 m/s, without = 2.37 ± 0.16 m/s). Road type had no effect in this analysis either (tarmac = 2.65 ± 0.21 and dirt = 2.15 ± 0.18 m/s), as the full model incorporating female class category and road type did not provide a significantly better fit to the data than the null model (Model 6: $AIC_{\text{null}} = 418.49$, $AIC_{\text{full}} = 420.49$, $\chi^2 = 2.008$, $P = 0.367$). Our predictions that females would cross the roads faster than males was supported, although our predictions for the effects of age, presence of clinging offspring and road type were not supported.

Table 5. Total number of observations of crossing speeds for each sex, age and presence of clinging infant class analysed.

Road crossing time observations									
Road type	Sex (Model 4)			Age class (Model 5)			Presence of clinging infant (Model 6)		
	Male	Female	Total	Adult	Immature	Total	AF W/I	AF	Total
Dirt road	16	68	84	84	5	89	8	60	68
Tarmac road	29	88	117	117	8	125	24	63	87
Total	45	156	201	201	13	214	32	123	155

AF W/I = Adult female with clinging infant; AF = adult female without a clinging infant.

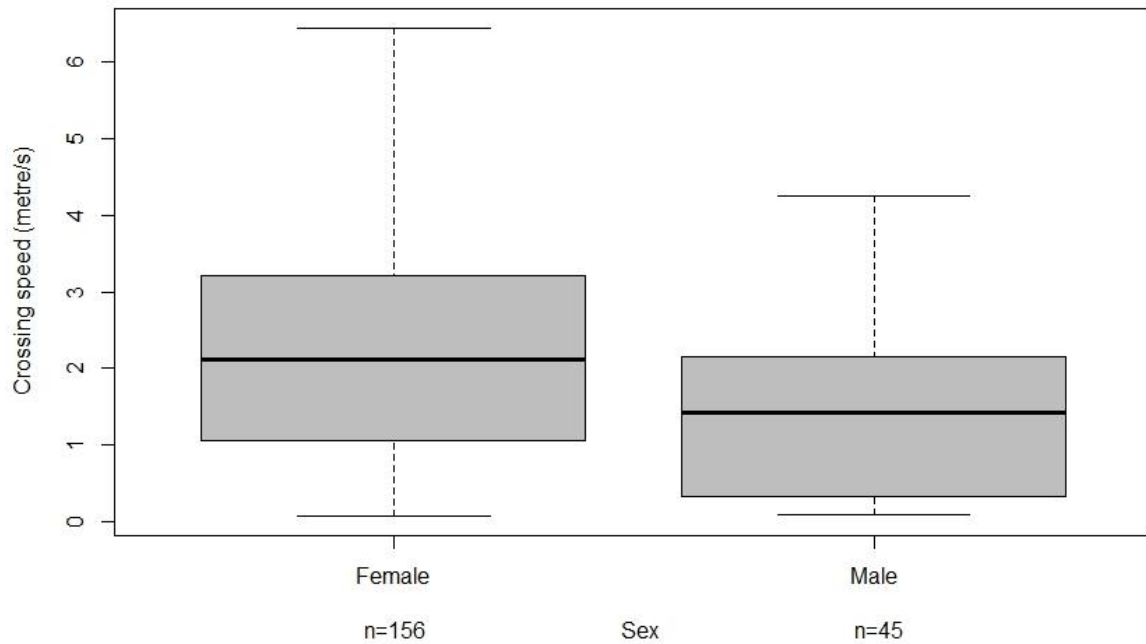


Fig 4. Road crossing speed of adult females and adult males

Table 6. Linear mixed-effects model output for factors predicting variation in adult crossing speeds.

Model 4: Sex differences in road crossing time (N male = 45, N female = 156 crossings).					
Log-likelihood ratio test:					
AIC Null	AIC Full	χ^2	P		
581.01	565.68	19.338	< 0.001		
Full-model output:					
	Estimate	Std. error	DF	T-value	P
Intercept	0.933	0.130	29.319	7.206	< 0.001
Sex (male)	0.641	0.162	187.488	3.949	< 0.001
Road (tarmac)	0.305	0.165	25.940	1.843	0.077

Sitting occurrence

Colobus sat on the road mid-crossing in 16.5% of individual crossing events (n = 230 individual crossing events, for which sitting occurrence could be established) (Table 7). Male crossing events showed sitting occurrence significantly more often than female crossing events (males = 38.3%, females = 10.5%; Fig. 5) but effect of road type on sitting occurrence

(tarmac = 20%, dirt = 10.8%) was not significant (Model 7; Table 8; Figure 6). There was no significant difference in sitting occurrence between age classes (immatures = 16.7%, adults = 16.5%). Road type had no significant effect in this analysis either (tarmac = 20% and dirt = 10.6%), as the full model incorporating age category and road type did not provide a significantly better fit to the data than the null model (Model 8: $AIC_{\text{null}} = 210.18$, $AIC_{\text{full}} = 210.52$, $\chi^2 = 3.663$, $P = 0.160$). There was no significant difference in sitting occurrence between females with clinging infant crossing events and females without infant crossing events (with infant = 15.2%, without = 9.4%). Road type had no significant effect in this analysis either (tarmac = 13.6% and dirt 5.9%), as the full model incorporating female class category and road type did not provide a significantly better fit to the data than the null model (Model 9: $AIC_{\text{null}} = 119.08$, $AIC_{\text{full}} = 119.84$, $\chi^2 = 3.237$, $P = 0.198$). Our predictions of differences between sexes in occurrence of sitting were supported although our predictions for the effects of age, presence of clinging offspring and road type were not supported.

Table 7. Total number of observations of sitting occurrences whilst crossing the road for each sex, presence of clinging infant and age class analysed.

Sitting occurrence during road crossings									
Road type	Sex (Model 7)			Age class (Model 8)			Presence of clinging infant (Model 9)		
	Male	Female	Total	Adult	Immature	Total	AF W/I	AF	Total
Dirt road	15	68	84	83	2	85	8	60	68
Tarmac road	32	103	135	135	10	145	25	78	103
Total	47	171	219	218	12	230	33	138	171

AF W/I = Adult female with clinging infant; AF = adult female without a clinging infant.

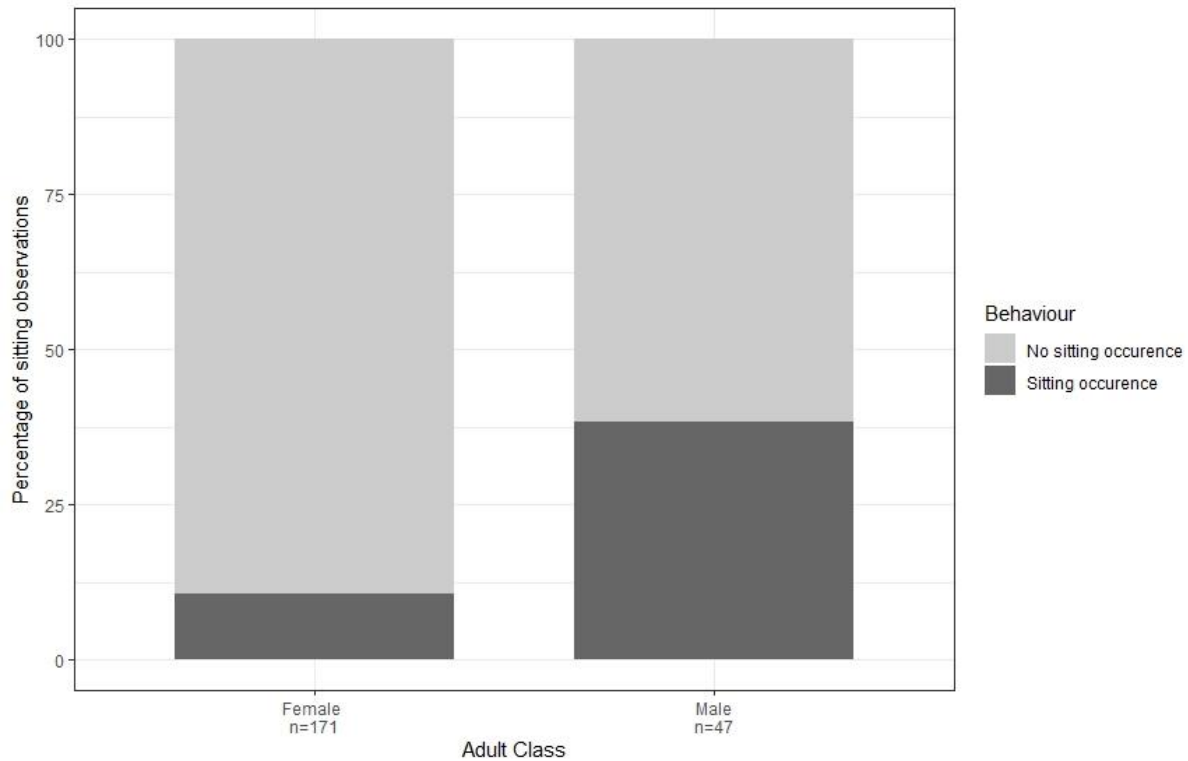


Fig 5. Sitting occurrence of adult females and adult males.

Table 8. Linear mixed-effects model output for factors predicting variation in adult sitting occurrence.

Model 7: Sex differences in sitting occurrence				
Likelihood ratio test:				
AIC Null	AIC Full	X ²	P	
199.37	183.12	20.253	< 0.001	
Full model output:				
	Estimate	Std. error	Z value	P
Intercept	-2.580	0.399	-6.470	< 0.001
Sex (Male)	1.639	0.393	4.168	< 0.001
Road (Tarmac)	0.663	0.431	1.541	0.124

Discussion

I found little evidence that Zanzibar red colobus perceived variation in risk when crossing a wider, busier tarmac road, compared with a narrower, little-used dirt road. Group crossing rate (number of colobus crossing per minute) as well as individual crossing speeds (m/s) did not differ between the tarmac road and the dirt road, suggesting that either the colobus were not perceiving the greater risk associated with the tarmac road, treating both roads as equally dangerous, or not perceiving roads as risky environments at all. Given that some individuals (and age-sex classes) did show some hesitancy when crossing roads, I consider the likelihood

of the colobus not perceiving any risk when on the road as unlikely. On the other hand, given that colobus sometimes sat mid-road while crossing (even when oncoming vehicles had to stop and wait for them to move: HO, pers. obs.), it is similarly difficult to conceive that they treated all roads as inherently risky places. That leaves us with the interpretation that while colobus do perceive some risk when crossing roads, they are not particularly attuned to the risk variance associated with roads of different traffic intensity and vehicle speed, and that there is significant inter-individual variation in general wariness towards open spaces.

I also found that, contrary to our prediction that the smaller colobus group would traverse the road more cohesively and quicker than the larger group, the study groups did not differ in their whole group crossing rate. This is despite the evidence from previous studies on Bighorn sheep (*Ovis canadensis*) that an increase in group size often relates to a decrease in individual-level vigilance (Rieucau & Martin, 2008). Group size effects on risk perception has been studied extensively in birds, where individual vigilance decreases as group size increases for two reasons. Firstly, additional individuals means higher vigilance, directly increasing predator detection (or, in our case, vehicles). Secondly, the greater number of individuals in a group dilutes the risk of predation to each individual (Beauchamp, 2008). Despite these previous studies not being entirely comparable to colobus and cars, what they suggest is that an increase in group size can be associated with a decrease in risk perception. This, however, is not seen in the colobus data. A potential explanation for this may be that colobus in larger groups do not perceive themselves to be safer than those in smaller groups and thus behave similarly during road-crossings. Alternatively, their high level of habituation to people (and, perhaps, vehicles) may reduce their risk perception. The contrast in size of the two groups selected for our study, was perhaps also not sufficiently large to affect their members' perception of risk. Although our larger study group, at ca. 31 - 35 individuals, was approximately twice as large as the smaller one, it was perhaps too small to demonstrate the effect of group size on risk perception in the predicted manner.

Considering colobus crossing behaviour at the individual level, road type did not have a significant effect on any of our three behavioural metrics of risk perception (hesitancy to cross, crossing speed, and mid-road sitting occurrence) in any of the sex-age class comparisons I conducted. Unlike the colobus, chimpanzees have been shown to perceive and respond differently to similar variation in risk (Hockings, *et al.*, 2006). When crossing a

busier road in Guinea, compared to a less busy one, chimpanzees showed a greater wait time before crossing (a measure similar to our ‘hesitation to cross’) and higher vigilance before and during crossing, indicating higher perception of road risk. This contrasting pattern in response to roads of different size and risk in chimpanzees and colobus may be due to differences in relative brain size. For example, in a comparative study of bird responses to vehicles, Husby & Husby (2014) found that birds with larger relative brain size avoided roads more often and could judge crossing times better. This suggests that brain size can be advantageous in adapting to novel anthropogenic environments such as roads (Husby & Husby, 2014). Previous studies have shown that for mammals, a larger relative brain size correlates with success of the species within such environments (Sol, *et al.*, 2008). The smaller relative brain size of the Zanzibar red colobus, in comparison to chimpanzees, may therefore suggest that these folivores are less able to respond to novel anthropogenic changes in their environment. Alternatively, our measures of ‘risk awareness’ may not have been as sensitive to the behavioural responses of the colobus as were the ones used by Hockings, *et al.* (2006) for chimpanzees, where they considered crossings from the first point of vigilance scanning until the final individual crossing as well as fully understanding and considering the role of social status in crossing strategy. With the issues around individual identification when recording colobus crossing events, pseudo-replication in the present study could bias the results and so they should be interpreted with caution. Without the ability to account of repeated observations of individual colobus during crossing, some monkeys that may be more or less risk averse than others may have been oversampled thus biasing the findings of this study. Additionally, in this analysis I was not able to account for the possible salient effect of social rank on risk-taking and avoidance. Future studies should aim to collect detailed individual-level data on vigilance rates in colobus or other folivores during crossing events to allow more robust interspecific comparisons and although there can be difficulty, individual identification should be attempted where possible.

While not all the behavioural metrics I considered differed between sex-age classes in the predicted direction, there were indications that: (a) females showed greater hesitancy of crossings roads in general than males; and (b) females with clinging infants were more risk-aware than females without clinging infants. Adult females differed from adult males in two of the three behavioural metrics: they crossed roads faster and sat mid-road less often during crossing. Females and males showed similar hesitancy before crossing a road. Female

Zanzibar red colobus are slightly smaller than males (Struhsaker, 2010). Given that longer limbs allow for faster locomotion (Zamora-Camacho, *et al.*, 2014), males would be expected to cross roads faster than females, all else being equal. This strengthens the interpretation that faster road crossing by females is linked to them having a stronger perception of roads as a riskier landscape than males do. Consistent with this is the fact that females were less likely to pause and sit in the road mid-crossing than males. Nevertheless, the fact that individual monkeys in general crossed the tarmac and the dirt road in a similar way and did not show awareness of the different levels of risk those roads presented, suggests that females are warier of travelling on the ground in general, rather than being appreciative of the particular risk that the roads may present. Studies of risk response in vervet monkeys (*Chlorocebus pygerythrus*), in the context of resource defence, suggest that males and females show equal responses to risk in most cases. When males were unable to provide support, female risk perception was shown to increase (Arseneau-Robar, *et al.*, 2017). Although male colobus cannot and do not provide ‘support’ to females while crossing roads, more males present in a group may cause female risk perception to reduce if they do perceive cars as “predators” when they cross the road. Studies of boldness and risk perception of individuals in multiple groups of varying sizes and compositions would help resolve this question.

Females with clinging infants exhibited a greater hesitancy before crossing a road than did females without clinging infants. However, there was no difference in road-crossing speed or tendency to sit on the road. The extra weight of a clinging infant may increase the perception of risk in such females, or they may be more hesitant to take offspring into riskier environments making them more likely to pause before stepping onto the road. Similarly, Arseneau-Robar, *et al.* (2017) found that female vervet monkeys with infants were less likely to participate in intergroup aggression to defend resources and territory as the presence of infants affected their perceived risk by increasing the potential costs of engaging in aggression.

Adult and immature individuals did not differ in any of the three road-crossing behaviours that may be linked to risk perception. This is surprising as I predicted that adults, having greater experience of successfully crossing roads would show a greater ability to reduce risk in their road-crossing behaviour by being warier when doing so. Survivorship bias should lead to a greater proportion of adults showing more risk-sensitive, by comparison with immature individuals, as has been demonstrated in Florida scrub jays (Mumme, *et al.* 2000).

Birds that were immature or naïve experienced reduced mortality rates once they have resided in roadside territories for approximately three years (Mumme, *et al.*, 2000). Why older colobus did not appear to show behavioural signs of greater wariness is therefore puzzling, although consistent with the observation that adult and immature individuals are killed on this road as often as would be expected from their relative abundance in the groups living in the vicinity of the roads (Olgun, *et al.*, 2022). There are three possible explanations for these findings. Firstly, Zanzibar red colobus may rapidly learn safe road-crossing strategies whilst still being dependent locomotors, carried by their mothers, leading to similar behavioural profiles of adults and immatures on the road. Even if this was the case, the relatively high rate of mortalities of colobus of all ages on this road does not support the idea of rapid learning during early development in this context (Olgun, *et al.*, 2022). Secondly, colobus may not perceive the level of risk that the road poses to them, no matter their experience with the road. Thirdly, behavioural responses that could be detected through the proxies used here were not sufficient to understand risk awareness that colobus may have when crossing roads. Longitudinal, rather than cross-sectional, observations on road crossing behaviour would be able to tease apart these alternative explanations. Additionally, studying new road developments could provide an opportunity for comparison with groups whose adults have no experience of crossing roads.

I previously showed that the roadkill rates of Zanzibar red colobus suggest that there is no difference in risk of crossing roads between sex-age classes (Olgun, *et al.*, 2022). Nevertheless, our findings in the present study show that females, especially those with clinging infants, showed road-crossing behaviours indicative of greater risk awareness than that of males. The contrast between this observed variation in behaviour and the similar mortality rates between the sexes suggests either that if it were not for the behavioural differences female colobus would be even more likely to be killed by vehicles than males, or that the behaviours do not actually alter the risk of roadkill mortality (which may be more closely linked to behaviours, exhibited in the time immediately preceding a potential collision). Resolving this remains an important question for future research seeking to inform strategies to reduce the current high rate of red colobus roadkill at JCBNP, as well as road-crossing primates elsewhere.

Despite no demographic differences in risk, we do know that this species is frequently killed on the road at Jozani-Chwaka Bay National Park (Olgun, *et al.*, 2022). The loss of one red colobus every 6 weeks in this locality translates to an annual mortality loss estimate of up to 3.24% of the total population per year. We can therefore infer that red colobus current road-crossing behaviour is not effective at proving a sufficient reduction in risk to this source of anthropogenic mortality to safeguard the survival of the population. With an almost certain increase in road risk facing Zanzibar red colobus in the coming years, should this area be subject to the estimated 60% global increase of road networks (Dulac, 2013), there is an increased need for mitigation and intervention strategies from management authorities. Redevelopment of the roads to give longer lines of sight for colobus crossing might be a useful, though costly measure. Relatively less expensive would be the construction of multiple additional speedbumps to span all areas where colobus are known to cross a road. The Zanzibar red colobus are not alone in facing these issues; it is estimated that around 46 other primate species face the risks posed by roads (Hetman, *et al.*, 2019). The likelihood of further primate populations being affected by roads is inevitable, and with 60% of primate species threatened with extinction and 75% of primate species having declining populations (Estrada, *et al.*, 2017) strategies must be developed to reduce this risk across species and habitats.

Conclusions

Our roadkill findings help us estimate that between 1.77% and 3.24% of the population of these local colobus groups are lost annually to roadkill, numbers comparable to predation levels of other primate groups. This could pose a greater risk to colobus population persistence when compared to natural predation as cars are “non-selective” killers. Unlike mortality from natural predators, cars may be less likely to specifically take out the less able and young individuals in a population. Car mortality may thus affect population growth more, as relatively more reproductively aged individuals may be lost. Unlike mortality from natural predators, cars may be less likely to specifically take out the less able and young individuals in a population. Car mortality may thus affect population growth more, as relatively more reproductively aged individuals may be lost. In addition, with no behavioural adaptations demonstrating a strong enough effect on risk mitigation, we see that all individuals are at equal risk still, wariness and naivety do not have a significant enough effect on this species. Although, future studies of this kind should incorporate a greater number of behavioural variables to examine the behavioural adaptations to understand fully the plasticity capabilities

of species when crossing roads, our research showed that the colobus are not capable of meaningful or effective behavioural adaptations to reduce the risk that roads pose to them. Speed bumps have been proven effective and may be the most reasonable measure to reduce roadkill and in turn support persistence of colobus populations living roadside. Although other mitigation strategy effectiveness is yet to be examined when considering the Zanzibar red colobus, it may prove effective to increase speed bump presence in other high risk identifiable areas where colobus may be crossing roads.

Bibliography

- Akrim, F., Mahmood, T., Andleeb, S., Hussain, R. & Collinson, W.J. 2019 Spatiotemporal patterns of wildlife road mortality in the Pothwar Plateau, Pakistan. *Mammalia*, 83, 487–495.
- Arroyo-Rodríguez, V., Cuesta-del Moral, E., Mandujano, S., Chapman, C.A., Reyna-Hurtado, R. and Fahrig, L., 2013. Assessing habitat fragmentation effects on primates: the importance of evaluating questions at the correct scale. In: Marsh & Chapman (Eds.), *Primates in Fragments*, pp. 13-28. Springer, New York, NY.
- Arseneau-Robar, T.J.M., Taucher, A.L., Schnider, A.B., van Schaik, C.P. and Willems, E.P., 2017. Intra-and interindividual differences in the costs and benefits of intergroup aggression in female vervet monkeys. *Animal behaviour*, 123: pp.129-137.
- Austin, C.M. and Ramp, D., 2019. Behavioural plasticity by eastern grey kangaroos in response to human behaviour. *Animals*, 9(5), p.244
- Balčiauskas, L., Stratford, J., Balčiauskienė, L. and Kučas, A., 2020. Importance of professional roadkill data in assessing diversity of mammal roadkills. *Transportation Research Part D: Transport and Environment*, 87: pp.102493.
- Beauchamp, G., 2008. What is the magnitude of the group-size effect on vigilance?. *Behavioral Ecology*, 19: pp.1361-1368.
- Benson-Amram, S., Dantzer, B., Stricker, G., Swanson, E.M. and Holekamp, K.E., 2016. Brain size predicts problem-solving ability in mammalian carnivores. *Proceedings of the National Academy of Sciences*, 113: pp.2532-2537.
- Bezanson, M. and McNamara, A., 2019. The what and where of primate field research may be failing primate conservation. *Evolutionary Anthropology: Issues, News, and Reviews*, 28: pp.166-178.
- Birot, H., Campera, M., Imron, M.A. and 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: p.e23076.
- Blix, A.S., 2016. Adaptations to polar life in mammals and birds. *Journal of Experimental Biology*, 219(8), pp.1093-1105.

Boesch, C., Uehara, S. & Ihobe, H. 2002 Variations in chimpanzee-red colobus interactions. In *Behavioural Diversity in Chimpanzees and Bonobos* (eds Boesch, C., Hohmann, G. & Marchant, L.F.), pp. 221–230. Cambridge University Press, Cambridge, UK.

Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T. and Humle, T., 2017. Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. *International journal of primatology*, 38: pp.282-302.

Bujoczek, M., Ciach, M. & Yosef, R. 2011 Road-kills affect avian population quality. *Biological Conservation*, 144, 1036–1039.

Bunnefeld, N., Linnell, J.D., Odden, J., Van Duijn, M.A.J. and Andersen, R., 2006. Risk taking by Eurasian lynx (*Lynx lynx*) in a human-dominated landscape: effects of sex and reproductive status. *Journal of Zoology*, 270(1), pp.31-39.

Burger, J.R., George Jr, M.A., Leadbetter, C. and Shaikh, F., 2019. The allometry of brain size in mammals. *Journal of Mammalogy*, 100: pp.276-283.

Carius, F. & Job, H., 2019. Community involvement and tourism revenue sharing as contributing factors to the UN Sustainable Development Goals in Jozani–Chwaka Bay National Park and Biosphere Reserve, Zanzibar. *Journal of Sustainable Tourism*, 27: 826–846.

Caro, T., Dobson, A., Marshall, A.J. & Peres, C.A. 2014 Compromise solutions between conservation and road building in the tropics. *Current Biology*, 24, R722–R725.

Chan, B.P.L., Lo, Y.F.P., Hong, X.J., Mak, C.F. and 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: pp.1-9.

Chapman, C.A., Ghai, R., Jacob, A., Koojo, S.M., Reyna-Hurtado, R., Rothman, J.M., Twinomugisha, D., Wasserman, M.D. and Goldberg, T.L., 2013. Going, going, gone: a 15-year history of the decline of primates in forest fragments near Kibale National Park, Uganda. In *Primates in fragments* (pp. 89-100). Springer, New York, NY.

Charnov, E. & Berrigan, D. 2005 Why do female primates have such long lifespans and so few babies? or Life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews*, 1, 191–194.

Cheney, D.L. & Wrangham, R.W. 1987 Predation. In *Primate Societies* (eds Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T. T.) pp. 227–239. University of Chicago Press, Chicago, USA.

Cibot, M., Bortolamiol, S., Seguya, A. and 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: pp.890-900.

Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A. and Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PloS one*, 7: p.e50611.

Clutton-Brock, T.H. and Harvey, P.H., 1980. Primates, brains and ecology. *Journal of zoology*, 190: pp.309-323.

Coffin, A.W. 2007 From roadkill to road ecology: a review of the ecological effects of roads. *Journal of Transport Geography*, 15, 396–406.

Collinson, W.J., Davies-Mosert, H., Roxburgh, L. & van der Ree, R. 2019a Status of road ecology research in Africa: do we understand the impacts of roads, and how to successfully mitigate them? *Frontiers in Ecology and Evolution*, 7, 479.

Collinson, W.J., Marneweck, C. & Davies-Mosert, H.T. 2019b Protecting the protected: reducing wildlife roadkill in protected areas. *Animal Conservation*, 22, 396–403.

Coulson, T., Catchpole, E.A., Albon, S., Morgan, B., Pemberton, J.M., Clutton-Brock, T.H. et al. 2001 Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292, 1528–1531.

Cruz, P., Iezzi, M.E., De Angelo, C., Varela, D., Di Bitetti, M.S. and Paviolo, A., 2018. Effects of human impacts on habitat use, activity patterns and ecological relationships among medium and small felids of the Atlantic Forest. *PloS one*, 13: p.e0200806.

Cunneyworth, P.M. and 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*, pp.1-16.

da Rosa, C.A. & Bager, A. 2012 Seasonality and habitat types affect roadkill of neotropical birds. *Journal of Environmental Management*, 97, 1–5.

Da Silva, A.C.F.B., De Menezes, J.F.S. and Santos, L.G.R.O., 2022. Roadkill risk for capybaras in an urban environment. *Landscape and Urban Planning*, 222, p.104398.

D'Amico, M., Román, J., De los Reyes, L. and Revilla, E., 2015. Vertebrate road-kill patterns in Mediterranean habitats: who, when and where. *Biological Conservation*, 191, pp.234-242.

Davenport, T., 2019. *Piliocolobus kirkii*. In The IUCN Red List of Threatened Species 2019: e.T39992A92630664. <https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39992A92630664.en> [accessed 5 December 2020].

Davenport, T., Fakihi, S., Kimiti, S., Kleine, L., Foley, L. & De Luca, D., 2019. Zanzibar's endemic red colobus *Piliocolobus kirkii*: first systematic and total assessment of population, demography and distribution. *Oryx*, 53: 36–44.

Davenport, T. 2019 *Piliocolobus kirkii*. In The IUCN Red List of Threatened Species 2019: e.T39992A92630664. dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T39992A92630664.en [accessed 9 January 2020].

de Almeida-Rocha, J.M., Peres, C.A. and Oliveira, L.C., 2017. Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. *Biological Conservation*, 215: pp.30-38.

Dean, W.R.J., Seymour, C.L., Joseph, G.S. and Foord, S.H., 2019. A review of the impacts of roads on wildlife in semi-arid regions. *Diversity*, 11: p.81.

Deaner, R.O., Isler, K., Burkart, J. and Van Schaik, C., 2007. Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, behavior and evolution*, 70(2), pp.115-124.

DeCasien, A.R., Williams, S.A. and Higham, J.P., 2017. Primate brain size is predicted by diet but not sociality. *Nature ecology & evolution*, 1(5), pp.1-7.

Dexter, C.E., Appleby, R.G., Scott, J., Edgar, J.P. and Jones, D.N., 2017. Individuals matter: Predicting koala road crossing behaviour in south-east Queensland. *Australian Mammalogy*, 40(1), pp.67-75.

Doherty, T.S., Hays, G.C. and Driscoll, D.A., 2021. Human disturbance causes widespread disruption of animal movement. *Nature Ecology & Evolution*, pp.1-7.

Dominoni, D.M., Greif, S., Nemeth, E. and Brumm, H., 2016. Airport noise predicts song timing of European birds. *Ecology and evolution*, 6: pp.6151-6159.

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, 89–100.

Dulac, J., 2013. Global land transport infrastructure requirements. Paris: International Energy Agency, 20: p.2014.

Dunbar, R.I., 1998. The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 6: pp.178-190.

Dunbar, R.I.M., 2010. Brain and behaviour in primate evolution. In: Kappeler P H & Silk J (Eds.), *Mind the gap* (pp. 315-330). Springer, Berlin, Heidelberg.

Epps, C.W., Nowak, K. & Mutayoba, B. (2015) Unfenced reserves, unparalleled biodiversity and a rapidly changing landscape: roadways and wildlife in East Africa. In *Handbook of Road Ecology* (eds van der Ree, R., Smith, D.J. & Grilo, C.), pp. 448–454. John Wiley & Sons Inc., Chichester, UK.

Estrada, A., Garber, P.A., Rylands, A.B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K.A.I., Nijman, V., Heymann, E.W., Lambert, J.E. and Rovero, F., 2017. Impending extinction crisis of the world's primates: Why primates matter. *Science advances*, 3: p.e1600946.

Farmer, R.G. and Brooks, R.J., 2012. Integrated risk factors for vertebrate roadkill in southern Ontario. *The Journal of Wildlife Management*, 76(6), pp.1215-1224.

Font, E., García-Roa, R., Pincheira-Donoso, D. and Carazo, P., 2019. Rethinking the effects of body size on the study of brain size evolution. *Brain, behavior and evolution*, 93: pp.182-195.

Fox J, Weisberg S (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>.

Gallagher, A.J., Creel, S., Wilson, R.P. and Cooke, S.J., 2017. Energy landscapes and the landscape of fear. *Trends in Ecology & Evolution*, 32: pp.88-96.

- Garrigia, N., Santos, X., Montori, A., Richter-Boix, A., Franch, M. & Llorente, G. 2012 Are protected areas truly protected? The impact of road traffic on vertebrate fauna. *Biodiversity and Conservation*, 21, 2761–2774.
- Georgiev, A., Melvin, Z., Warkentin, A., Winder, I. & Kassim, A. 2019 Two cases of dead-infant carrying by female Zanzibar red colobus (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park, Zanzibar. *African Primates*, 13, 57–60.
- Goldman, H.V. & Walsh, M.T. 2002 Is the Zanzibar leopard (*Panthera pardus adersi*) extinct? *Journal of East African Natural History*, 91, 15–25.
- González-Gallina, A., Benítez-Badillo, G., Rojas-Soto, O.R. and Hidalgo-Mihart, M.G., 2013. The small, the forgotten and the dead: highway impact on vertebrates and its implications for mitigation strategies. *Biodiversity and Conservation*, 22: pp.325-342.
- Grilo, C., Koroleva, E., Andrášik, R., Bíl, M. and González-Suárez, M., 2020. Roadkill risk and population vulnerability in European birds and mammals. *Frontiers in Ecology and the Environment*, 18: pp.323-328.
- Habig, B., Chiyo, P.I. and Lahti, D.C., 2017. Male risk-taking is related to number of mates in a polygynous bird. *Behavioral Ecology*, 28(2), pp.541-548.
- Hart, B.L., 2011. Behavioural defences in animals against pathogens and parasites: parallels with the pillars of medicine in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1583), pp.3406-3417.
- Harvey, P.H. and Clutton-Brock, T.H., 1985. Life history variation in primates. *Evolution*, 39: pp.559-581.
- He, F., Langhans, S.D., Zarfl, C., Wanke, R., Tockner, K. and Jähnig, S.C., 2020. Combined effects of life-history traits and human impact on extinction risk of freshwater megafauna. *Conservation Biology*. Early view: <https://doi.org/10.1111/cobi.13590>
- Hels, T. & Buchwald, E. 2001 The effect of road kills on amphibian populations. *Biological Conservation*, 99, 331–340.
- Hetman, M., Kubicka, A.M., Sparks, T.H. and Tryjanowski, P., 2019. Road kills of non-human primates: a global view using a different type of data. *Mammal Review*, 49(3), pp.276-283.

Hill, R.A. and Lee, P.C., 1998. Predation risk as an influence on group size in cercopithecoid primates: implications for social structure. *Journal of Zoology*, 245(4), pp.447-456.

Hockings, K.J., 2011. Behavioral flexibility and division of roles in chimpanzee road-crossing. In *The chimpanzees of Bossou and Nimba* (pp. 221-229). Springer, Tokyo.

Hockings, K.J., Anderson, J.R. and Matsuzawa, T., 2006. Road crossing in chimpanzees: a risky business. *Current Biology*, 16: pp.R668-R670.

Holderegger, R. and Di Giulio, M., 2010. The genetic effects of roads: a review of empirical evidence. *Basic and Applied Ecology*, 11(6), pp.522-531.

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 *Handbook of Road Ecology* (eds van der Ree, R., Smith, D.J. & Grilo, C.), pp. 198–212. John Wiley & Sons Inc., Chichester,

Husby, A. and Husby, M., 2014. Interspecific analysis of vehicle avoidance behavior in birds. *Behavioral Ecology*, 25: pp.504-508.

Iranzo, E.C., Wittmer, H.U., Traba, J., Acebes, P., Mata, C. and Malo, J.E., 2018. Predator occurrence and perceived predation risk determine grouping behavior in guanaco (*Lama guanicoe*). *Ethology*, 124(5), pp.281-289.

Jacobs, A. 2015 Factors affecting the prevalence of road and canopy bridge crossings by primates in Diani Beach, Kenya. Unpublished master's thesis, University of Kent, Canterbury, UK.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT 2005 Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. *Ecological Modelling* 185(2–4):329–348.

Jeganathan, P., Mudappa, D., Kumar, M.A. & Shankar Raman, T.R. 2018 Seasonal variation in wildlife roadkills in plantations and tropical rainforest in the Anamalai Hills, Western Ghats, India. *Current Biology*, 114, 619–626.

Jones JH 2011 Primates and the evolution of long, slow life histories. *Curr Biol*, 21(18):R708-R717.

Junker, J., Köhl, H.S., Orth, L., Smith, R.K., Petrovan, S.O. and Sutherland, W.J., 2017. Primate conservation: Global evidence for the effects of interventions.

Kamilar, J.M. and Cooper, N., 2013. Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368: p.20120341.

Khadaroo, J. & Seetanah, B. 2008 The role of transport infrastructure in international tourism development: a gravity model approach. *Tourism Management*, 29, 831–840.

Kioko, J., Kiffner, C., Jenkins, N. and Collinson, W.J., 2015. Wildlife roadkill patterns on a major highway in northern Tanzania. *African Zoology*, 50(1), pp.17-22.

Krief, S., Iglesias, Gonzales, A., Appenzeller, B.M.R., Okimat, J.P., Fini, J.B., Demeneix, B. et al. 2020 Road impact in a protected area with rich biodiversity: the case of the Sebitoli road in Kibale National Park, Uganda, *Environmental Science and Pollution Research*, 27, 27914-27925.

Kuznetsova, A., Brockhoff, P.B. and Christensen, R.H., 2017. lmerTest package: tests in linear mixed effects models. *Journal of statistical software*, 82, pp.1-26.

Lampe, U., Reinhold, K. and Schmoll, T., 2014. How grasshoppers respond to road noise: developmental plasticity and population differentiation in acoustic signalling. *Functional Ecology*, 28: pp.660-668.

Laundré, J.W., Hernández, L. and Ripple, W.J., 2010. The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, 3: pp.1-7.

Laurance WF, Goosem M, Laurance SGW 2009 Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24(12):659–669.

Leen, Y., Ruppert, N. & Rosely, N.F.N. 2019 Activities, habitat use and diet of the wild Dusky langurs. *Journal of Sustainability Science and Management*, 14, 71–85.

Lima, S.L., Blackwell, B.F., DeVault, T.L. and Fernández-Juricic, E., 2015. Animal reactions to oncoming vehicles: a conceptual review. *Biological Reviews*, 90(1), pp.60-76.

Linden, B., Foord, S., Horta-Lacueva, Q.J. & Taylor, P.J. 2020 Bridging the gap: how to design canopy bridges for arboreal guenons to mitigate road collisions. *Biological Conservation*, 246, 108560.

Lone, K., Loe, L.E., Meisingset, E.L., Stamnes, I. and Mysterud, A., 2015. An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*, 102: pp.127-138.

López-Sepulcre, A. and Kokko, H., 2012. Understanding behavioural responses and their consequences. In *Behavioural Responses to a Changing World*. Oxford University Press.

Machado, F., Fontes, M., Mendes, P., Moura, A. & Romao, B. 2015 Roadkill on vertebrates in Brazil: seasonal variation and road type comparison. *North-Western Journal of Zoology*, 11, 247–252.

Maor, R., Dayan, T., Ferguson-Gow, H. and Jones, K.E., 2017. Temporal niche expansion in mammals from a nocturnal ancestor after dinosaur extinction. *Nature ecology & evolution*, 1: pp.1889-1895.

Markham, A.C., Gesquiere, L.R., Alberts, S.C. and Altmann, J., 2015. Optimal group size in a highly social mammal. *Proceedings of the National Academy of Sciences*, 112(48), pp.14882-14887.

Mass, V., Rakotomanga, B., Rakotondratsimba, G., Razafindramisa, S., Andrianaivo mahefa, P., Dickinson, S. et al. 2011 Lemur bridges provide crossing structures over roads within a forested mining concession near Moramanga, Toamasina Province, Madagascar. *Conservation Evidence*, 8, 11–18.

Mazerolle, M.J., Huot, M. & Gravel, M. 2005. Behavior of amphibians on the road in response to car traffic. *Herpetologica*, 61, 380 – 388.

McGregor, R.L., Bender, D.J. and Fahrig, L., 2008. Do small mammals avoid roads because of the traffic?. *Journal of Applied Ecology*, 45: pp.117-123.

McLennan, M.R. and Asiimwe, C., 2016. Cars kill chimpanzees: case report of a wild chimpanzee killed on a road at Bulindi, Uganda. *Primates*, 57: pp.377-388.

McLennan, M.R., Spagnoletti, N. and Hockings, K.J., 2017. The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *International Journal of Primatology*, 38: pp.105-121.

Meijer, J.R., Huijbregts, M.A., Schotten, K.C. and Schipper, A.M., 2018. Global patterns of current and future road infrastructure. *Environmental Research Letters*, 13: p.064006.

Miksis-Olds, J.L., Donaghay, P.L., Miller, J.H., Tyack, P.L. & Reynolds, J.E. 2007. Simulated vessel approaches elicit differential responses from manatees. *Marine Mammal Science* 23, 629 – 649.

Møller, A.P. and Erritzøe, J., 2017. Brain size in birds is related to traffic accidents. *Royal Society open science*, 4(3), p.161040.

Monge-Nájera, J., 2018. What can we learn about wildlife killed by vehicles from a citizen science project? A comparison of scientific and amateur tropical roadkill records. *UNED Research Journal*, 10.

Mumme, R.L., Schoech, S.J., Woolfenden, G.E. and Fitzpatrick, J.W., 2000. Life and death in the fast lane: Demographic consequences of road mortality in the Florida Scrub-Jay. *Conservation biology*, 14(2), pp.501-512.

Narayan, E. 2019 Physiological stress levels in wild koala sub-populations facing anthropogenic induced environmental trauma and disease. *Scientific Reports*, 9, 6031.

Newmark, W.D. (2008) Isolation of African protected areas. *Frontiers in Ecology and the Environment*, 6, 321–328.

Ngoprasert, D., Lynam, A.J. and Gale, G.A., 2007. Human disturbance affects habitat use and behaviour of Asiatic leopard *Panthera pardus* in Kaeng Krachan National Park, Thailand. *Oryx*, 41: pp.343-351

Njovu, H., Kisingo, A., Hesselberg, T. & Eustace, A. 2019 The spatial and temporal distribution of mammal roadkills in the Kwakuchinja Wildlife Corridor in Tanzania. *African Journal of Ecology*, 57, 423–428.

Nowak, K. and Lee, P.C., 2013. Status of Zanzibar red colobus and Sykes's monkeys in two coastal forests in 2005. *Primate Conservation*, 2013(27), pp.65-73.

Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S., Hoshino, Y. and Toda, H., 2013. Differences in the activity pattern of the wild boar *Sus scrofa* related to human disturbance. *European Journal of Wildlife Research*, 59: pp.167-177.

Okita-Ouma, B., Koskei, M., Tiller, L., Lala, F., King, L., Moller, R., Amin, R. and Douglas-Hamilton, I., 2021. Effectiveness of wildlife underpasses and culverts in connecting elephant habitats: a case study of new railway through Kenya's Tsavo National Parks. *African Journal of Ecology*, 59(3), pp.624-640.

Olgun, H., Mohammed, M.K., Mzee, A.J., Green, M.L., Davenport, T.R. and Georgiev, A.V., 2022. The implications of vehicle collisions for the Endangered endemic Zanzibar red colobus *Piliocolobus kirkii*. *Oryx*, 56(2), pp.268-276.

Park, D., Jeong, S.M., Kim, S.K., Ra, N.Y., Lee, J.H., Kim, J.K., Kim, I.H., Kim, D.I. and Kim, S.B., 2017. Patterns of snake roadkills on the roads in the northeast region of South Korea. *Korean Journal of Environment and Ecology*, 31: pp.42-53.

Pinto, F.A., Clevenger, A.P. and Grilo, C., 2020. Effects of roads on terrestrial vertebrate species in Latin America. *Environmental Impact Assessment Review*, 81: p.106337.

Porto Peter, F., Molina-Vacas, G., Rodriguez, J. and Grilo, C., 2013. Effects of roads on spatial behaviour and abundance of small mammals: gaps in knowledge. *Oecol Aust*, 17: pp.63-76

Pozo-Montuy, G., Serio-Silva, J.C., Chapman, C.A. and Bonilla-Sánchez, Y.M., 2013. Resource use in a landscape matrix by an arboreal primate: evidence of supplementation in black howlers (*Alouatta pigra*). *International Journal of Primatology*, 34: pp.714-731.

Purvis, A., Gittleman, J.L., Cowlishaw, G. and Mace, G.M., 2000. Predicting extinction risk in declining species. *Proceedings of the royal society of London. Series B: Biological Sciences*, 267: pp.1947-1952.

R Core Team 2018 R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [R-project.org](https://www.R-project.org) [accessed 19 November 2020].

Rieucan, G. and Martin, J.G., 2008. Many eyes or many ewes: vigilance tactics in female bighorn sheep *Ovis canadensis* vary according to reproductive status. *Oikos*, 117: pp.501-506.

Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., Dirzo, R., Galetti, M., Levi, T., Lindsey, P.A., Macdonald, D.W., Machovina, B. and Newsome, T.M., 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society open science*, 3: p.160498.

Rondinini, C. and Doncaster, C.P., 2002. Roads as barriers to movement for hedgehogs. *Functional Ecology*, 16(4), pp.504-509.

Root, T.L. and Schneider, S.H., 2002. Climate change: overview and implications for wildlife. *Wildlife responses to climate change: North American case studies*, 10: pp.765-766.

Rosati, A.G., 2017. Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in cognitive sciences*, 21(9), pp.691-702.

RStudio Team 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL <http://www.rstudio.com/>

Rytwinski T, Soanes K, Jaeger JA, Fahrig L, Findlay CS, Houlahan J, Van Der Ree R, van der Grift EA (2016) How effective is road mitigation at reducing road-kill? A meta-analysis. *PLoS one*, 11(11):0166941.

Rytwinski, T. and Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. *Biological Conservation*, 147: pp.87-98.

Saunders, F., 2011. It's like herding monkeys into a conservation enclosure: the formation and establishment of the Jozani-Chwaka Bay national park, Zanzibar, Tanzania. *Conservation and Society*, 9: pp.261-273.

National Park, Zanzibar, Tanzania. *Conservation and Society*, 9, 261–273.

Schutt P 2008 Analysis of road kill data from Ankarafantsika National Park, Madagascar. Masters Dissertation, Duke University.

Schwartz, A.L.W., Shilling, F.M. & Perkins, S.E. (2020) The value of monitoring wildlife roadkill. *European Journal of Wildlife Research*, 66, 18.

Schwartz, A.L.W., Williams, H.F., Chadwick, E., Thomas, R.J. & Perkins, S.E. 2018 Roadkill scavenging behaviour in an urban environment. *Journal of Urban Ecology*, 4, juy006.

Siex, K.S. and Struhsaker, T.T., 1999. Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *International Journal of Primatology*, 20(2), pp.163-192.

Siex, K.S., 2003. Effects of population compression on the demography, ecology, and behavior of the Zanzibar red colobus monkey (*Procolobus kirkii*). Duke University. PhD thesis.

Siex, K.S. & Struhsaker, T.T. 1999 Ecology of the Zanzibar red colobus monkey: demographic variability and habitat stability. *International Journal of Primatology*, 20, 163–192.

Smith DJ, Ree R van der, Rosell C 2015 Wildlife Crossing Structures. In: *Handbook of Road Ecology*. John Wiley and Sons, Ltd, pp 172–183

Sol, D., Bacher, S., Reader, S.M. and Lefebvre, L., 2008. Brain size predicts the success of mammal species introduced into novel environments. *the american naturalist*, 172: pp.S63-S71.

Sorato, E., Gullett, P.R., Griffith, S.C. and Russell, A.F., 2012. Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. *Animal Behaviour*, 84(4), pp.823-834.

Stillfried, M., Gras, P., Börner, K., Göritz, F., Painer, J., Röllig, K., Wenzler, M., Hofer, H., Ortmann, S. and Kramer-Schadt, S., 2017. Secrets of success in a landscape of fear: urban wild boar adjust risk perception and tolerate disturbance. *Frontiers in Ecology and Evolution*, 5: p.157.

Street, S.E., Navarrete, A.F., Reader, S.M. and Laland, K.N., 2017. Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences*, 114: pp.7908-7914.

Struhsaker, T.T. & Siex, K.S., 1998. The Zanzibar red colobus monkey: conservation status of an endangered island endemic. *Primate Conservation*, 18: 51–58.

Struhsaker, T.T., 2005. Conservation of red colobus and their habitats. *International Journal of Primatology*, 26: 525–538.

Struhsaker, T.T., 2010. The red colobus monkeys: variation in demography, behavior, and ecology of endangered species. Oxford University Press.

Suraci, J.P., Clinchy, M., Zanette, L.Y. and Wilmers, C.C., 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology letters*, 22: pp.1578-1586.

Suscke, P., Presotto, A. and Izar, P., 2020. The role of hunting on *Sapajus xanthosternos*' landscape of fear in the Atlantic Forest, Brazil. *Mdsoar.org*, <http://hdl.handle.net/11603/19372> [Accessed 13/02/2021]

Teelen, S. 2008 Influence of chimpanzee predation on the red colobus population at Ngogo, Kibale National Park, Uganda. *Primates*, 49, 41–9.

Teixeira, F.Z., Printes, R.C., Fagundes, J.C.G., Alonso, A.C. and Kindel, A., 2013. Canopy bridges as road overpasses for wildlife in urban fragmented landscapes. *Biota Neotropica*, 13: pp.117-123.

Thieltges, D.W. and Poulin, R., 2008. Parasites and pathogens: avoidance. *eLS*.

Thurfjell, H., Ciuti, S. and Boyce, M.S., 2017. Learning from the mistakes of others: How female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PloS one*, 12: p.e0178082.

Trombulak, S.C. & Frissell, C.A. 2000 Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14, 18–30.

Tuomainen, U. and Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biological Reviews*, 86(3), pp.640-657.

Valladares-Padua, C.B., Cullen, L.J. & Padua, S.M. 1995 A pole bridge to avoid primate road kills. *Neotropical Primates*, 3, 13–15.

Van Allen, B.G., Dunham, A.E., Asquith, C.M. and Rudolf, V.H., 2012. Life history predicts risk of species decline in a stochastic world. *Proceedings of the Royal Society B: Biological Sciences*, 279: pp.2691-2697.

van der Ree, R Smith DJ, Grilo C 2015 The Ecological Effects of Linear Infrastructure and Traffic. In: *Handbook of Road Ecology*. John Wiley and Sons, Ltd, pp 1–9

Venables, W.N. & Ripley, B.D. 2002 *Modern Applied Statistics with S*. 4th edition. Springer, New York, USA.

Warkentin, A.S., 2019. Effects of Tourist Presence and Activity on the Behaviour of Zanzibar Red Colobus Monkeys (*Piliocolobus kirkii*) at Jozani-Chwaka Bay National Park (Masters dissertation, Bangor University, UK).

Watts, D.P. and Mitani, J.C., 2015. Hunting and prey switching by chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. *International Journal of Primatology*, 36(4), pp.728-748.

White, J.W., Hoogenboom, G., Wilkens, P.W., Stackhouse, P.W. & Hoel, J.M. 2011 Evaluation of satellite-based, modeled-derived daily solar radiation data for the continental United States. *Agronomy Journal*, 103, 1242–1251.

Whiten, A. and Byrne, R.W. eds., 1997. *Machiavellian intelligence II: Extensions and evaluations*. Cambridge University Press.

Zamora-Camacho, F.J., Reguera, S., Rubino-Hispán, M.V. and Moreno-Rueda, G., 2014. Effects of limb length, body mass, gender, gravidity, and elevation on escape speed in the lizard *Psammodromus algirus*. *Evolutionary Biology*, 41(4), pp.509-517.