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Vehicle Collisions Among Four Species of Monkeys Between 2000 and 2018 on a Suburban Road in Diani, Kenya

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

Keywords Diani · Kenya · Primate · Road-crossing behavior · Road mortality · Wildlife–vehicle collision

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Introduction

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

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

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

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

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

Rainfall affects collision rates, because daily path length increases in the dry season. Thus, we predict more collisions in the dry season than in the wet season.

Methods

Study Site

Diani is an international tourist beach resort in Kwale County, southeastern coastal Kenya (Fig. 1). The suburban town contains remnant patches of the coastal Zanzibar–Inhambane undifferentiated forest floristic region, which extends from southern Somalia to the mouth of the Limpopo River in Mozambique (Schipper and Burgess 2004; White 1983). The climate is bimodal. A shorter dry season occurs between July and September and a longer dry season occurs between December and March, whereas April–June and October–November are the typically rainy months (J. Beakbane *unpubl. data*).

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

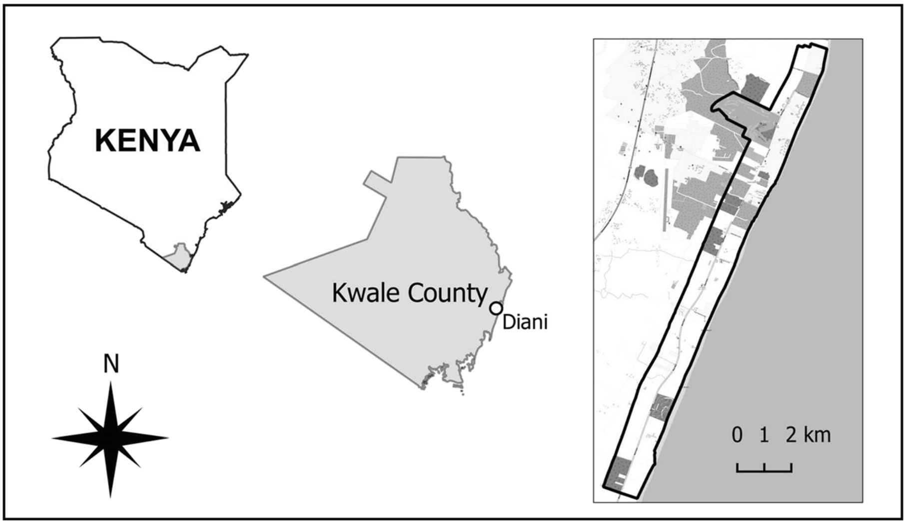

Fig. 1. Location of the study site in Diani, Kwale County, Kenya. Beach Road is indicated by the thin line bisecting the town. The bold line shows the annual monkey census area from which we derived population data.

There are eight speed bumps and a few painted lines and traffic signs. The speed limit is 50 km/h.

Study Species

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

Data Collection

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

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

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

Table I Monkey species of Diani, Kenya with species' attributes

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

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

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

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

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

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

Statistical Analysis

Using SPSS statistic software (IBM Corp, Version 24), we tested assumptions prior to performing all statistical analyses. We rejected the null hypothesis at a 0.05 significance level.

We first calculated the percentage of illness and each type of anthropogenic cause of injury and death in the dataset (vehicle–primate collisions, electrocutions, snares, poison, domestic dog attacks, primate pets, and human abuse) that occurred in the study area surrounding the 10 km section of Diani's Beach Road. We then calculated the Constant Annual Growth Rate to determine the overall population trend of each species. The formula is expressed as follows:

$$\text{Constant annual growth rate} = \left(\frac{\text{Final population}}{\text{Beginning population}}\right) \wedge (1/(15-1)) - 1,$$

where Beginning population = the number of individuals based on the 2004 annual census; Final population = the number of individuals based on the 2018 annual census; and 15 is the number of years between the beginning population and final population.

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

To examine age-class involvement in vehicle collisions, we summed the number of cases of infant, juvenile, subadult, and adult for each species for those years with corresponding census data (2004–2006 and 2010–2018). We also determined the size of each age class in the population for the same years using age-class data collected during the annual census. We then calculated the annual proportion of the population involved in collisions for each age class for each species. We used a Kruskal–Wallis test to assess the null hypothesis that within species, the mean ranks are equal across age classes. For species that were not consistent with the null hypothesis ($P < 0.05$), we carried out *post hoc* testing in pairwise comparisons using a Mann–Whitney U test to identify the age classes that were significantly different. We reported the nonadjusted P values as these tests were planned and limited to a small number of tests (Armstrong 2014).

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

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

Ethical Note

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

Data Availability The datasets generated and analyzed during the current study are available in the supplementary files or from the corresponding author upon request.

Results

Between January 2000 and December 2018, Colobus Conservation received 1896 reports from the community relevant to primate illnesses, injuries, and deaths. Vehicle–monkey collisions were the most frequent cause reported, accounting for 37% ($N = 705$) of the cases. The monthly frequency of vehicle–monkey collisions ranged 0–10 cases with a mean of 3.1 ± SD 2.0 ($N = 228$ months) (Fig. 2). Survival rates were low, as only 15% (104 of 705) of individuals were either alive and not

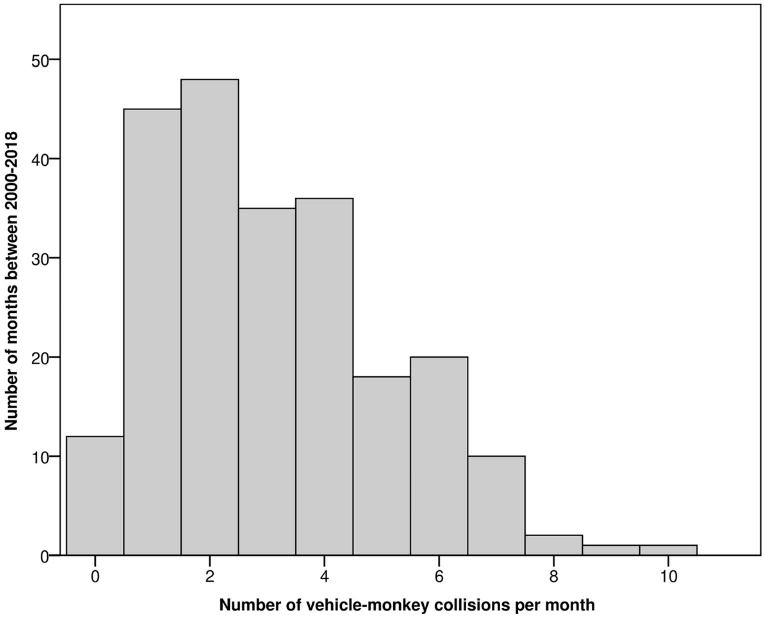

Fig. 2. Distribution of the monthly number of vehicle–monkey collisions on Beach Road in Diani, Kenya for four monkey species combined (colobus, Sykes's monkey, vervet, and baboon) for 2000–2018 (N = 19 yr).

captured or treated and released. Death occurred in 83% of cases (N = 588); these 588 cases were made up of 80% dying on impact or shortly thereafter, 9% dying during treatment, and 11% euthanized as a result of the injuries. In 2% of cases, the team did not find the monkeys when they followed the report up in the field.

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

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

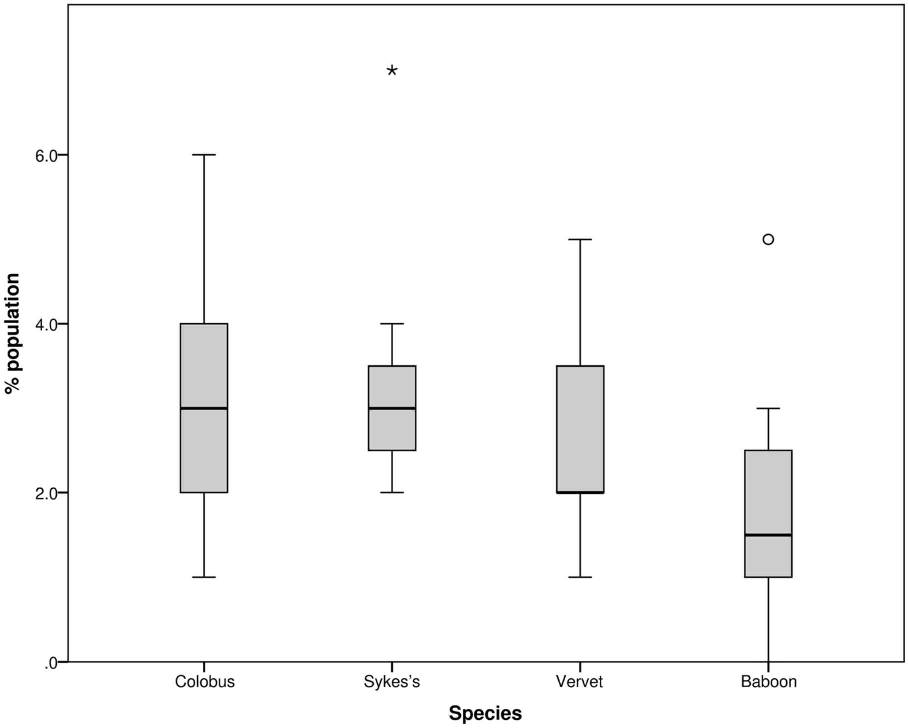

Fig. 3. Percentage of the population involved in vehicle–monkey collisions on Beach Road in Diani, Kenya, for four monkey species in 2004–2006 and 2010–2018 (N = 12 yr). Bars show the median, boxes the interquartile range, whiskers the minimum and maximum values, open circle an outlier, and the asterisk an extreme outlier.

Constant annual growth rate varied between species, with colobus showing negative growth while Sykes's monkeys, vervets, and baboons showed positive growth (Table II). When standardized across years by dividing the number of cases by the annual population size, collision rates differed significantly across species ($\chi^2 = 8.451$, $N = 12$, df = 3, $P = 0.038$) (Fig. 3). In pairwise *post hoc* comparisons, we found significant differences only between colobus and Sykes's monkeys, and baboons (colobus–Sykes's: $\chi^2 = -0.92$, $N = 12$, df = 3, $P = 0.87$; colobus–vervet $\chi^2 = 5.04$, $N = 12$, df = 3, $P = 0.37$; colobus–baboon: $\chi^2 = 13.54$, $N = 12$, df = 3, $P = 0.02$; Sykes's–vervet: $\chi^2 = 5.96$, $N = 12$, df = 3, $P = 0.29$; Sykes's–baboon: $\chi^2 = 14.46$; $N = 12$, df = 3, $P = 0.01$; vervet–baboon: $\chi^2 = 8.5$, $N = 12$, df = 3, $P = 0.13$).

The pattern of collisions by age class (infant, juvenile, subadult, adult) varied. For colobus and vervets, rates did not differ significantly across age-classes (colobus: $\chi^2 = 5.17$, $N = 48$, df = 3, $P = 0.16$; vervet: $\chi^2 = 2.35$, $N = 48$, df = 3, $P = 0.50$). However, for Sykes's monkeys, infants were involved in collisions more often than the other age classes ($\chi^2 = 15.94$, $N = 48$, df = 3, $P = 0.001$) and subadults were involved less often than adults, whereas for baboons, infants were involved less often than all other age classes but this was significant only with juveniles ($\chi^2 = 11.2$, $N = 48$, df = 3, $P = 0.011$). There were no statistically significant differences in rates of vehicle–monkey collisions between the sexes in colobus and baboons;

Table III Vehicle–monkey collisions by sex for four species of monkey on Beach Road in Diani, Kenya, 2000–2018 (*N* = 19 yr)

Species	Female	Male	χ^2	*P*
Colobus	72	82	0.649	0.420
Sykes's	207	152	8.426	0.004**
Vervet	35	59	6.128	0.013*
Baboon	17	22	0.641	0.423

Pearson chi-square analyses assume 50:50 sex ratios.

*$P \leq 0.05$; **$P \leq 0.01$.

however, female Sykes's monkeys were involved in significantly more vehicle–monkey collisions than were males, whereas the opposite was true for vervets (Table III).

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

Discussion

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

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

Variable	Colobus		Sykes's		Vervet		Baboon	
	R	*P*	*r*	*P*	*r*	*P*	*r*	P
Hotel bed-nights	0.152	0.117	0.065	0.502	-0.057	0.560	0.068	0.487
Rainfall	−0.165	0.048*	−0.171	0.041*	−0.001	0.988	−0.030	0.722

*$P \leq 0.05$.

roadside vegetation (Danks and Porter 2010; Lee *et al.* 2004; Philcox *et al.* 1999). Quantification of the infrastructure in future studies would allow comparisons of risk factors across sites.

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

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

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

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

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

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

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

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

(Robinson and Bodmer 1999). Rates of vehicle collisions exceed this percentage in 2 yr for colobus and vervets and in 1 yr for Sykes's monkeys and baboons. Based on the constant annual growth rate, Sykes's monkeys and vervet populations appear to be increasing despite the impact of the road, indicating that these species can withstand the occasional year of higher mortality. The baboon population, which experienced low rates of vehicle collision, showed steady population growth. Vehicle collisions may, however, contribute to the negative population growth rate recorded in colobus. Assessing cumulative risk from multiple environmental stressors, rather than our single factor analysis, however, would better inform decision-based conservation strategies.

In conclusion, we present patterns of vehicle–monkey collisions for four species along a 10-km section of road through a suburban town with a 50 km/h speed limit. This study highlights the risks of roads for monkeys and shows that collision rates vary with species, age class, and, in some species, sex. A spatial analysis of collision locations would further advance the understanding of road-crossing risks to primates.

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Author Contributions PC conceived and designed the study. JD performed the original analysis of the dataset and wrote the first draft of the manuscript. PC added additional years to the dataset and developed the analyses and the discussion. PC wrote the final version of the manuscript. Both authors gave final approval for publication.

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