**Traffic volume and long-distance foraging movements to migratory prey shape roadkill patterns in Serengeti spotted hyenas**

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**ABSTRACT**

Collisions between wildlife and vehicles are a major cause of death for wild species worldwide. In Africa, many protected areas are traversed by roads whose traffic volume has substantially increased in the past few decades. In the same period, wildlife tourism has grown which has contributed to an increase in the number of roads and traffic volume. Yet, knowledge on wildlife killed by vehicles (roadkills) within protected areas is limited. Here we investigate the incidence and pattern of spotted hyena (*Crocuta crocuta*) roadkills inside the Serengeti National Park, Tanzania, between 1989 and 2020. We expected roadkill incidence to increase over time, to occur on main roads more often and to involve mostly adult females who regularly travel long-distances, particularly during lactation. Patterns of roadkills were expected to reflect seasonal changes in the locations of vast migratory ungulate herds, which are the main prey of hyenas. Roadkills (n = 87) were indeed more likely on main roads, which are ‘commuting’ routes for hyenas to both distant foraging areas and local anthropogenic food sources, and where traffic was highest. Adult females, particularly high-ranking ones, suffered the highest levels of road mortality. Our results reveal the threat posed by traffic to wildlife in protected areas and the importance of mitigation measures such as the enforcement of existing regulations on night driving and speed limits, especially during the seasons that the prey herds are present (or something like thatS).

**KEYWORDS**

roadkills, road ecology; protected areas; human-wildlife conflicts; *Crocuta crocuta*; large carnivore; predator-prey relationships; carnivore ecology, wildlife conservation

**ARTICLE IMPACT STATEMENT**

Three decades of Serengeti spotted hyena roadkills show increased risk for high-ranking females, on main roads and close to migratory prey.

**INTRODUCTION**

Large protected areas that limit human activities within their boundaries are considered a cornerstone of biodiversity conservation, particularly for large carnivores (Hofer & Mills 1998; Woodroffe & Ginsberg 1998). Although they have proven useful in this respect (Watson et al. 2014; Gray et al. 2016), protected areas are not free of anthropogenic pressure (Hofer et al. 2006; Geldmann et al 2019), and wildlife populations are still declining in some of them due to human activities (Craigie et al. 2010; Laurance et al. 2012; Veldhuis et al. 2019). Among anthropogenic direct impacts, roadkills , and are one of the main sources of wildlife mortality in some protected areas (Garriga et al. 2012; Grilo et al. 2015; Hill et al. 2019, 2020a).

Within protected areas, vehicles are typically expected to give way to wildlife and vehicle speed is often regulated to reduce wildlife roadkills (Collison et al 2019). However, the human population, and therefore the traffic volume,in regions surrounding most protected areas is increasing (Wittemyer et al. 2008) which poses a threat to conservation, and particularly to carnivore populations (Parks & Harcourt 2002; Cardillo et al. 2004). In addition, wildlife tourism has expanded in recent decades, further contributing to the expansion of road networks and traffic volume and speed within protected areas ( Drews 1995; Mkanda & Chansa 2011; Caro et al. 2014; Lyamuya et al 2021). All these factors challenge conservation within protected areas (Wittemyer et al. 2008; Estes et al. 2012; Veldhuis et al. 2019). Knowledge of the spatiotemporal patterns of roadkills can help identify sections within road networks where a specific species is particularly vulnerable to vehicle collisions and where mitigation strategies should be implemented (Seiler 2005; Steiner et al. 2014). Additionally, demographic information on roadkilled individuals can provide an assessment of the scale of loses and possible demographic consequences for a given species (Grilo et al. 2015; Gunson & Teixeira 2015; Garriga et al. 2017).

Large carnivores are particularly vulnerable to road accidents as they typically i) range over large distances and thus may cross roads more frequently (Grilo et al. 2015), ii) often travel along roads and tracks (Hill et al. 2020b), and iii) may forage on prey or carcasses on roads (Planillo et al. 2018; Hill et al. 2020b). Within a given carnivore species, sex or age specific differences in movement patterns may modulate the risk of being hit by a vehicle. For instance, adult male otters (*Lutra lutra*) (Philcox et al. 1999), adult male and female badgers (*Meles meles*) during the biannual peaks of female fertility (Davies et al. 1987) and dispersing adult male black bears (*Ursus americanus*) (Grilo et al. 2015) are particularly susceptible to being killed by vehicles.

Most studies on roadkills of large carnivores have been conducted in North America and Europe outside protected areas (e.g. Planillo et al. 2018; Bencin et al. 2019). Relatively little is known about large carnivores killed on roads in protected areas in Africa (Drew 1995; Mkanda & Chansa 2010; Njovu et al. 2018; Lyamuya et al. 2021), even though they often host a high diversity of large carnivores and most have experienced an increase in tourism in recent decades (Caro et al. 2014; Tablado & D’Amico 2017; Larsen et al. 2020). Here we use long-term data from the past three decades to investigate the patterns of deaths of a keystone predator, the spotted hyena (*Crocuta Crocuta*), caused by vehicle accidents on roads in the Serengeti National Park (Serengeti NP), in northwestern Tanzania. The Serengeti NP and associated protected areas together form the Serengeti ecosystem which is one of the largest protected landscapes in Africa, and it contains one of the largest populations of this highly social carnivore (Hofer and Mills 1998).

In the Serengeti NP, the main prey of spotted hyenas are migratory wildebeest (*Connochaetes taurinus*), Thomson’s gazelles (*Eudorcas thomsoni*), and zebras (*Equus* *quagga*) (Hofer & East 1993a) (Hofer & East 1993a). At the start of the rain season aroundNovember, these migratory species leave their dry season refuges in the north and west of the park to move to the nutritious short-grass plains in the southeast (Fig. 1a, b). When the rains end around May, the migratory herds return to their dry season refuge (Pennycuick 1975; McNaughton 1979; Hopcraft et al. 2015). As a result, hyena clans experience major fluctuations in prey abundance in their clan territories throughout the year (Hofer & East 1993a). During periods when migratory prey are absent from the clan territory, subadult and adult hyenas regularly commute alone or in small groups between their territory and locations containing large migratory herds (Hofer & East 1993b) with round trips covering up to 150 km (Hofer & East 1993b). When commuting, hyenas typically travel on game trails, vehicle tracks and roads (Hofer & East 1993b) where they may encounter vehicles both within and outside their clan territory. Hyenas are mostly active from dusk to dawn (Kruuk 1972). As vehicles in the Serengeti are generally not permitted to drive at night, the threat they pose to hyenas is expected to be maximum during the sunset and sunrise times, when hyena activity and traffic overlap. On the other hand, during daylight hours, hyenas walk along roads, rest on roads and rest or drink from pools of water on roads, which will also expose them to vehicles, particularly in tourist areas where hyenas are to some extent habituated to wildlife-viewing vehicles and on main roads where vehicles can travel at high speed.

Our study aims at understanding the factors that determine hyena roadkill mortality within the protected area of the Serengeti NP. To this goal, we study hyena roadkills in relation to landscape and environmental characteristics, spatio-temporal shifts in prey distribution and hyena individual characteristics. We expected roadkill incidence to be higher: (i) on main roads than on tracks, because of the greater traffic volume and speed (Grilo et al. 2009, 2015; McCown et al. 2009; Bencin et al. 2019; Gunson et al. 2020), (ii) on roads close to human habitation (lodges, tented camps, campsites, staff housing) which may provide hyenas with anthropogenic food resources (Mills & Hofer 1998; Kolowski & Holekamp 2009; Belton et al. 2018), (iii) in areas close to water bodies, which may provide water to drink, attract prey and provide resting sites (Kolowski & Holekamp 2009; Červinka et al. 2015; Pagany 2020), and (iv) in areas with dense woodland where hyenas may be more likely to walk along roads and where the visibility of drivers may be reduced (Abrahms et al. 2016; Hill et al. 2020b). We expected the seasonal spatio-temporal pattern of roadkills to (i) to increase over time, (ii) reflect fluctuations in tourism, i.e., increase during the peak in tourism in July-August and to a lesser extent during the Christmas-New Year period in December and January (Larsen et al. 2020), and (iii) change with the migratory movements of the migratory herds, i.e., to increase in the southeastern area of the park between December and April, and increase in areas to the northwest between August and October.

Finally we expected differences in the incidence of roadkills between animals in different age, sex, and social status categories, as these are associated with the extent of their ranging behavior. This should affect road usage and thus the chance of encountering vehicles (Grilo et al. 2015). As cubs typically remain close to the clan communal den whereas subadult and adult hyenas range over a larger area (Mills & Gorman 1987; Hofer & East 1993a), we expected subadults and adults to experience a proportionally higher road mortality than cubs. Among adults, we expected the incidence of roadkills to be higher in: (i) females than males because they typically commute more often than males and hence should be more likely to encounter vehicles (Hofer & East 1993b, 1993c), (ii) low-ranking than high-ranking females because access to food resources within the clan territory is determined by social status, thus low-ranking females commute more frequently than high ranking females (Hofer & East 1993a; Gicquel et al. 2022).

**METHODS**

**Study area**

The study was conducted within the Serengeti NP, in northwestern Tanzania (2.3° South, 34.8° East, Fig. 1a) between 1989 and 2020. The Serengeti NP is an internationally famous tourist destination and since 1989, tourist lodges, tented camps and campsites have substantially increased, together with the number of vehicles used for viewing wildlife and those supplying lodges and tented camps with supplies (equipment, food and water).

We consider two categories of roads, which we term 1) main roads and 2) tracks (Fig. 1c). All main roads are graded ‘murram’ roads which are used throughout the year by trucks, national bus services and private cars in transit through the park, as well as vehicles associated with transporting tourists and supplies to tourist facilities within the park and beyond, vehicles used in park management and wildlife research. One main road (B144) passes from the south of the park northwards to link to towns in northern Tanzania such as Loliondo, the Kenyan border and the Maasai Mara National Reserve (MMR). From this main road, another main road branches north of Seronera westward through the Western Corridor of the Serengeti NP, providing access to towns in the Lake Victoria region, and another branch northwest towards the headquarters of the Serengeti NP at Fort Ikoma near the park boundary, and towns beyond. ~~During the study, the volume of traffic on these main roads has increased.~~ We term all other game viewing tracks and access roads to facilities ‘tracks’.

The network of tracks in the Serengeti NP has considerably expanded during the study, some tracks have been closed and the routes of others have changed. The volume of traffic on tracks has increased, particularly in areas containing tourist facilities. There is an official speed limit (50 km/hour) set for all roads and tracks within the Serengeti NP, and vehicles are mostly prohibited from driving at night, but these park rules are not always observed.

**Spotted hyena roadkills**

Data on hyena roadkills were collected by members of the Serengeti spotted hyena research project and included hyena roadkills they encountered and those provided by park staff, scientists, veterinarians, and tourists. For each hyena roadkill, the date on which the carcass was found or reported was recorded and this date was used in the analysis. For most carcasses this date was within approximately one or two days (maximum approximately 7 days) of death because scavengers ensure that carcasses typically only persist for a shorter period. The location of roadkills was either estimated using map grid references or, more recently, determined using GPS coordinates. The total number of carcasses was 87, of which 69 had GPS coordinates, acquired at the time of observation or determined using the location indications provided by the observer when sufficiently accurate (Fig. 1b-d).

**Individual characteristics**

Adult carcasses exhibiting clear evidence of lactation were sexed as females, otherwise sex was determined using the dimorphic glans morphology of the genitalia (Frank et al. 1990). Age at death was categorized as cub (< 1 year), subadult (1-2 years) or adult (> 2 years of age) based on body size, pelage characteristics and dentition (Kruuk 1972; Hofer & East 1993a, Hofer et al. 1993). When age was not provided (n = 8, 9%), individuals were considered adults by default, as a younger age category would most likely have been reported.

Based on unique spot patterns, other individually unique features and microsatellite profiling (East et al. 2009), 13 carcasses (15%) were identified as members of three hyena clans (Isiaka, Pool, Mamba) studied continuously since 1987, 1989 and 1990, respectively, as part of the ongoing Serengeti spotted hyena research project (for details see Hofer and East 2003)*.* For these individuals, information about their social status on the death date was available. The social status of adult females in each clan was determined using submissive behaviors during dyadic interactions (Hofer & East 2003). Each adult female within a clan was assigned a standardized rank, equally spaced between -1 (lowest rank) and +1 (highest rank), with 0 as the median rank (see e.g. Hofer & East 2003 or Gicquel et al. 2022 for further details).

**Spatial data**

We downloaded the Tanzanian road network from the OpenStreetMap (OSM) dataset on the Geofabrik download server (Geofabrik GmbH 2020) and processed it for analysis using QGIS (QGIS Development Team 2020). This map included both the main roads and tracks in the Serengeti NP in 2020. We used the road network represented on a 2013 map of the Serengeti National Park (ISBN: 9781851374045) produced by Frankfurt Zoological Society (FZS) as a baseline. We removed from the OSM dataset tracks that do not appear on the FZS map. Conversely, we added the tracks that appear on the FZS map but were not present in the OSM dataset, using Google Earth satellite images. Tracks that were not distinguishable on the satellite images were not added (Fig. 1c).

We acquired the locations of amenities such as accommodation for tourists (lodges, tented camps and campsites) and housing for those working in the park (Fig. 1e), and the perennial and seasonal rivers and other water bodies (hereafter “water sources”, Fig. 1f) from OSM. We used the land cover map from Reed et al. (2009) to characterize vegetation along roads and tracks (Fig. 1g).

**Commuting movements and roadkill risk**

To determine whether individuals from study clans were killed by vehicles when commuting, i.e. when being outside their respective clan territories, we calculated the average territory for each clan as follows. Study clan territories are estimated to cover roughly 55 km2 (Hofer & East 1993c). We thus represented each territory by a circle with a radius of 4.2 km centered on the average position of the communal den (as in Gicquel et al. in 2022). Thus, when roadkill victims were found further than 4.2km from their clan communal den at the time of their death, we considered that they were outside their territory and thus killed during commuting.

**Data analysis**

To determine which variables affected the spatial distribution of hyena roadkills, we analyzed the determinants of the number of carcasses per unit length of road using a generalized linear model (GLM). We considered roads and tracks for which it was likely that we would receive reports of a carcass. We divided roads and tracks into 2.5km long segments (Fig. 1h). End segments shorter than 2km (representing 10.6% of the length of roads and tracks considered) were excluded. (Fig. 1b, c). The number of carcasses found per segment was used as the response variable for the GLM. In total there were 69 carcasses with GPS coordinates included in this analysis. To account for overdispersion, we fitted a negative binomial model. The variables used as predictors were i) the type of road (*RoadType*, main roads and tracks as previously defined), ii) the distance between the midpoint of each segment and the closest amenity (*DistanceAmenity*), iii) the distance between the midpoint of each segment and the closest riverine vegetation, which may indicate a seasonal river or a permanent water body (*DistanceWater*); and iv) the percentage of woodland cover in a 1km wide buffer (500m on each side) along the road (*Woodland*). We tested the significance of the predictors using the likelihood ratio test (test statistic abbreviated as G) to compare the full model with reduced models. Model assumptions were verified by inspecting model residuals.

To test for a potential temporal pattern in relation to the movements of migratory herds, we defined two time intervals. These corresponded to the period during which the migratory herds are located in the short-grass plains in the southeast (December through May), and in their dry season refuge in the north and the MMR (August through October) (Hopcraft et al. 2015). Although we defined these periods based on the location of the migratory herds, we sometime refer to them as ‘seasons’ for simplicity, as the periods during which the wildebeest are in the southeast or in the north broadly correspond to the wet and dry seasons, respectively. We compared the distribution of carcasses of adults and subadults found during these two periods (n = 54) to the expected uniform distribution using a binomial test. For this comparison, we excluded the year 2020 as records terminated in March.

To determine whether there was a spatial shift in the roadkill locations during the year following the location of the migratory herds (the spatiotemporal analysis), we tested for differences in median latitude and longitude of carcasses across the two periods described in the previous paragraph using a Wilcoxon test. The year 2020 was included as this analysis was not affected by the termination of records. We only included carcasses of adults or subadults found during the aforementioned periods and located by GPS coordinates (n = 52).

To investigate risks associated with age, sex or social status, we compared the observed proportions of individuals of a given age class or sex among roadkills with the expected proportions given the age distribution and sex ratio in different age classes in the study population, using binomial tests. For this purpose, we calculated the expected proportion of cubs, subadults and adults as well as females and males for each year, then calculated the averages across the study period. We compared the median standardized social status of roadkilled females belonging to the study clans to the expected median (0) if social status did not influence road mortality, using a one-sample Wilcoxon test.

Data are presented as means ± standard error of the mean (SE), and p values are reported for two-tailed tests. We used Rstudio v1.3.959 (RStudio Team 2020) and R v 4.0.1 (R Core Team 2020), along with the package MASS (Ripley et al. 2020) for the analyses. We used the packages ggplot2 (Wickham et al. 2020) and tmap (Tennekes et al. 2020) for the figures.

**RESULTS**

In total, 87 hyena roadkills were recorded in the Serengeti National Park between 1989 and 2020. Thirteen of the 87 carcasses were identified as members of the study clans. The median roadkill rate was 0.71±0.27 hyena/100 km/year on main roads and 0.07±0.03 on tracks, The number of roadkills per road segment was significantly higher on main roads than on tracks (β*RoadType:Track* = -2.64 ± 0.29, G = 66.34, df = 516, p < 0.001, Fig. 2a), closer to than further from amenities (β*DistanceAmenity* = -0.53 ± 0.16, G = 13.48, df = 516, p < 0.001, Fig. 2b), and closer to than further from riverine habitat/water sources (β*DistanceWater* = -0.40 ± 0.17, G = 6.06, df = 516, p = 0.01, Fig. 2c). Additionally, the number of roadkills per segments decreased with increasing percentage of woodland cover around the road (β*Woodland*= -1.02 ± 0.23, G = 24.14, df = 516, p < 0.001, Fig. 2d).

Roadkills were unevenly distributed over the months, with a peak in March-April (Fig. 3a). There was a significant excess in the observed number of roadkills of adults and subadults during the wet season, which corresponds to the time period when migratory herds are on the short-grass plains (binomial test, n = 52, p < 0.01, Fig. 3b). The location of roadkills of adults and subadults changed with the location of migratory herbivores. When migratory herds were on the short-grass plains in the southeast, the median latitude and longitude of roadkills were 0.11° and 0.07° (or 12.2 km and 8.2 km) further south and east than when the herds were in their dry season refuge (two-sample Wilcoxon test, n = 41, W = 352, p = 0.02, and W = 86, p = 0.001, respectively, Fig. 3c).

Roadkills consisted of 56 adults, 16 subadults, 7 cubs and 8 individuals whose age was not reported and who were considered to be adults. Compared to the representation of each of these age classes in the population over the study period (66% adults, 13% subadults and 21% cubs, n = 2458 individuals), adults and subadults taken together were significantly over-represented (exact binomial test, n = 87, p < 0.001, Fig. 4a). This difference was still significant when only cases for which we knew the age with certainty were included (n = 79, p < 0.01). The proportion of males in roadkill cases of adults was 0.31, significantly lower than 0.45, the adult sex ratio in the study population (exact binomial test, n = 52, p = 0.01, Fig. 4b). This bias in the sex ratio was still significant when only cases for which we knew the age with certainty were included (n = 51, p = 0.01). Females were thus overrepresented among roadkill cases in adults.

Among the 13 carcasses of study clan members, nine were females (seven adults, one subadult, one cub), and four were (adult) males. Among adult and subadult females, high-ranking individuals were over-represented (one-sample Wilcoxon test, V = 34, p = 0.023, µ = 0, Fig. 4c). Among the 12 carcasses of adults and subadults, 11 died outside their clan territory, i.e. during commuting.

**DISCUSSION**

Using three decades of roadkill data of spotted hyenas in the Serengeti NP, we showed that the main risk is posed by main roads in proximity to touristic amenities, water sources, or dense vegetation. Additionally, we found a seasonal pattern of roadkills parallel to the migration of the large herbivores, and that roadkill mortality risk affect disproportionally to high ranking adult females in the population.

In line with many studies on carnivore roadkills outside protected areas (Grilo et al. 2015; Bencin et al. 2019; Gunson et al. 2020; Dennehy et al. 2021), we found a higher incidence of hyena roadkills on main roads, where traffic volume and speed are typically higher, than on side tracks (Fig. 1b,c, Fig. 2a). Roadkill incidence was also higher close to amenities (Fig. 2b), possibly because hyenas are attracted to anthropogenic food associated with housing and tourist accommodation (Kolowski & Holekamp 2008; Yirga et al. 2012: Kalyahe et al. in press) and typically access facilities using vehicle tracks which would increase their chance of encountering vehicles approaching and leaving these amenities. Roadkill risk close to amenities is probably exacerbated by the fact that traffic around housing and tourist campsites is particularly high at dawn and dusk when hyenas are active and highly mobile, as tourist cars and support vehicles typically leave early and arrive late. Roadkill incidence was also higher close to riverine habitat and potential water, probably because hyenas are directly attracted there (to drink and/or rest)). Such habitats also may attract some prey species (Redfern et al. 2003; Valeix et al. 2010). Roadkill incidence was lower on woodland-surrounded roads and tracks, potentially because the density of hyenas is lower there (Hofer & East 1995).

Our results indicate that the long-distance commuting behavior of hyenas to and from areas containing large migratory herds contribute to the hyena roadkill patterns. First, the locations of hyena roadkills were linked to the location of migratory herds (Fig. 1b, 3c). The incidence of roadkills was higher during the wet season, when the migratory herds are clumped on the short-grass plains in the southeast (Fig. 3b). This is probably because the southeast to northwest main road serves as an important commuting route for hyenas belonging to clans in the north and west of the park that travel to and from the short-grass plains (Fig. 1c). Coupled with increased tourist traffic in areas containing large migratory herds (Larsen et al. 2020), this may contribute to the concentration of roadkills in the south of the Serengeti NP in the wet season. In the dry season, the migratory herds move to their wider dry season refuges in the northwest, where they are less concentrated and there are fewer roads. Second, most roadkills of adult and subadult clan membershappened outside their clan territories, suggesting hyenas are particularly vulnerable when commuting (see supporting information for further details). Third, age and sex categories of hyenas that commute more often were more likely to be killed by vehicles, i.e. adults and subadults as opposed to cubs (Fig. 4a), and adult females as opposed to adult males (Fig. 4b).

In line with other studies, our results suggest that the risk of being killed by a vehicle increases with mobility, range size or distance travelled (Davies et al. 1987; Philcox et al. 1999; Grilo et al. 2015) and that prey distribution can affect carnivore roadkill patterns (Barrientos and Bolonio 2009; Planillo et al. 2018). As predicted, our findings indicated that regular long-distance foraging trips by hyenas to areas with large concentrations of migratory ungulates increased the risk of individual being killed by vehicles.

Even though low-ranking adult females commute more often than high-ranking females (Hofer & East 2003; Gicquel et al. 2022), they were less often found as roadkills. Personality and individual experience may modulate roadkill risks in wild species (). It is possible that more frequent commuting might decrease road mortality risk to some extent through learning and experience. Alternatively, high-ranking females might have suffered proportionately more roadkills because of a bolder and more risk-prone personality (Yoshida et al. 2016).

Our estimates of roadkill rates for hyenas on roads (0.71±0.27 hyena/100 km/year) and tracks 0.07±0.03 hyena/100 km/year) are undoubtedly underestimates as carcasses may have gone undetected, unreported or been consumed by scavengers before detection (Santos et al. 2011; Teixeira et al. 2013). Even so, our results provide a conservative estimate of these rates, and as predicted the rate was substantially higher on main roads than tracks. This was probably due to the greater volume of vehicles and higher speed of traffic on main roads. In line with this suggestion, a recent roadkill survey in the Serengeti NP reported that 69.4% of wildlife roadkills occurred on roads in a good condition and with a high volume of traffic (Lyamuya et al. 2021).

Although our study is based on incidences of hyenas killed by vehicles including those found by members of the project and those reported by people engaged in other activities in the Serengeti NP, we think that the seasonal pattern revealed by our analysis is likely to be robust. For instance, traffic volume is reduced during the wet season, which is mostly outside the peak tourist periods. This would reduce search effort and make it harder to detect a peak in hyena roadkills in relation to migratory herd presence in the southeast of the park, yet this is what we found. Within the study area of the Serengeti spotted hyena project, research effort was essentially homogenous in time and space (Supporting Information, Fig. S1), owing to the long-term and ongoing nature of our project. We also think our findings are reasonable, since the results of our spatial analyses were consistent with the results of other studies on large carnivores.

Hyena roadkills are likely to intensify as the human population continues to grow around the Serengeti NP (e.g., Campbell & Hofer 1995; Estes et al. 2012) and the development of wildlife tourism in this area increases (Larsen et al. 2020), potentially threatening the long-term viability of the Serengeti hyena population. This perspective is all the more likely as r andadult females, particularly high-ranking ones who contribute most to the population growth rate (Benhaiem et al. 2018), are the most affected by both roadkills and snaring (Benhaiem et al. in revision.).

Based on our results, we suggest mitigation measures should be urgently imposed to reduce large carnivore roadkills, and they should prioritize main roads, such as the enforcement of existing regulations on night driving and speed limits, especially around the locations of the migratory herds. As it is known from traffic accidents involving humans, the enforcement of speed limits would effectively reduce roadkill incidence, particularly so during the evening when many tour cars and support vehicles often race to get to the campsites and other amenities before it gets completely dark.

**Supporting Information**

Locations of the wind-energy facilities (Appendix S1),

estimated average carcasses/turbine (Appendix S2), and

notes on interpretation of raw data and hypotheses (Ap-

pendix S3) are available online

Locations of the wind-energy facilities (Appendix S1),

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Supplementary results (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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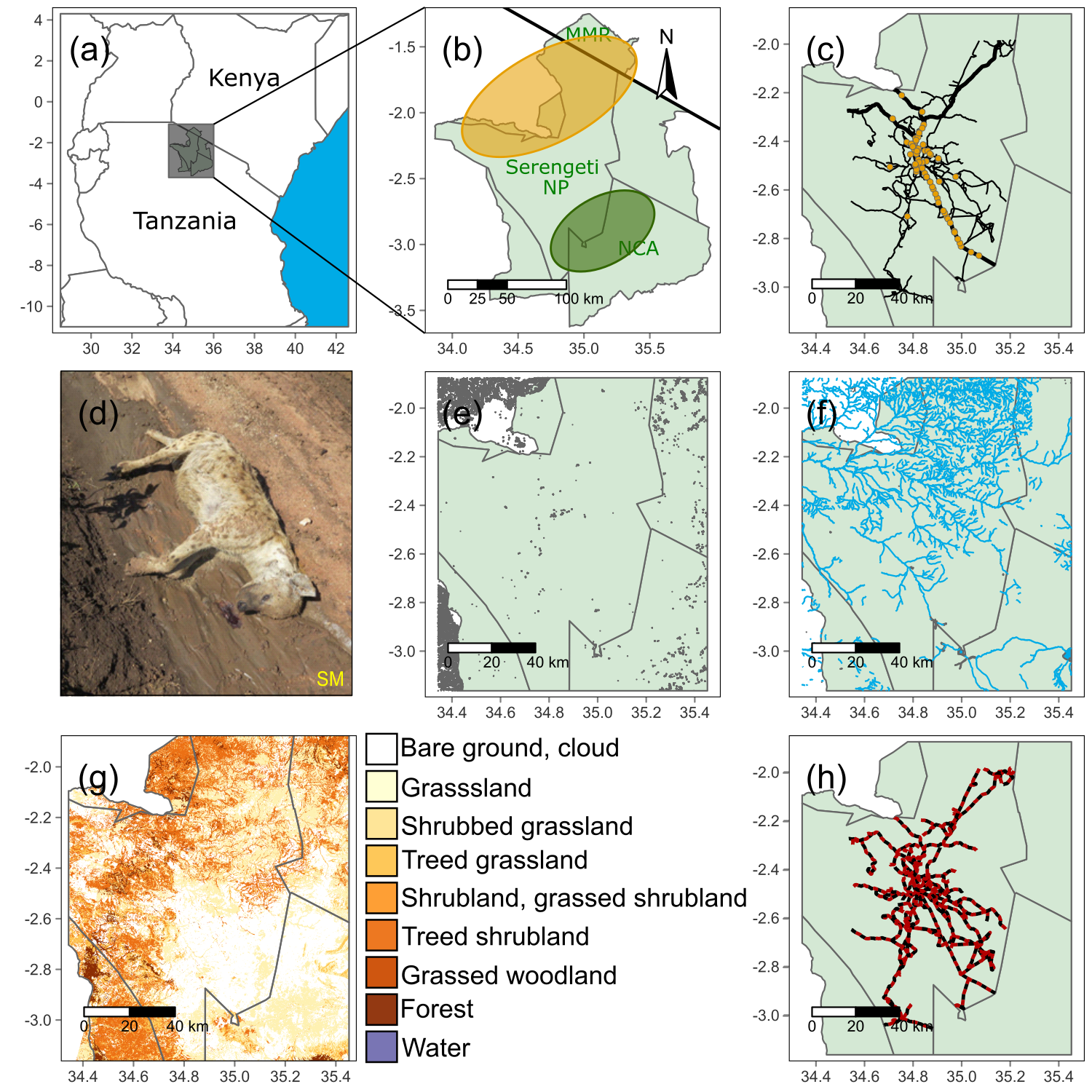
# **Figure legends**

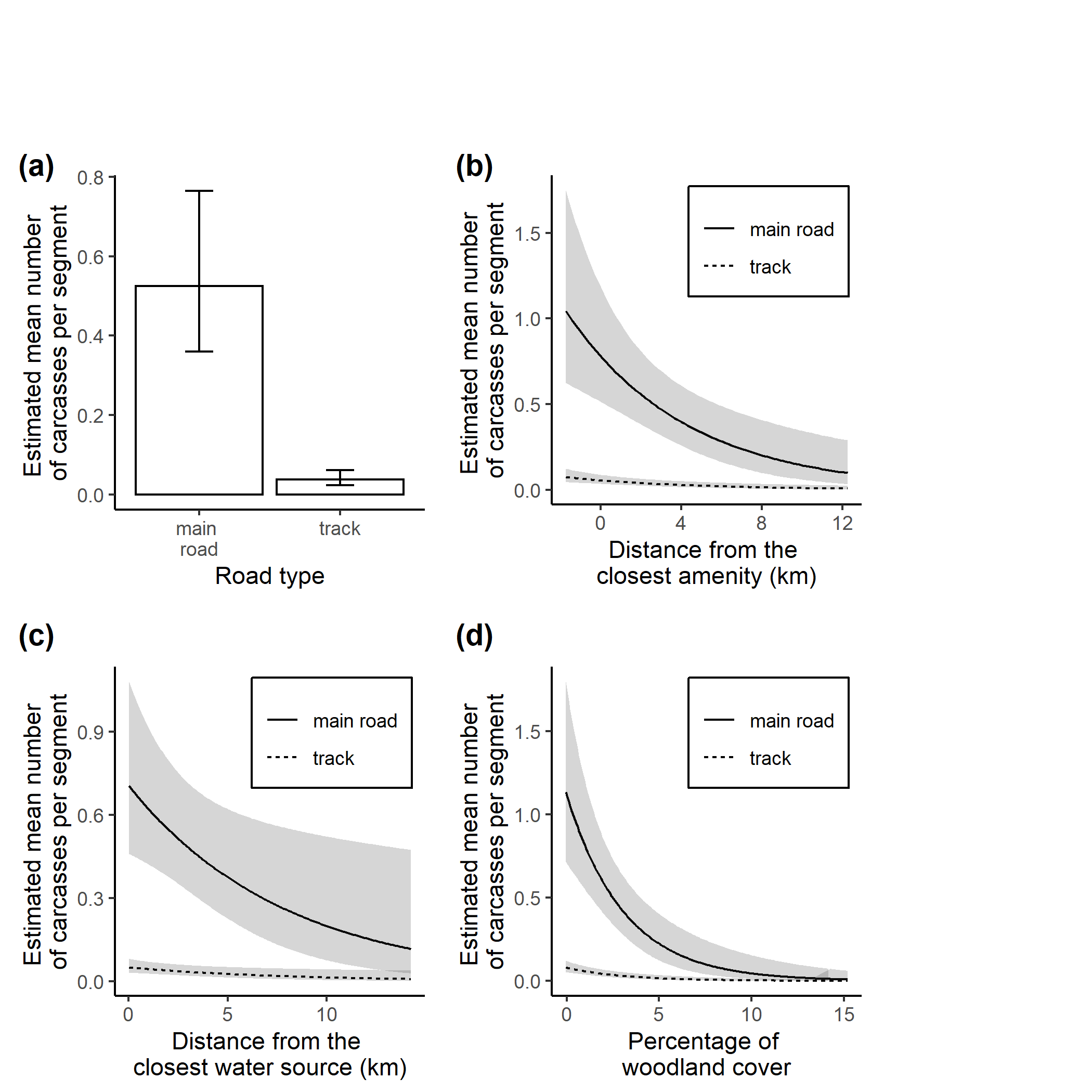
**Figure 1. Study area, spatial data, and hyena roadkill distribution. (a)** Location of the Serengeti ecosystem in Tanzania. **(b)** The Serengeti ecosystem, and the broad location of the migratory wildebeest herds between August and October (yellow) and between late December and early May (green). Serengeti NP: Serengeti National Park, NCA: Ngorongoro Conservation Area, MMR: Maasai Mara Reserve. **(c)** The road network of the Serengeti NP considered in our analysis and recorded roadkills with GPS coordinates. Thick lines represent the main ‘murram’ roads; thin lines represent the tracks used for ranger patrols, safari drives and access to lodges and campsites; yellow dots represent roadkills. **(d)** Adult male killed by a vehicle on a safari road. Photograph by Sonja Metzger. **(e-g)** Amenities (e), waterways and waterbodies (f), and land cover (g) in the study area. **(h)** The road network considered in our analysis segmented into 2.5km long segments for statistical analysis. Alternating colors (black and red) identify individual segments.

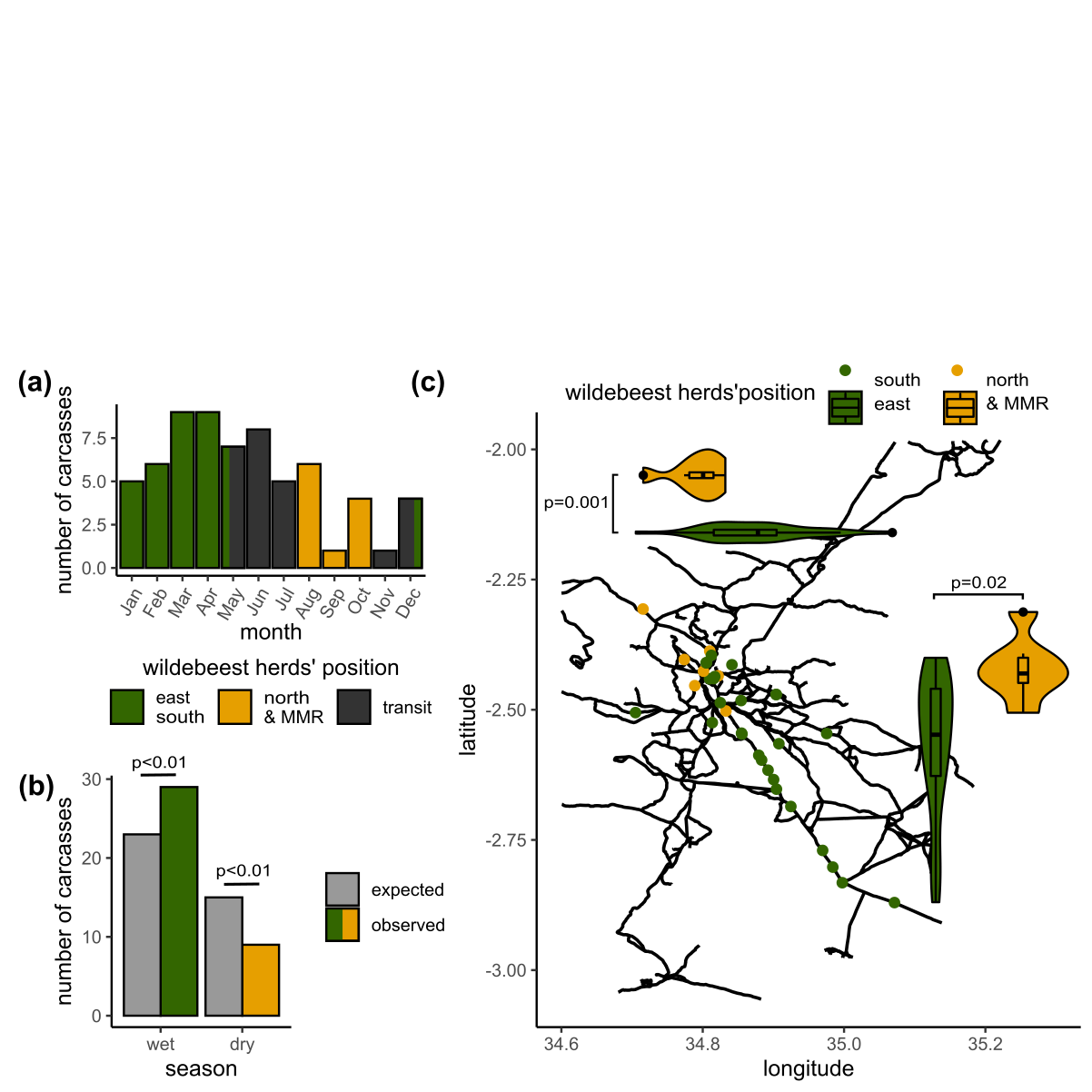
**Figure 2. Effect of environmental characteristics and road types on hyena roadkill incidence. (a)** Estimated mean number of carcasses per segment on the main road and on tracks. Error bars indicate 95% confidence intervals. **(b-c)** Estimated mean number of carcasses per segment as a function of the distance to the (b) closest building, (c) closest water source or riverine habitat on main roads and on tracks. Ribbons indicate 95% confidence intervals. **(d)** Estimated mean number of carcasses per segment as a function of the percentage of woodland cover in a 1km-wide buffer along the road. Numerical variables were set at their mean value.

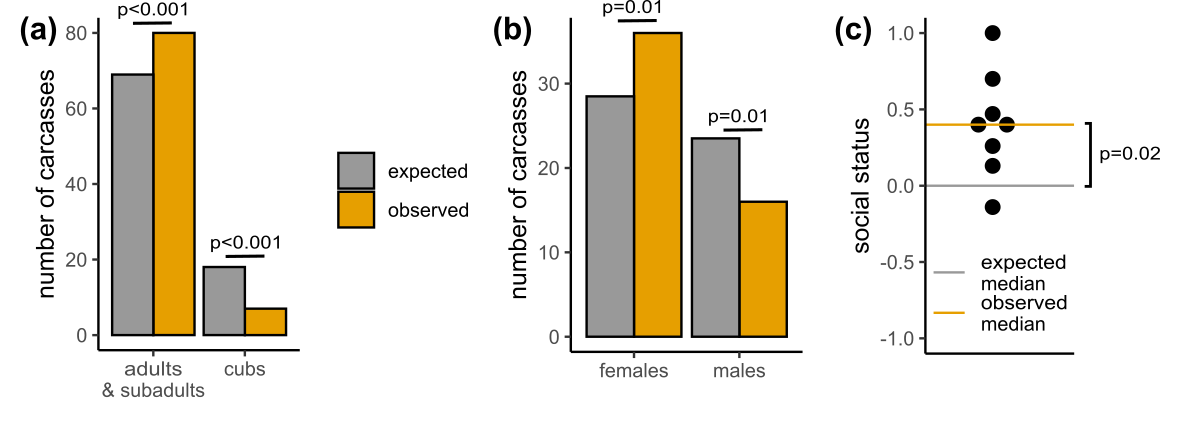
**Figure 3. Temporal and spatiotemporal patterns of hyena roadkills. (a)** Number of hyena roadkill carcasses recorded between 1989 and 2019 by month. **(b)** Expected and observed number of carcasses of adults and subadults recorded between 1989 and 2019 by season. **(c)** Spatial distribution of adult and subadult roadkills recorded between 1989 and 2020 by season. Violin plots show the distribution of roadkills by season along the latitudinal and longitudinal axes. Migratory herds are located in the southeast during the wet season (dark green) and in the north and Maasai Mara National Reserve (MMR) during the dry season (yellow).

**Figure 4. Effect of age, sex and social status on hyena roadkills. (a).** Expected and observed number of individuals of each age classes among roadkilled hyenas. **(b)** Expectedandobserved number of females and males among roadkilled adults. **(c)** Social status of the seven adult females and the subadult female belonging to the three study clans. -1, 0, and +1 are the lowest, the median and the highest rank, respectively.

**Figure 1**

**Figure 2**

**Figure 3**

**Figure 4**