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

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

Keywords – cost-effectiveness analysis, crossing rate, horizontal ladder canopy bridge, road barrier effect, traffic volume.

Introduction

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

For primates, canopy bridge overpasses (horizontal ladder or single pole or rope bridges: Birot *et al.*, 2020) are exclusively used to increase habitat connectivity, such as across

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agricultural lands (Das *et al.*, 2009; Birot *et al.*, 2020; Nekaris *et al.*, 2020), where intervening habitat is unsuitable (Hernández-Pérez, 2015; Chan *et al.*, 2020), and over roads (Valladares-Padua and Cullen Jr., 1995; Lokschin *et al.*, 2007; Mass *et al.*, 2011; Martín, 2012; Teixeira *et al.*, 2013; Donaldson and Cunneyworth, 2015; Lindshield, 2016; Saralamba and Menpreeda, 2018; Flatt *et al.*, 2022; Langur Project Penang, 2022; Ow *et al.*, 2022). Canopy bridges are intended to reduce the impact of landscape fragmentation by increasing the amount and quality of available habitat (Spellerberg, 2002; Forman *et al.*, 2003) while lessening genetic diversity erosion among the subpopulations (Reed, 2004; Holderegger and Di Giulio, 2010).

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

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

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

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

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

In the suburban town of Diani, south-eastern Kenya, Colobus Conservation, a local conservation organisation, installs horizontal ladder canopy bridges across a 9 km section of Beach Road (Eley and Kahumbu, 1997; Donaldson and Cunneyworth, 2015) in response to monkey-vehicle collisions for four sympatric species of monkeys: colobus (*Colobus angolensis palliatus*), Sykes' monkey (*Cercopithecus mitis albogularis*), vervet (*Chlorocebus pygerythrus hilgerti*), and baboon (*Papio cynocephalus cynocephalus*) (Cunneyworth and Duke, 2020). While crossing structures over and under roads are typically installed to reduce both wildlife-vehicle collisions and the barrier effect, we limited our study to evaluate whether the canopy bridges reduced the road barrier effect and whether this was an economical mitigation to do so. To achieve our aim, we observed monkey road crossings on the ground and the canopy bridges in three survey years (2004, 2011, 2020). We tested predictions arising from the following hypotheses: 1) Terrestrial species use bridges less frequently than arboreal species because terrestrial species are already on the ground and cross directly rather than move to a bridge to cross the road. Thus, we predict bridge use to vary according to the species substrate preference, where arboreal species use bridges more often than those that are terrestrial. 2) As body mass increases, the centre of gravity shifts higher, and therefore an individual's stability on a bridge decreases. Thus, we predict more frequent bridge use among smaller species than larger species. 3) Foraging areas, water, and sleeping sites occur on opposite sides of the road, and therefore, monkeys cross the bridges bidirectionally to access these spatially discrete resources. Thus, we predict that the number of bridge crossings east-west and west-east did not differ significantly. 4) Monkeys perceive higher road crossing risk on the ground than on bridges because individuals on the ground are closer to the oncoming vehicles. Thus, we predict that bridges facilitate crossings at higher traffic volumes than ground crossings. Lastly, we assessed the financial costs of bridges against the frequency of use to determine if bridges were an economically viable mitigation strategy to the road barrier effect.

Materials and methods

Study species and site

Four species of monkeys occur sympatrically in the suburban town of Diani, on the south-eastern coast of Kenya (−4.26757°, 39.59554°): Peters' Angolan colobus (colobus), Zanzibar Sykes' monkey (Sykes' monkey), Hilgert's vervet (vervet), and the southern yellow baboon (baboon). These species crosscut a broad taxonomic range, and amongst other variables, they vary in the degree of arborealism and body mass, with all species being sexually dimorphic (table 1).

The economic base of Diani is beach tourism, and consequently, there are many hotels of which most retain some original forest trees, forest patches, and other vegetation. As typical for an anthropogenically modified area, the monkeys move around their range above the ground using vegetation as well as electrical and

Table 1. Attributes of Diani's four sympatric species of monkeys.

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

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

telephone cables, building roofs, fences, and walls.

Beach Road was built in 1971 through Diani's primary forest, part of the Coastal Forests of East Africa, Global Biodiversity Hotspot (Myers *et al.*, 2000). Set inland 200-450 m, the road bisects the town approximately north to south. The asphalt road is 6 m wide, and the speed limit is 50 km/h.

Canopy bridge design

All of the canopy bridges in this study are horizontal ladder-style design (fig. 1). The team chooses trees offset from the road's verge and secures the bridges to the trees using T-bars and anchors. They install additional bridge segments with support poles and platforms when the tree line occurs far from the road's edge.

Data collection

Road crossings on the ground and canopy bridges

In 2004, 2011, and 2020, we conducted road crossing surveys of the colobus, Sykes' monkey, vervet, and baboon along a 9 km section of Diani's Beach Road. We standardized the methods and included all canopy bridges present on the road in each survey year. While we observed all bridges on the road, the number of bridges varied across the survey years (2004: $N_{\text{bridges}} = 21$; 2011: $N_{\text{bridges}} = 27$; 2020: $N_{\text{bridges}} = 29$) (fig. 2). Eighteen bridges occurred in a similar location across all three survey years, ten bridges occurred in a similar location across two survey years, and three bridge locations were surveyed only in one year. We defined similar locations across years as situations when bridges were relocated to within 50 m. This occurred when a tree could no longer safely support a bridge (died, lost branches, cut down).

Two-person teams sat on the roadside and recorded ground and canopy bridge crossings for two twelve-hour days (06:00 h-17:59 h) for each bridge (table 2). The teams sat near the roadside where the road transect and the bridge were visible but where their presence did not appear to influence road crossings. On datasheets, the teams recorded information for each individual that crossed the road: the species of monkey, whether the crossing was on the ground or the bridge, the time to the minute of the start of the crossing, and the crossing direction (east-west, west-east).

To record ground crossings, we created road transects at each canopy bridge, within which the teams limited the recording of crossings (fig. 3). Using a tape measure, we measured the transects along the road north and south of each bridge and used rocks as markings on the road

Figure 1. Horizontal ladder canopy bridges over Diani's Beach Road. a) Sykes' monkey crossing with bridge rungs visible, b) two Sykes' monkeys crossing, c) bridge components are: i) 30 cm rubber pipe, ii) 30 cm PVC conduit pipe, iii) 45 cm pressure pipe, iv) 3/16" galvanized wire rope grips, v) 3/16" galvanized wire, vi) turnbuckle.

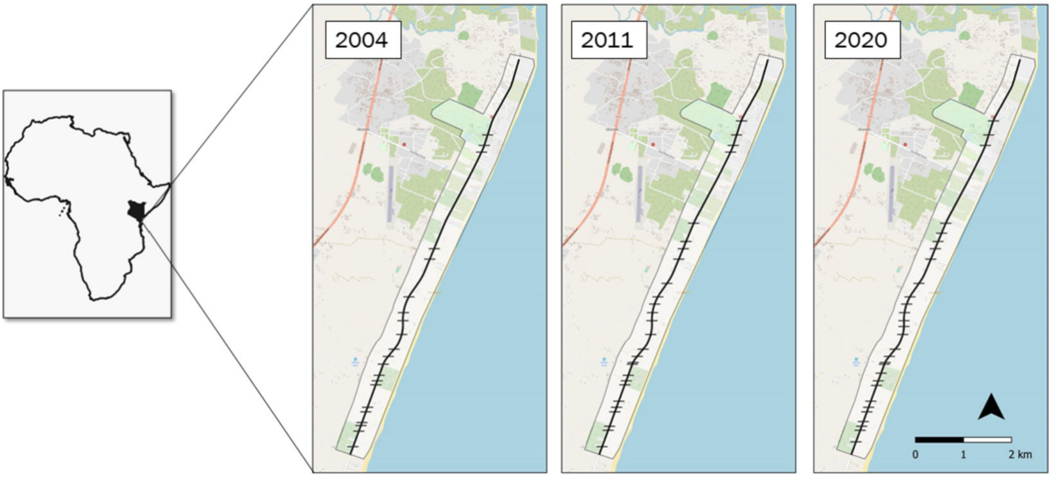

Figure 2. Maps of the canopy bridge locations in each survey year (2004, 2011, 2020) on Diani's Beach Road, Kenya. Beach Road is denoted as the bold line approximately north to south, and the lighter polygon defines the monkey census area, which determines the population size for each species in this study. The short black lines across the road indicate bridge locations.

Table 2. Sampling effort by survey year (2004, 2011, 2020), noting the standardised number of survey days and hours for each bridge while the sampling effort varied by year.

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

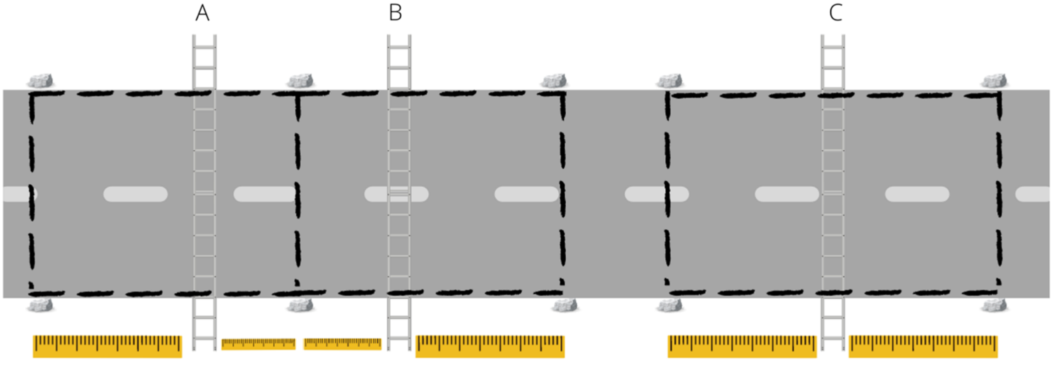

Figure 3. Method for determining road transects for recording ground crossings. Grey ladders indicate canopy bridges, and bold dashed boxes indicate the associated transects with the rock symbols denoting how the transect extents were marked on the road. The large yellow tape measures denote the standardised 100 m transect on either side of the bridge (bridge C) where bridges were greater than 100 m apart, and the smaller yellow tape measures measure half the distance between the two bridges (bridge A and B) where bridges were less than 100 m apart..

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

Traffic volume

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

Monkey population size

Censuses of Diani's monkeys were conducted in each survey year (2004, 2011, 2020). These censuses applied survey methods standardised across the years within a defined 7 km^2 area (ref. polygon in fig. 2). The censuses surveyed the east and west sides of the 9 km section of Diani's Beach Road, where the teams recorded the road crossing and traffic volume data. The census distance varied between 200-450 m on either side of the road (east: between the road and the Indian Ocean beach, west: between the road and the edge of the town). In only one location (golf course), the census distance extended beyond this width to 1250 m.

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

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

We compiled the census data and calculated the population size of each species for each survey year (2004, 2011, 2020). As the teams used standardized census methods across the properties and removed double counts, we considered the dataset to estimate the minimum population size. Situations where estimating complete counts are rare (Plumptre *et al.*, 2013), but given the unique nature of our census area and its relatively small size, made this practical. Furthermore, Diani's monkeys are bound to the east by the Indian Ocean, the north by the Kongo River, and the west by Ukunda town. There are limited opportunities for immigration and emigration to the area south of Diani because of the highly fragmented habitat due to small-scale agriculture, informal businesses, and urban development. Given these ranging constraints, their exposure to the census area is relatively stable across seasons and years, as corroborated by several longer-term studies (Donaldson, 2017; Dunham, 2017).

Data analysis

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

Crossings by substrate preference and body mass

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

confidence interval, and applied a Bonferroni correction for multiple tests ($\alpha = 0.05/9 = 0.006$).

Bridge crossing direction

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

Traffic volume

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

Cost-effectiveness

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

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

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

Results

For all survey years combined (2004, 2011, 2020), we observed 8344 road crossings by the four species of monkeys (colobus, Sykes' monkey, vervet, baboon). Of these, 4931 were ground crossings (colobus: $N = 42$, 1%; Sykes': $N = 1187$, 24%; vervet: $N = 622$, 13%; baboon: $N = 3080$, 62%) and 3413 were canopy bridge crossings (colobus: $N = 159$, 5%; Sykes': $N = 2982$, 87%; vervet: $N = 269$, 8%; baboon: $N = 3$, 0%).

Crossings by substrate preference and body mass

We compared the bridge crossing rate between species based on their population sizes (fig. 4). All nine tests were significantly different (table 3). Yet, bridge use (result: Sykes'>vervet>colobus>baboon) did not follow the predicted order based on stratum preference, arboreal to terrestrial (prediction: colobus>Sykes'>vervet>baboon) or body mass, smallest to largest (prediction: vervet> Sykes'>colobus>baboon). There was some ranking ambiguity in the crossing rate between colobus and vervets because, in one survey year (2004), colobus used the bridges more than vervets; and in the other two years (2011, 2020), vervets used the bridges more than colobus. Yet, the mean crossing rate over the three survey years for colobus is 0.3 and for vervets is 0.7.

Bridge crossing direction

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

Traffic volume

Differences in traffic volume at the location of the crossing (fig. 5) were significant for colobus and vervets yet in the opposite direction. For colobus, the mean rank of traffic volume at the time of bridge crossings was higher

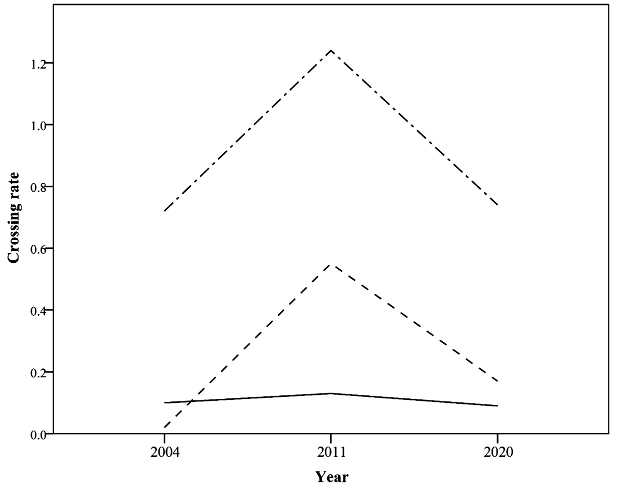

Figure 4. Crossing rate expressed as the number of bridge crossings by population size for each species (colobus, Sykes' monkey, vervet) in the three survey years (2004, 2011, 2020). The crossing rate for baboons equals 0. Colobus = solid, Sykes' monkey = dash-dot, vervet = dash.

Table 3. Poisson exact test comparing the rate (number of bridge crossings/population size (Pop)) for species (sp) pairs (colobus, Sykes' monkey, vervet) by survey year (2004, 2011, 2020). The 95% confidence interval (CI) is given. The direction of the result is displayed as < where the crossing rate of species 1 is less than that of species 2, or > where the crossing rate of species 1 is greater than that of species 2. Asterisks indicate where the direction of the result between species 1 and species 2 is significant.

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

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

Cost-effectiveness

The mean cost of each bridge was USD 157. The cost increased with fewer crossings, yet the cost per crossing was < USD 0.10 in all three survey years (table 5).

Discussion

We observed the four species of monkeys living sympatrically in Diani-colobus, Sykes'

Table 4. Number of bridge crossings for colobus, Sykes' monkeys, and vervets in each direction, east to west and west to east, by year. The significance value is 0.006 for multiple tests.

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

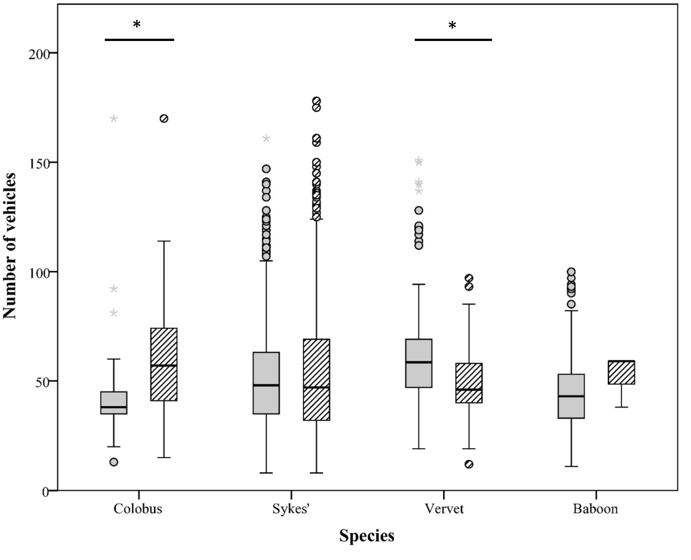

Figure 5. For each crossing, the number of vehicles passing at the crossing location (ground: solid; bridge: hatched) counted as a 15-minute block, categorized by species (colobus, Sykes' monkey, vervet, baboon). The data were combined for the three survey years (2004, 2011, 2020). Significant results are denoted with an underlined asterisk.

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

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

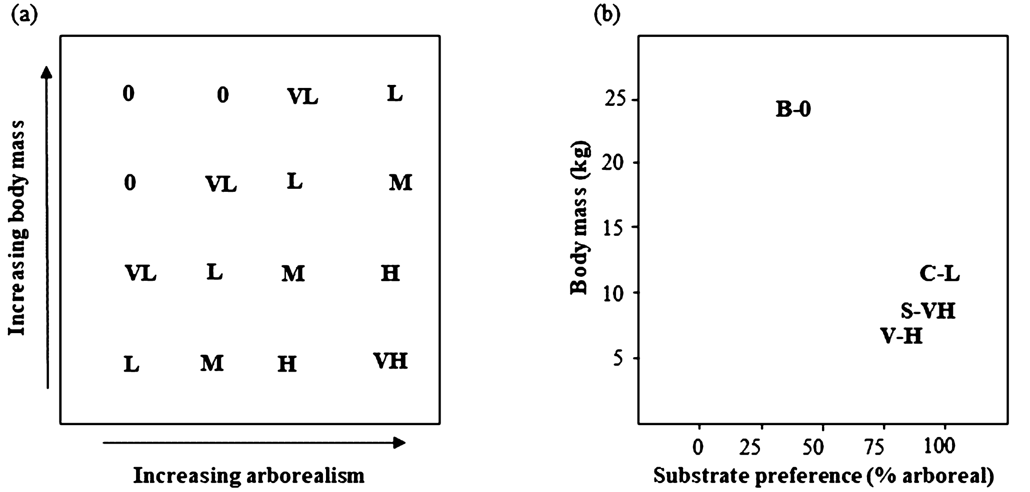

Figure 6. Representation of species' attributes, substrate preference and body mass (kg of Diani's adult males), hypothesised to constrain the canopy bridge crossing rate (a) predictions, and (b) our results (C = colobus, S = Sykes' monkey, V = vervet, B = baboon). Crossing rates (number of bridge crossings/population size) defined as 0 = few to no crossings, VL (Very Low) = 0.1, L (Low) = 0.25, M (Medium) = 0.5, H (High) = 0.75, VH (Very High) = 0.9.

monkey, vervet, and baboon – crossing Beach Road on the ground, but only colobus, Sykes' monkey, and vervet regularly used the canopy bridges.

Crossings by substrate preference and body mass

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

We suggest the interaction between stratum preference and body mass may be more informative (fig. 6). While our results are, to some extent, consistent with these predictions, the addition of crossing rates for other species will determine if stratum preference and body mass together are predictive of species canopy bridge use. We note that there are additional factors that possibly constrain bridge use. For example, the colobus hand does not have a thumb, the typical morphology of the African colobines (Davies and Oates, 1994), which with their larger body size, may contribute to greater instability on the bridges resulting in a lower crossing rate than otherwise would be expected. Interestingly, but perhaps coincidentally, the spider monkey (*Ateles* spp.), a genus also lacking a thumb, has not been observed to use bridges (Aureli *et al.*, 2022).

While we observed baboons crossing the road frequently on the ground, we only recorded three bridge crossings. These were observed in 2004; within 8 minutes, 2 individuals crossed west, and 1 crossed east. Although the bridges do not mitigate the road barrier effect for this species, the annual proportion of the population involved in vehicle collisions on Diani's Beach Road is $<1.75\%$ (Cunneyworth and Duke, 2020), which is likely sustainable (Robinson and Bodmer, 1999). We found only one reference of bridge use by baboons elsewhere. Subadult chacma baboons (*Papio ursinus*) in South Africa infrequently used pole bridges (Linden *et al.*, 2020). Baboons are a large, highly terrestrial species, and together these attributes may contribute to their lack of bridge use. Perhaps at higher traffic volumes, baboons will use the bridges. Yet, testing various bridge designs is warranted for baboons (and other large, terrestrial species). Specifically, the overall width of the bridge (side to side) could mitigate the larger body mass, and incorporating netting from the ground to the top end of the canopy bridge, could mitigate the high degree of terrestrialism by providing access to the bridge from the ground (P. Cunneyworth & B. Linden, pers. comm.). Alternatively, speed calming measures (speed bumps) may also mitigate the road barrier effect for large, terrestrial primates. Two papers discuss speed bumps but to mitigate primate-vehicle collisions rather than reduce the road barrier effect (Zanzibar red colobus (*Piliocolobus kirkii*): Struhsaker and Siex, 1996; chimpanzees (*Pan troglodytes schweinfurthii*): Cibot *et al.*, 2015).

Bridge crossing direction

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

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

Traffic volume

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

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

Cost-effectiveness

A study calculated a cost-benefit analysis for 13 various mitigation measures against the costs of large ungulate vehicle collisions (Huijser *et al.*, 2009). That study calculated the difference between construction, installation, and maintenance costs of the mitigations and the costs associated with collisions such as vehicle damage, human injury and death, loss of the hunting value of the animal, carcass removal and disposal, and towing and investigation. We, instead, calculated a cost-effectiveness analysis calculating the cost of the mitigation (construction, installation, and maintenance) against the cost of each crossing. We did not do a cost-benefit analysis because, of the collision costs associated with the large ungulate study, only carcass removal and disposal applied to our study. We chose not to include carcass removal and disposal because while Colobus Conservation carries out these activities, it would not necessarily be a service available at other study sites. We calculated the cost of each crossing as USD <0.10.

A cost-benefit analysis places a net benefit in a dollar value of the program (= cost of mitigation less cost of collisions). In other words, the program is cost-effective when the net benefit is greater than zero. In contrast, the result of a cost-effectiveness analysis (= cost/outcome) is open to interpretation. We consider Diani's bridge project as an economical mitigation to the road barrier effect for the three species of monkeys that use the bridges, but ultimately donors and road engineers will determine if it is so. Within the primate canopy bridge literature, some studies include the bridge cost (construction and installation), but none include the annual maintenance cost or the bridge's life span before replacement. We encourage authors to include this information in their reporting so that cost-effectiveness analyses can be compared across sites.

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

The cost-effectiveness analysis formula did not incorporate the non-tangible value of bridge use, which economists largely ignore (Chardonnet *et al.*, 2002). For example, Diani's monkeys contribute to ecosystem services such as seed dispersal. To date, their role in dispersing seeds of rare and endemic tree species across the road has been unrecognized. But as Diani's indigenous forest is part of the Coastal Forests of East Africa, a Global Biodiversity Hotspot (Myers *et al.*, 2000), the benefit may be substantial. There are also tourism benefits. We also did not consider colobus crossings more valuable though they are a species vulnerable to extinction (de Jong *et al.*, 2020).

Survey limitations and recommendations for future studies

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

While we collected a large sample of crossings, we recognise three limitations of our study. 1) The study was conducted on only two days in each survey year. Our assumption is that these days represent an 'average' crossing day in that year though we were unlikely to record all species that crossed each bridge. We do not expect substantial differences from what we observed because the species are closely bound to the study area and likely remain close to the bridges throughout the year. 2) In general, Diani's monkeys appear habituated to the suburban sights and sounds. The monkeys display indicators of high levels of habituation to the bridges. For example, across the years, we have observed matings, playing, grooming, and resting on bridges, and individuals crossing back and forth and immediately back again. However, future studies should consider including variables such as traffic noise, the presence of pedestrians, and including motorcycles as vehicles, as we recognise that some monkeys will be more fearful than others, on a species and an individual level. These additional variables may help further to explain differences in crossing rates within and across species. 3) Other studies report periods of bridge habituation. An early Colobus Conservation report writes that, of Diani's monkeys, only colobus delayed using the first bridge (Eley and Kahumbu, 1997). Though the report does not specify the habituation time for colobus, it indicates that colobus were using them regularly at least by eight months post-installation. None of our bridges were installed less than eight months before the survey; therefore, we believe that bridge habituation does not factor into our results.

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

Conclusion

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

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

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Statement of ethics

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

Conflict of interest statement

The authors have no conflicts of interest or competing financial interests.

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Author contribution

PMKC: Conceptualization, Funding acquisition, Methodology, Investigation, Validation, Project Administration, Data Curation, Formal Analysis, Writing – Original draft preparation. AD: Investigation, Data Curation, Writing – Review & Editing. FO: Funding acquisition, Investigation, Data Curation, Writing – Review & Editing.

Supplementary material

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

References

Amick D (2018). *Road crossing behaviour of four wild primate species in Diani, Kenya*. Master's thesis, University of Roehampton, UK.

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

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

Ascensão F, Yogui DR, Alves MH, Alves AC, Abra F, Desbiez ALJ (2021). Preventing wildlife roadkill can offset mitigation investments in short-medium term. *Biological Conservation* 253: 108902. DOI: 10.1016/j.biocon.2020.108902.

Aureli F, Hutschenreiter A, Araya D, Arévalo-Huezo E, Avila T, Boiledieu C, *et al.* (2022). Do spider monkeys use artificial canopy bridges to cross linear infrastructure? *Folia Primatologica* 93: 1–10. DOI: 10.1163/14219980-20211204.

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

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

Birot H, Campera M, Imron MA, Nekaris KAI (2020). Artificial canopy bridges improve connectivity in fragmented landscapes: the case of Javan slow lorises in an agroforest environment. *American Journal of Primatology* 82(4): 1–10. DOI: 10.1002/ajp.23076.

Boardman AE, Greenberg DH, Vining AR, Weimer D (2018). Cost-effectiveness analysis and cost-utility analysis. In *Cost-Benefit Analysis: Concepts and Practice*, 5th ed. (Boardman AE, Greenberg DH, Vining AR, Weimer DL, eds.), pp. 511–536. Cambridge, Cambridge University Press.

Brehme CS, Tracey JA, Mcclenagha LR, Fisher RN (2013). Permeability of roads to movement of scrubland lizards and small mammals. *Conservation Biology* 27(4): 710–720. DOI: 10.1111/cobi.12081.

Chan BPL, Lo YFP, Hong XJ, Mak CF, Ma Z (2020). First use of artificial canopy bridge by the world's most critically endangered primate the Hainan gibbon *Nomascus hainanus*. *Scientific Reports* 10(1): 15176. DOI: 10.1038/s41598-020-72641-z.

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

Chen HL, Koprowski J (2019). Can we use body size and road characteristics to anticipate barrier effects of roads in mammals? A meta-analysis. *Hystrix, Italian Journal of Mammalogy* 30: 1–7. DOI: 10.4404/hystrix--00185-2018.

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

Cuarón AD (1995). Pole bridges to avoid primate kills: a sequel to Valladares-Padua et al. *Neotropical Primates* 3(3): 74–75.

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

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

Davies AG, Oates JF (1994). What are the colobines?. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Davies AG, Oates JF, eds.), pp. 1–10. Cambridge, Cambridge University Press.

de Jong YA, Cunneyworth PMK, Butynski TM, Maisels F, Hart JA, Rovero F (2020). Colobus angolensis. In *The IUCN Red List of Threatened Species 2020*.

de Oliveira PRR, Alberts CC, Francisco MR (2011). Impact of road clearings on the movements of three understory insectivorous bird species in the Brazilian Atlantic forest. *Biotropica* 43(5): 628–632. DOI: 10.1111/j.1744-7429.2010.00744.x.

Diaz-Varela ER, Vazquez-Gonzalez I, Marey-Pérez MF, Álvarez-López CJ (2011). Assessing methods of mitigating wildlife-vehicle collisions by accident characterization and spatial analysis. *Transportation Research Part D: Transport and Environment* 16(4): 281–287. DOI: 10.1016/j.trd.2011.01.002.

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

Donaldson A, Cunneyworth P (2015). Case study: canopy bridges for primate conservation. In *Handbook of Road Ecology* (van der Ree R, Smith DJ, Grilo C, eds.), pp. 341–343. John Wiley & Sons Ltd. DOI: 10.1002/9781118568170.ch41.

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

Eley R, Kahumbu P (1997). *Diani's Monkeys*. (Kahumbu P, Eley R, eds.). Nairobi, Kenya.

Fahrig L (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515. DOI: 10.1146/annurev.ecolsys.34.011802.132419.

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

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

Flatt E, Basto A, Pinto C, Ortiz J, Navarro K, Reed N, *et al.* (2022). Arboreal wildlife bridges in the tropical rainforest of Costa Rica's Osa Peninsula. *Folia Primatologica* 93: 1–17. DOI: 10.1163/14219980-20211109.

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, *et al.* (2003). *Road Ecology. Science and Solutions*. Washington, DC, Island Press.

Garcia F de O, Culot L, de Carvalho REWF, Rocha VJ (2022). Functionality of two canopy bridge designs: successful trials for the endangered black lion tamarin and other arboreal species. *European Journal of Wildlife Research* 68(2): 20. DOI: 10.1007/s10344-022-01569-8.

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

Gregory T, Carrasco-Rueda F, Alonso A, Kolowski J, Deichmann JL (2017). Natural canopy bridges effectively mitigate tropical forest fragmentation for arboreal mammals. *Scientific Reports* 7(1): 3892. DOI: 10.1038/s41598-017-04112-x.

Hernández-Pérez E (2015). Rope bridges: a strategy for enhancing habitat connectivity of the black howler monkey (*Alouatta pigra*). *Neotropical Primates* 22(2): 94–96.

Hetman M, Kubicka AM, Sparks TH, Tryjanowski P (2019). Road kills of non-human primates: a global view using a different type of data. *Mammal Review* 49(3): 276–283. DOI: 10.1111/mam.12158.

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

Huijser MP, Duffield JW, Clevenger AP, Ament RJ, McGowen PT (2009). Cost justification and examples of cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada. *Proceedings of the 2009 International Conference on Ecology and Transportation* 14(2): 625–639.

Kelly C, Diggins C, Lawrence A (2013). Crossing structures reconnect federally endangered flying squirrel populations divided for 20 years by road barrier. *Wildlife Society Bulletin* 37(2): 375–379. DOI: 10.1002/wsb.249.

Kumar A, Devi A, Gupta AK, Sarma K (2013). Population, behavioural ecology and conservation of hoolock gibbon in northeast India. *Rare Animals of India* 1: 242–266. DOI: 10.2174/9781608054855113010014.

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

Linden B, Foord S, Horta-Lacueva QJB, Taylor PJ (2020). Bridging the gap: how to design canopy bridges for arboreal guenons to mitigate road collisions. *Biological Conservation* 246: 108560. DOI: 10.1016/j.biocon.2020.108560.

Linder JM, Oates JF (2011). Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation* 144(2): 738–745. DOI: 10.1016/j.biocon.2010.10.023.

Lindshield SM (2016). Protecting nonhuman primates in peri-urban environments: a case study of Neotropical monkeys, corridor ecology, and coastal economy in the Caribe Sur of Costa Rica. In *Ethnoprimatology* (Waller MT, ed.), pp. 351–369. Springer. DOI: 10.1007/978-3-319-30469-4.

Little SJ, Harcourt RG, Clevenger AP (2002). Do wildlife passages act as prey-traps? *Biological Conservation* 107(2): 135–145. DOI: 10.1016/S0006-3207(02)00059-9.

Lokschin LX, Rodrigo CP, Hallal Cabral JN, Buss G (2007). Power lines and howler monkey conservation in Porto Alegre, Rio Grande do Sul, Brazil. *Neotropical Primates* 14(2): 76–80. DOI: 10.1896/044.014.0206.

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

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

Mass V, Rakotomanga B, Rakotondratsimba G, Razafindramisa S, Andrianaivomahefa 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.

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

Myers N, Mittermeler RA, Mittermeler CG, Da Fonseca GAB, Kent J (2000). Biodiversity hotspots for conservation priorities. *Nature* 403(6772): 853–858. DOI: 10.1038/35002501.

Narváez Rivera GM, Lindshield SM (2016). An experimental evaluation of artificial wildlife bridges crossing structures for New World monkeys in Costa Rica. In *Joint Meeting of the International Primatological Society and the American Society of Primatologists*.

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

Ow S, Chan S, Toh YH, Chan SH, Lakshminarayanan J, Jabbar S, *et al.* (2022). Bridging the gap: assessing the effectiveness of rope bridges for wildlife in Singapore. *Folia Primatologica* 93: 1–12. DOI: 10.1163/14219980-20211110.

Plumptre AJ, Sterling EJ, Buckland ST (2013). Primate census and survey techniques. In *Primate Ecology and Conservation: a Handbook of Techniques* (Sterling EJ, Bynum N, Blair ME, eds.), pp. 10–26. Oxford, Oxford University Press. DOI: 10.1093/acprof:oso/9780199659449.003.0002.

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

Reed DH (2004). Extinction risk in fragmented habitats. *Animal Conservation* 7(2): 181–191. DOI: 10.1017/S1367943004001313.

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

Robinson JG, Bodmer RE (1999). Towards wildlife management in tropical forests. *Journal of Wildlife Management* 63(1): 1–13.

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

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

Seidler RG, Long R, Berger J, Bergen S, Beckmann JP (2015). Identifying impediments to long-distance mammal migrations. *Conservation Biology* 29(1): 99–109. DOI: 10.1111/cobi.12376.

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

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

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

Spellerberg IF (2002). *Ecological Effects of Roads: the Land Reconstruction and Management. Ecological Effects of Roads*. CRC Press. DOI: 10.1201/9781482279931.

Struhsaker T (1981). Census methods for estimating densities. In *Techniques for the Study of Primate Population Ecology* (National Research Council, ed.), pp. 36–80. Washington DC, National Academy Press.

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

Sunnucks P, Balkenhol N (2015). Incorporating landscape genetics into road ecology. In *Handbook of Road Ecology* (van der Ree R, Smith DJ, Grilo C, eds.), pp. 110–118. John Wiley & Sons Ltd.

Teixeira FZ, Printes RC, Fagundes JCG, Alonso AC, Kindel A (2013). Canopy bridges as road overpasses for wildlife in urban fragmented landscapes. *Biota Neotropica* 13(1): 117–123. DOI: 10.1590/S1676-06032013000100013.

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

van der Grift EA, van der Ree R, Fahrig L, Findlay S, Houlahan J, Jaeger JAG, *et al.* (2013). Evaluating the effectiveness of road mitigation measures. *Biodiversity and Conservation* 22(2): 425–448. DOI: 10.1007/s10531-012-0421-0.

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

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