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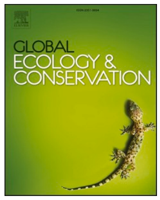

Rapid behavioral responses of endangered tigers to major roads during COVID-19 lockdown

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ABSTRACT

Roads pose a major, and growing, challenge for the conservation of endangered species. However, very little is known about how endangered species behaviorally respond to roads and what that means for road mitigation strategies. We used the nation-wide lockdown in Nepal during the COVID-19 pandemic as a natural experiment to investigate how dramatic reductions in traffic volume along the national highway affected movements of two GPS-collared tigers (*Panthera tigris*)—a globally endangered species. This work is the first systematic research on tigers in Nepal using radiotelemetry or GPS tracking data since the 1980s. We found that the highway more strongly constrained the space use and habitat selection of the male in Parsa National Park than the female in Bardia National Park. Over the entire study period, the female on average crossed 10 times more often per week than the male, and when he was near the highway, he was over 11 times more probable to not cross it than to cross during the day. However, we also found that the cessation of traffic during the pandemic lockdown relaxed tiger avoidance of roads and made the highway more permeable for both animals. They were 2–3 times more probable to cross the highway during the lockdown than before the lockdown. In the month following the lockdown, the space use area of the male tiger tripled in size (160–550 km^2), whereas the female's shrunk to half its previous size (33–15 km^2). These divergent patterns likely reflect differences between the two parks in their highway traffic volumes and regulations as well as ecological conditions. Our results provide clear evidence that vehicle traffic on major roads impede tiger movements, but also that tigers can respond quickly to reductions in human pressures. We conclude by identifying various actions to mitigate road impacts on tigers and other endangered species.

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1. Introduction

Roads threaten endangered species worldwide (Beaudry et al., 2008; Schmidt et al., 2020). They cut through many protected habitats and are projected to cut through many more in the future (Laurance et al., 2015). In addition to fragmenting habitats, road networks can negatively impact wildlife by impeding gene flow between populations, increasing animal mortality via vehicle collisions, and increasing human disturbance through settlement growth, hunting, or traffic noise and lights (Fahrig and Rytwinski, 2009). Carnivores are particularly susceptible to the impacts of roads because they often require large habitats, have low reproductive output, and occur in low densities (Grilo et al., 2015). In Iran, for example, collisions with vehicles on roads increases the mortality and thus extinction risk of the endangered Asiatic cheetah (*Acinonyx jubatus venaticus*, Parchizadeh et al., 2018). Road networks in the northern Andes of South America severely fragment habitats of spectacled bears (*Tremarctos ornatus*), threatening their long-term survival (Kattan et al., 2004). Moreover, road infrastructure is expanding rapidly in some of the most biodiverse regions on Earth (Laurance et al., 2014). Understanding the effects of roads on endangered carnivores will therefore lead to significant conservation gains. Although studies have elucidated a range of road impacts on wildlife (Van Der Ree et al., 2015), little is known about how roads constrain the movements of endangered carnivores (Poessel et al., 2014). This knowledge gap reduces our ability to mitigate the negative, and increasing, effects of road networks on endangered carnivores.

The globally endangered tiger (*Panthera tigris*)—a conservation flagship species—is vulnerable to the impacts from road networks throughout their range (Goodrich et al., 2015). A recent study found that 134,000 km of roads already exist within the 13-country range of the tiger in Asia and 24,000 km of new roads will be added by 2050 (Carter et al., 2020). As with much of Asia, Nepal is experiencing rapid growth in transport infrastructure in the lowlands (Terai), which encompass all of the country's ~250 tigers (MoFSC, 2015). The ongoing widening of the 1028 km East-West (Mahendra) Highway to support greater traffic volume is especially concerning for biodiversity conservation, as the road bisects all tiger-bearing parks in Nepal as well as important habitat corridors and bottlenecks (Quintana et al., 2022). Widening the highway without putting alternative structures and mitigation measures in place will likely lead to more severe impacts on tigers, their prey, and other wildlife in these parks and adjoining forests. Construction of the expansion project is already underway and will continue over several years in various stages. Yet, this project and others are being constructed with little to no mitigation of their impacts on tigers, in part because we know very little about road effects on the biology and ecology of the species (Poudel et al., 2020). Disparate evidence suggests roads can increase tiger mortality, decrease their prey, and reduce tiger gene flow and dispersal across landscapes (Goodrich et al., 2008; Jiang et al., 2014; Kerley et al., 2002; Thatte et al., 2018). However, we lack a strong understanding of how, when, and why tigers interact with roads, and what that means for implementing better mitigation measures.

Using the COVID-19 pandemic lockdown as a natural experiment, we assessed how reductions in human activities and traffic volume affected the space use of tigers along the national park portions of the East-West Highway in Nepal. The reduction of human activity and mobility during the COVID-19 pandemic, particularly during lockdowns when people were confined to their homes, lowered human pressures on natural systems (Bíl et al., 2021). These dramatic abruptions in global human activity have created the greatest natural experiments of our time, allowing the robust assessment of anthropogenic effects on ecological systems (Rutz et al., 2020). Notably, global lockdowns significantly decreased road traffic, with vehicle use dropping by over 50% in many countries (Perkins et al., 2022). Recent work has shown that reduced vehicular traffic during the lockdowns has caused animals to shift their space use near roads and urban areas (Benson et al., 2021; Corradini et al., 2021; Wilmers et al., 2021). These studies suggest that animals can move across structural barriers, such as roads and human settlements, in the absence of active human disturbance including vehicle traffic (Corradini et al., 2021; Koju et al., 2021). In our case, this natural experiment allows us the unique opportunity to gain insights on tiger movements near roads with varying traffic patterns that can, for example, guide decisions on the placement of wildlife crossing structures, inform how and when to regulate traffic volumes, and develop spatial zoning plans that aim to shrink the road effect zone on endangered tigers.

We equipped two wild tigers in Nepal with GPS collars—one in Bardia National Park and one in Parsa National Park—to record detailed information on their movements and behaviors around the East-West Highway prior to expanding from two to four lanes. Systematic research on tigers using radiotelemetry or GPS tracking data from collars has not occurred in Nepal since the 1980s (Smith, 1993). Collar technology and data quality has improved considerably since then. We focused on both parks because the way traffic is regulated between them differs greatly. Traffic volume and speed is strictly regulated in Bardia with army guards set at the entry and exit of the park, recording the identity and speed of vehicles and issuing fines to vehicles going too fast or too slow (i.e., lingering along the road for too long). In contrast, traffic volume and speed are not regulated along the highway intersecting Parsa National Park, except for signs showing speed limits (40 km/hr). The highway traffic volume along the section of Parsa is much higher as it is the shortest route for supplying goods and services from India to Kathmandu, the capital city. By comparing between these two sites, we can better understand how variation in traffic regulation and volume affect tiger space use around the highway. Furthermore, during the study, the government of Nepal instituted its second national COVID-19 lockdown between 30 April and 1 September, 2021 (Pandey et al., 2022). During the lockdown, road use dramatically reduced as trade was postponed, many businesses were closed, and social activities were heavily restricted. The lockdown therefore enabled us to evaluate how dramatic changes to traffic volume affected individual tigers' space use and the permeability of the highway.

We evaluated three specific aspects in this research: (1) when, where, and to what degree the tigers cross the highway; (2) how the tigers structure their movement behaviors near and far from roads; and (3) how these crossings and behaviors varied between the periods before, during, and after the COVID-19 lockdown. We anticipate that the tigers will avoid areas closer to roads and that the highway will reduce overall permeability of the landscape for tiger movements. In addition, we anticipate that these negative impacts will be reduced during the COVID-19 lockdown due to declines in traffic volume. Based on our analyses, we synthesize recommendations for reducing the impact of transport infrastructure on tigers. We also more broadly point to future research directions to assess the multitudinous effects of transport development on tigers to inform tiger-friendly infrastructure planning.

2. Methods

2.1. Study areas

Bardia National Park, located in south-western Nepal, was established in 1976 and is 968 km^2. Bardia is home to a large, and growing, source population of tigers in the region. Tiger numbers in Bardia have increased from 18 to 125 from 2009 to 2022 (DNPWC and DOFSC, 2022). Bardia is connected to the Banke National Park to the east and has important corridors that link to forests in the south and the west. Bardia has an elevation range of 150–1565 m, although about 70% of the park is in the flat lowlands (Upadhyaya et al., 2020). The highway's ~30 km stretch passes through the Park and bisects its highly productive Karnali River floodplain. This area is rich with tigers, other large carnivore species, such as the common leopard (*Panthera pardus*), and various ungulate prey species (Karki et al., 2016).

Parsa National Park, located in south-central Nepal, was established in 1984 as a wildlife reserve with an area of 499 km^2, which was extended eastward to 627 km^2 in 2015, and then upgraded to a National Park in 2017 (Thing et al., 2022). As with Bardia, Parsa has seen a rapid rise in tiger numbers in recent years from 4 to 41 from 2009 to 2022 (DNPWC and DOFSC, 2022; Lamichhane et al., 2018). The park also hosts a diversity of large predator and ungulate species. The park is connected to the Chitwan National Park to the west, which is considered to have the largest tiger population in Nepal (128 in 2022; DNPWC and DOFSC, 2022), and has important forest corridors further east. Parsa has an elevation range of 100–950 m. The highway bisects a flat, narrow portion of the park that is part of the recent extension area. Unlike Bardia, Parsa has a highly alluvial substrate that restricts water availability throughout the non-monsoonal months (Thing et al., 2022).

Both Bardia and Parsa generally experience three distinct seasons: winter (late September–mid February), summer (mid February–mid June) and monsoon (mid June–mid September). However, the 2021 monsoon season began on 11 June and ended on 16 October (MoEWRI, 2022). The maximum temperature is 45 °C and mean annual rainfall is 1500 mm (Dinerstein, 1979; Upadhyaya et al., 2020).

2.2. Quantifying road traffic

To estimate how much traffic was reduced during the COVID lockdown, we obtained data on daily traffic counts before, during, and after lockdown, where available. Daily traffic count data pre- (Feb 2021) and post-lockdown (Feb 2022) were obtained from the Nepal Department of Roads (MoPIT, 2022) for the exact highway segment passing through Parsa (station: Pathlaiya North) and for a segment of the highway near our study site in Bardia (station: Kohalpur West). We used these data from the Kohalpur West traffic station adjacent to Bardia to reflect traffic counts at our study site in Bardia, assuming the numbers are very similar given their proximity in space. During lockdown, daily traffic counts in Parsa were estimated using camera traps. Specifically, we collected the traffic data by placing camera traps perpendicular to the roads at three locations along the highway passing through Parsa. Single camera traps (Bushnell HD) were placed at each location for one week during the lockdown period (11–17 May, 2021). Cameras were set to take 3 pictures in each detection without delay. We then recorded the date, time, and vehicle type for each picture and summed all vehicles for each day. As we were not able to obtain traffic counts in Bardia during the lockdown, we assumed that the pattern of change in traffic volume during the lockdown in Parsa is approximately the same for Bardia. We believe this assumption is reasonable as the lockdown applied equally and at the same time across the whole country.

2.3. Tiger capture and GPS data

A field team captured one male tiger (M01) inside Parsa National Park on February 14, 2021 (75 days prior to lockdown), and one female tiger (F01) inside Bardia National Park on March 26, 2021 (35 days prior to lockdown). The animals were immobilized and anesthetized with a combination of Medetomidine (0.07 mg/kg) and Ketamine (3 mg/kg), using Atipamezole (5 mg/ml) as the antidote. We fit both individuals with a Vertex PLUS (Vectronic, Germany) GPS-collar with bi-directional Iridium satellite link. The collars recorded GPS fixes every 1.5 h, accurate to within 8–15 m on average. All capture, handling, and immobilization were in accordance with the University of Michigan IACUC Protocol #PRO00010077, recommendations in the ARRIVE Guidelines, and the "Operational manual for the satellite telemetry on Royal Bengal tiger 2021" approved by the Nepal Department of National Parks and Wildlife Conservation.

Both animals were native to the parks (i.e., not translocated) with territories overlapping the highway based on images from camera traps that were set prior to capture. The male was estimated to be 8 years old and weighed approximately between 200 and 220 kg, and the female was estimated at 5 years old and weighed approximately between 150 and 160 kg. Both animals were healthy. The female was not pregnant and there was no evidence that she had any cubs at the time.

2.4. Road crossing analysis

To understand how roads influence the movements of tigers, we first examined road crossing behaviors related to time of day and COVID lockdown policy. We calculated the frequency of road crossings per tiger during day and night per week during the length of time they were collared. Road crossings were determined by identifying the movement paths of each tiger that intersected the highway using ArcGIS Pro version 2.8. The time of day for each location was determined using the "crepuscule" function in the R package maptools (Bivand and Lewin-Koh, 2021). The function assigns each location the sun's altitude associated with its timestamp. We categorized those locations with the sun's altitude at less than 6 degrees from the horizon as night and more than 6 degrees as day (Bivand and Lewin-Koh, 2021). Next, we determined the weekly crossing rates per tiger before, during, and after the COVID lockdown to determine whether shifts in traffic patterns during the lockdown affected crossing behaviors. We tested the difference in number of crossings per week by time of day and during each lockdown period using a robust two-way ANOVA with 20% trimmed means with R package WRS2, function "t2way" to avoid violating assumptions of normality and homogeneity of variances due to skewed data (Mair and Wilcox, 2020). Post-hoc tests of the pairwise trimmed means ($\widehat{\psi}$) were conducted with the "mcp2atm" function of that package.

We also examined the influence of the highway on tigers' movement speeds. We compared movement speeds when crossing the highway and compared them to all other movement speeds when not crossing the road. Movement speed was calculated for each GPS path, that is, between two sequential locations (distance / time). The speed of movement paths that intersected the highway were compared to all other movement paths by performing a bootstrapped Welch two sample t-test with 10,000 iterations using the R package MKinfer (Kohl and Kohl, 2020). A bootstrapped t-test was chosen to adjust the confidence interval to account for the left-skewed distribution of speeds (Tibshirani and Efron, 1993). We then examined if movement speeds while crossing the highway varied by lockdown and by time of day using robust one-way ANOVAs with 20% trimmed means with R package WRS2, function "t1way" (Mair and Wilcox, 2020). We also plotted movement speeds pre-COVID lockdown, during the lockdown, and post-lockdown in the day and nighttime in relation to distance to the highway.

2.5. Calculating tiger space use area and daily distance moved

To determine the effects of the COVID lockdown on tiger space use areas, we estimated space use area per month before, during, and after the lockdown period. Space use areas for each tiger were modeled using area-corrected Autocorrelated Kernel Density Estimation with an Ornstein-Uhlenbeck process in the R package ctmm (Calabrese et al., 2016; Fleming and Calabrese, 2017). This method fits continuous time-movement models to the telemetry data that incorporate temporal autocorrelation structures, including Ornstein-Uhlenbeck and Ornstein-Uhlenbeck Foraging (Calabrese et al., 2016; Fleming and Calabrese, 2017). The most likely model is selected by AIC and then used to estimate the individual's space use area. To determine the effects of the COVID lockdown on tiger movements, we calculated the daily cumulative distance moved by each tiger. Step lengths were computed using the R package amt (Signer et al., 2019). Noon was used as the starting point of each day because tigers are typically active at night (Carter et al., 2012; Sunquist, 1981). We tested the differences in daily distance moved during each COVID policy period using a robust one-way ANOVA with 20% trimmed means in R package WRS2, function "t1way" (Mair and Wilcox, 2020). Post-hoc tests of the pairwise trimmed means ($\widehat{\psi}$) were conducted with the "lincon" function of that package.

2.6. Modeling tiger habitat selection

To determine the effect of the highway and the COVID lockdown policy on each tiger's behavior and ability to move through the landscape, we fit the GPS-collar location data to integrated step-selection functions (Avgar et al., 2016). These functions compare the values of covariates where the animal moved with those from a set of empirically-derived random locations to estimate habitat selection at the finest scale allowable by the data (Avgar et al., 2016; Fortin et al., 2005). They model habitat selection while also taking into account how the animal moves (length of steps, turn angles) under different conditions (Avgar et al., 2016; Fieberg et al., 2021).

To model the effects of the highway on habitat selection, we included the covariates: distance to road (m), distance to road squared (m), and permeability of the highway. We included distance to road squared because we suspected the effect of the highway on tiger movements could be non-linear (Benítez-López et al., 2010). Permeability was modeled as a binary covariate (0 or 1) indicating whether or not an individual tiger step crossed the highway. As such, steps taken by a tiger when not within crossing distance of the highway (i.e., the highway is not available to cross) did not contribute to the permeability effect size calculation (Robb et al., 2022). In addition, we expected that time of day (day or night, as defined above) and COVID lockdown policy period (pre-lockdown, during lockdown, or post-lockdown) would interact with distance to road and highway permeability. To rule out potential covarying effects, we also included the environmental attributes of distance to nearest river (m), canopy height (m), and distance to crop and built areas (m). River GIS data were extracted from OpenStreetMap using the R package osmdata. Canopy height data with 30 m horizontal resolution was derived from the Global Ecosystem Dynamics Investigation (Potapov et al., 2021). The highway GIS data were obtained from the Nepal Department of Roads. Crop and built areas were extracted from the European Space Agency's Sentinel-2 10 m land-cover dataset (Karra et al., 2021).

Next, we hypothesized that the movement characteristics of step length and turning angle would be influenced by distance to the nearest road, and further that step length would vary by time of day. Movement characteristics were parameterized as step length, log step length, and cosine of turning angle following Fieberg et al. (2021). Available steps were quantified by generating 10 random steps for each observed step using the "random_steps" function of the R package amt (Signer et al., 2019). All continuous variables were standardized by subtracting the mean and dividing by the standard deviation. Prior to inclusion in the model, Spearman's rank order correlation tests were run for all the observed and randomly generated covariate values of each tiger. Only distance to roads and distance to crop and built areas had a ρ value ≥ 0.7. Because this analysis is focused on roads, we eliminated distance to crop and built areas.

We used integrated step-selection models to fit the covariates to each tiger's steps with the function "fit_issf" in the R package amt (Signer et al., 2019). Beta coefficients with 95% confidence intervals were generated for each covariate as well as significance at the $p < 0.05$ level. We used the beta coefficients from the model to calculate Relative Selection Strength (RSS) between specific points in space and time, such as pre-lockdown and during lockdown or near and far from the highway (Avgar et al., 2017). This represents the ratio of the probability of a tiger occurring at a given point in space and time with particular attributes relative to another available point (Avgar et al., 2017; Fieberg et al., 2021). RSS values were based on each tiger's average step length.

The RSS for highway permeability is the probability that a tiger may have crossed the highway relative to if the highway were not present (Robb et al., 2022). RSS of < 1 suggests the highway acted as a barrier to tiger movement, and a RSS > 1 suggests that the highway increases tiger movement (Robb et al., 2022; Wadey et al., 2018). Interaction terms indicate the covariate's difference with respect to the reference category. For time of day, the reference category was day, and for COVID policy, the reference category was the pre-lockdown period. To illustrate differences in selection across a range of covariate values, we also calculated the log RSS. A log RSS of 0 indicates neutral selection, negative is selection against habitat with that attribute, and positive is selection for habitat with that attribute.

3. Results

3.1. Highway road traffic

The average daily traffic along the East-West Highway that passes through Parsa National Park declined 85% during the lockdown from 11,318 vehicles in February 2021 (pre-lockdown) to 1802 vehicles in May 2021 (lockdown). By February 2022 (post-lockdown)

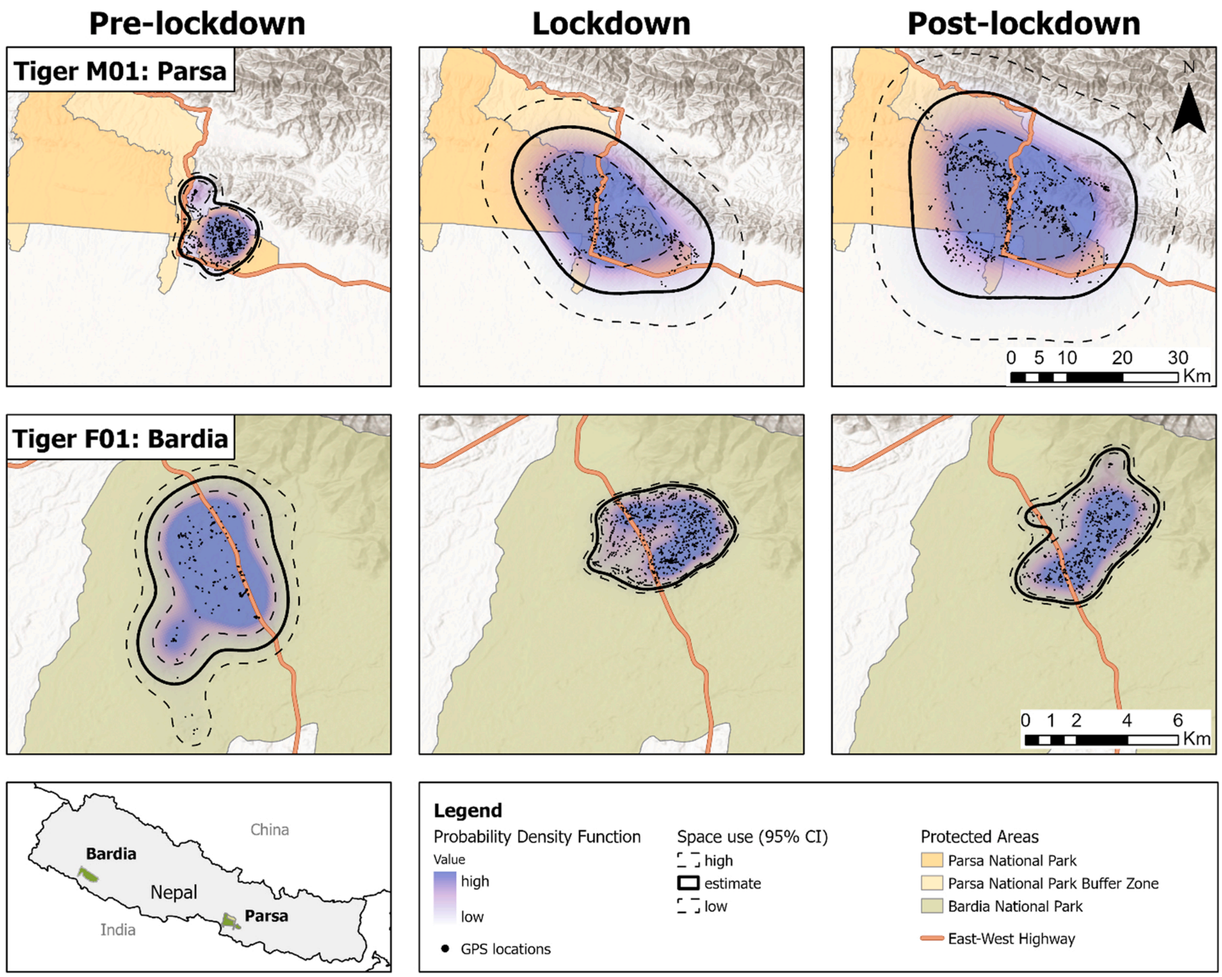

Fig. 1. Individual tiger space use areas in Bardia National Park (western Nepal) and Parsa National Park (central Nepal) during each COVID policy period (pre-lockdown, during lockdown, and post-lockdown). Space use areas and utilization probability density function were modeled using area-corrected Autocorrelated Kernel Density Estimation (OUF anisotropic model). The solid black outline represents the estimate and the dashed lines represent the low and high 95% confidence intervals.

average daily traffic counts increased to 9718 vehicles, nearly back to levels pre-lockdown. Average daily traffic on the highway adjacent to Bardia National Park (near the study site) was 10,633 vehicles in April 2021 (pre-lockdown) and increased post-lockdown to 12,123 vehicles. Although we do not have empirical data during lockdown within Bardia, we assumed that traffic reductions in Bardia were comparable to those in Parsa.

3.2. Tiger GPS data

Between February 2021 and March 2022, 8180 GPS locations were successfully obtained (2568 for the female tiger, 5612 for the male tiger; Fig. 1). The female and male tiger's GPS-collar stopped transmitting in November 2021 and March 2022, respectively. The overall GPS fix success rate for both tigers was 0.82 (number of successful fixes / number of attempted fixes).

3.3. Tiger road crossing

The male tiger crossed the highway 38 times over 56 weeks, approximately 0.68 times per week (Fig. 2). He crossed the highway significantly more during the lockdown period (0.79 times per week) than pre-lockdown (0.19 times per week), and significantly more at night (36 times) than during the day (2 times) (Table S1, $Q = 17.43$, $p = 0.002$). Additionally, during the lockdown, the male tiger was significantly more likely to cross the highway during the day compared to pre-lockdown ($Q = 17.43$, $p = 0.002$). The female tiger crossed the highway 204 times over 32 weeks, approximately 6.37 times per week. She also crossed approximately the same amount during the day (105 times) and the night (99 times). She showed no significant differences in crossing patterns by COVID policy or time of day.

Both the male ($t = 10.98$, $p < 0.0001$) and female ($t = 11.09$, $p < 0.0001$) tigers moved at significantly greater speeds when crossing the highway than when not crossing (Fig. S1). The male tiger moved especially fast, moving about 2.5 times as fast as the female (0.36 m/s compared to 0.14 m/s) when crossing the highway. While he crossed significantly faster during the night than day ($F[1, 21.8] = 106.29$, $p < 0.0001$), there was no difference in crossing speeds across COVID policy periods. However, during the lockdown, his movement speed for any step starting near (within 1 km linear distance) the highway reduced by more than half (e.g., 0.075–0.03 m/s during the daytime) compared to pre-lockdown (Fig. S2, Table S2). Like the male tiger, the female tiger's speeds while crossing the highway did not vary by COVID policy period, but were significantly higher at night ($F[1, 115.38] = 25.34$, $p < 0.001$). However, her speeds within 1 km of the highway were lower than the male tiger's speed, and did not vary by COVID policy period, averaging between 0.04 and 0.08 m/s across all periods and times of day.

3.4. Tiger space use areas and daily distances

The first month after lockdown the male tiger's space use area more than tripled in size (552.3 km^2 in May 2021) compared to the two months prior (~160 km^2 in both March and April 2021) (Fig. S3a). His space use area expanded even further in the post-lockdown period (Fig. 1). In contrast, the female tiger's space use area was at its maximum in the month before lockdown (April 2021) at 33.05 km^2 (Fig. S3b). It subsequently shrank to 15.53 km^2 in the first month of lockdown (May 2021). Her space use area expanded slightly post-lockdown to 16.75 km^2 in September and 20.93 km^2 in October 2021.

The male tiger's average daily distance moved was significantly less during lockdown (5.02 km/day) and post-lockdown (4.67 km/

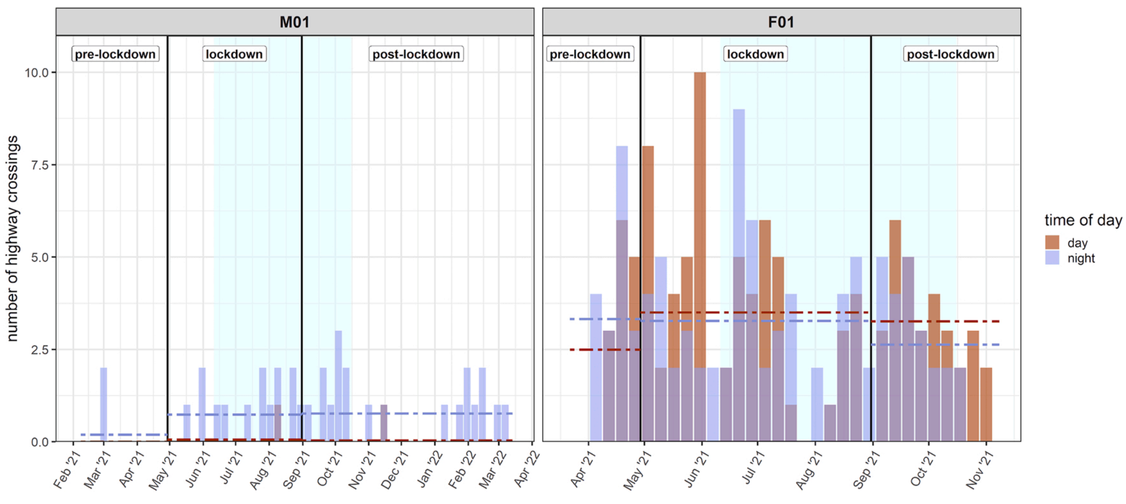

Fig. 2. Number of times per week each individual tiger crossed the East-West Highway during daytime and nighttime. The dashed lines indicate the number of crossings per week across each COVID policy period (pre-COVID lockdown, during COVID lockdown, or post-COVID lockdown) in the daytime and nighttime. The light blue shading represents the monsoon season in Nepal from 11 June to 16 October, 2021.

day) than pre-lockdown (7.74 km/day, $F[2, 103.33] = 8.04, p < 0.001$) (Table S3, Fig. S4). In contrast, the female tiger's average daily distance moved was significantly greater during lockdown (3.92 km/day) and post-lockdown (4.41 km/day) than pre-lockdown (2.78 km/day, $F[2, 53.6] = 7.57, p = 0.001$).

3.5. Tiger habitat selection

Both tigers changed their habitat selection and movement behaviors with respect to distance to roads, highway permeability, the COVID lockdown policy, and time of day (Fig. 3, Table S4). We found that the male tiger was significantly more likely to select locations further from a road, though this effect lessens slightly when he was far from a road ($\beta = -0.129$ [95% CI = −0.02, −0.24], $p < 0.0001$) (Fig. 4a). Distance to roads had a stronger negative effect on his habitat selection during the day than at night. For example, prior to the lockdown period and during the day he was 3.2 times more probable to select a location 2 km away from a road than 100 m away. Likewise, although the highway was a clear barrier to his movements, it was more permeable at night (Fig. 5a); when he was near the highway, he was 11.3 times more probable to not cross it than to cross during the day, and 2.2 times more probable to not cross it than to cross it at night. His avoidance of roads relaxed somewhat during the COVID lockdown and post-lockdown periods compared to the pre-lockdown period (Fig. 4a). He was also over 3 times more probable to cross the highway after the lockdown than before; however, the highway still reduced landscape permeability for the male during this period (Fig. 5a).

Unlike the male tiger, the female tiger was significantly more likely to select locations closer to a road (the highway was the only road in her site) rather than farther away from it ($\beta = -1.27$ [95% CI = 1.6, 0.95], $p < 0.0001$), and especially during the day ($\beta = -1.06$ [95% CI = −0.80, −1.32], $p < 0.001$) (Fig. 4b). In general, the highway acted as a barrier to her movement, though less so at night than during the day. This suggests that she preferred to stay close to the highway during the daytime but tended to cross it at night. However, the highway became more permeable to her during the lockdown period. She was over twice as probable to cross the highway during the lockdown than before.

4. Discussion

We found clear differences in movement patterns between the two tigers, likely reflecting differences in highway traffic patterns and regulations as well as ecological conditions at the two sites (Parsa and Bardia). The male tiger occupied an area in Parsa National Park where traffic speed limits on the highway were not enforced and traffic is constantly shipping goods back and forth between Nepal and India at all times of the day. The highway acted as a major barrier to his movement, evidenced by reduced permeability and his avoidance of areas near it. When he did walk near it, he often walked parallel to it instead of crossing it. Reductions in landscape permeability and space use related to major roads has been found elsewhere in other species, such as Asian elephants (*Elephas maximus*) in Malaysia, gray wolves (*Canis lupus*) in eastern Canada, and black bears (*Ursus americanus*) in Massachusetts, US (Lesmerises et al., 2013; Wadey et al., 2018; Zeller et al., 2020). In our study, the male tiger was especially cautious of the highway during the day when traffic was highest. Before the lockdown, he never crossed during the day. Combined, these multiple lines of evidence suggest that the male tiger is strongly avoiding human disturbance on the highway and this avoidance is pronounced during the day when traffic is greatest.

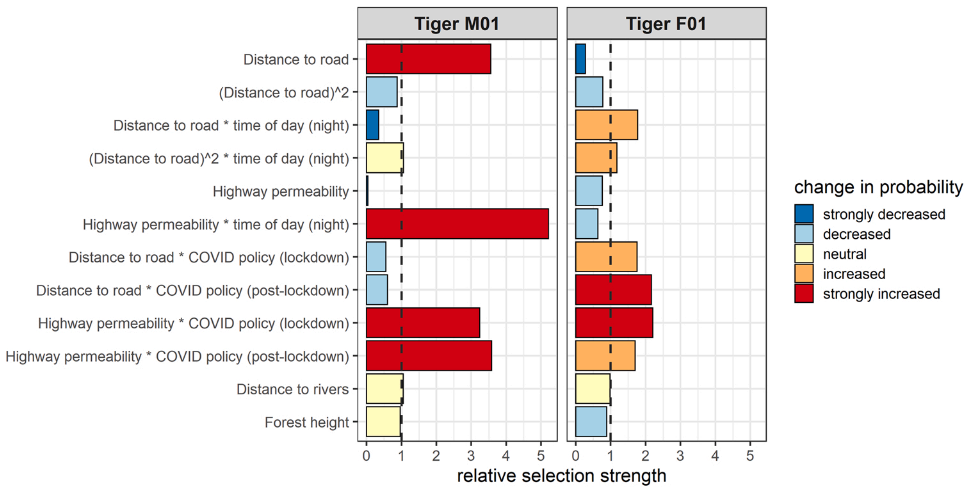

Fig. 3. Relative Selection Strength (RSS) for habitat covariates by individual tigers (Male, M01; Female, F01) in Nepal. RSS values are the exponentiated beta coefficients generated by the step-selection function. RSS$<$ 1 indicates a tiger has a decreased probability of selecting a given habitat covariate for one unit increase in that covariate. Conversely, for RSS > 1, a tiger has an increased probability of selecting a given habitat covariate for one unit increase. A covariate with RSS of 1 has no effect. Interaction terms indicate the difference with respect to the reference category. For time of day, the reference category is day, and for COVID policy, the reference category is the pre-lockdown period.

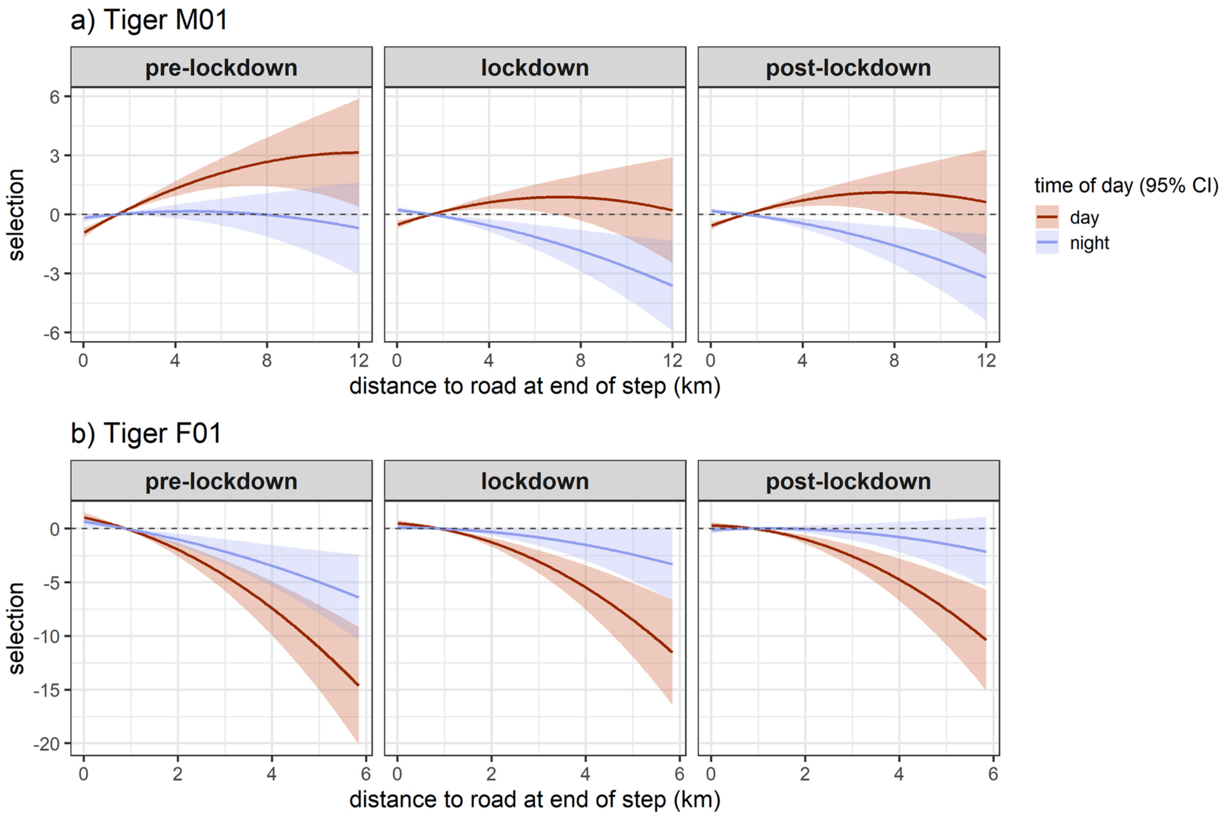

Fig. 4. Tiger habitat selection by distance to the nearest road for the male (a) and female (b) tiger pre-, during, and post-COVID lockdown periods in Nepal and during day and night with 95% confidence intervals. Selection is defined as the log Relative Selection Strength (RSS), which is measured relative to each tiger's mean distance from the road (male: 2.14 km; female: 1.24 km). Positive values indicate a preference relative to the mean distance, whereas negative values indicate avoidance relative to the mean distance.

Although the male tiger's space use and habitat selection were constrained by the highway, they were considerably relaxed during the COVID-19 lockdown when traffic volume declined dramatically. Instead of avoiding the road at all times, during the lockdown he began selecting locations near roads at nighttime. He also crossed the highway more frequently, especially at night but even a couple times during the day. With greater use of areas near roads and increased likelihood of crossing the highway, the male tiger greatly expanded his space use area to the west side of the highway immediately following the onset of the lockdown (Fig. 1) and before the start of the monsoon. This rapid expansion suggests that the high traffic pre-lockdown had constrained the male tiger's movements to one side of the highway. Cessation of traffic released the tiger from those constraints to roam more broadly. A similar pattern was found in Trento, Italy, where brown bears (*Ursus arctos*) approached roads more often and expanded their use of suitable areas after the pandemic lockdown (Corradini et al., 2021). Interestingly, in our case, the male tiger's space use area was never as small as it was before the lockdown, even after the lockdown had ended. It is possible that interactions with conspecifics (e.g., competition with another male) or greater familiarity with the road altered his ranging patterns post-lockdown compared to pre-lockdown. Furthermore, his space use area, especially after lockdown, was relatively large for the Terai region (Chanchani et al., 2014). In July, for example, he took large exploratory movements outside his typical core area, leading to a large space use area with large confidence intervals (Fig. S3). His large space use area reflects a lower prey density in Parsa than in the adjacent Chitwan National Park or more distant Bardia National Park (Lamichhane et al., 2018). However, prey densities have increased in Parsa over the last few years contributing to a growing tiger population in the area (Lamichhane et al., 2018).

Both the male and female tiger moved more quickly when near the highway, and especially while crossing, than when far from the highway (Fig. S1 and S2). The tigers' differential speed relative to the road also suggests they use energy differently in the presence of the highway than they would if it were absent. Furthermore, the greater daily distance moved by the male tiger before the lockdown suggests that the high-traffic disturbance during that period likely increased his energy use. Higher energy use near roads has been shown for other species. For example, turtles and snakes in North America traveled longer and expended more energy per day when roads were present in their home ranges than when they were not (Paterson et al., 2019). Cougars also have higher energetic costs and resource requirements in human-dominated landscapes (Wang et al., 2017). Energy used to frequently avoid a road might come at the expense of other metabolic functions and behaviors, as well as have lasting effects on individual fitness. An assessment of energetic usage (e.g., metabolic demands, hunting success) by tigers relative to the highway is an important aspect of research in the future.

In contrast to the male tiger in Parsa, the female tiger occupied an area where traffic speed was highly controlled using a timed

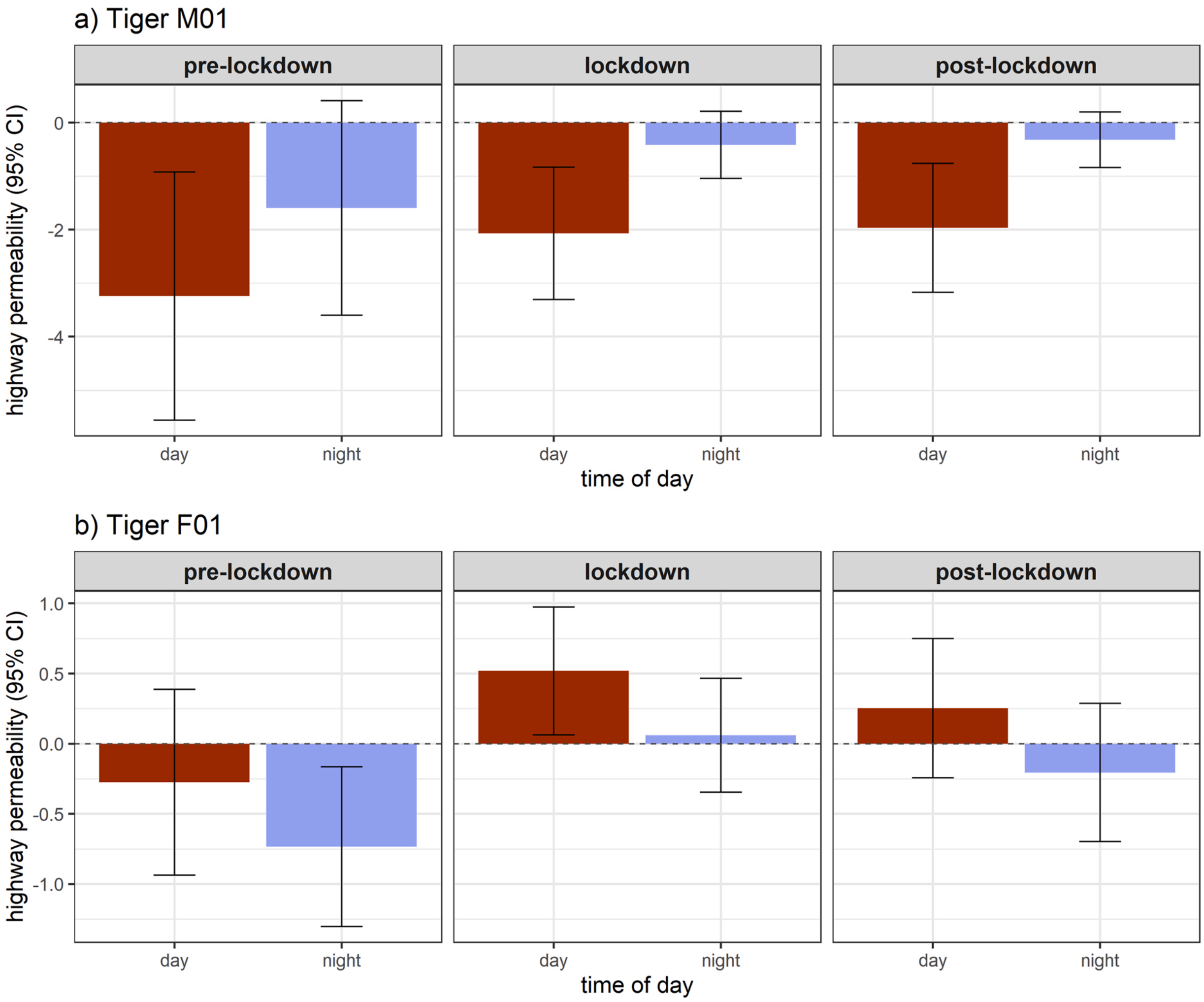

Fig. 5. Permeability of the highway by tigers in Nepal. Permeability for the male (a) and female (b) are represented by log Relative Selection Strength (RSS) pre-, during, and post-COVID lockdown periods and during day and night with 95% confidence intervals. Here, permeability is the degree to which tigers choose to cross the highway relative to remaining on the same side. Negative values indicate a tiger avoids crossing the highway, and positive values indicate that a tiger prefers to cross it. All other covariate values not mentioned are held constant.

entry/exit system enforced with fines by armed park guards. She crossed frequently before, during, and after the lockdown. In fact, she crossed about 10 times more often per week than the male tiger, despite the male having longer movements and a much larger space use area. The lower traffic volume and strict regulation of speed in Bardia via fines likely reduced overall disturbance from vehicles on the female, enabling her to cross the highway more freely than the male in Parsa. In addition, the flow of traffic in Bardia is likely more predictable than it is in Parsa, as vehicle entry in Bardia is controlled, and motorists are not allowed to stop and are kept within a small range of speeds. Previous work shows that predictable stimuli—e.g., smooth flowing traffic that stays on roads—are less evocative of a behavioral response by animals than less predictable stimuli—e.g., bikers or hikers off road (Ciuti et al., 2012; Stankowich, 2008). We posit that the female has habituated to the highway traffic in Bardia, evoking a limited behavioral response.

Although the female's movements appear less constrained by the highway than the male, normal traffic patterns before the lockdown may still have suppressed her movements. The near elimination of traffic volume during the lockdown likely reduced human disturbance from vehicles, making the highway more permeable to the female tiger during that time period. Her space use area was centered on the highway throughout the period she was collared. However, her space use area shrank to less than half its size (33–15 km^2) after the start of the lockdown (Fig. 1). She also started moving greater distances within her space use area. It is unclear whether these different movement patterns were because of changes in traffic patterns during the lockdown or because of other ecological interactions, such as changes to prey distributions or interactions with conspecifics (e.g., mates). It is possible, for example, that she adjusted her movements to take advantage of more abundant, concentrated prey during and directly after the monsoon. Indeed, higher tiger prey abundances were found post-monsoon compared to pre-monsoon periods in Similipal Tiger Reserve, India (Upadhyay et al., 2019). However, it is unlikely the monsoon caused the shrinkage in her space use area since it shrank immediately following the lockdown and just before the onset of the monsoon. Furthermore, there was no evidence (from pug marks or camera trap photos) that she had any cubs while collared, which may have altered her space use patterns. These unknowns underscore the need for future research to understand how the highway affects tiger interactions with prey and other tigers.

Although we are unable to make inferences on population-level responses to road networks in the Nepal Terai, we found that the highway and its road traffic clearly affects the space use, habitat selection, and movements of individual tigers. Based on the precautionary principle—to take action before the harm occurs—we urge policy makers to mitigate the impacts and human disturbances to tigers caused by the expansion of the highway from two to four lanes before it is too late (Kanongdate et al., 2012). In Parsa, where unregulated road traffic impeded male movements, placing wildlife crossing structures (underpasses or overpasses) at optimal locations will likely enable tigers and their prey to move across the highway more freely and thus support tiger recovery. Likewise, enforcing speed limits on the highway through Parsa—through signs, speed bumps, speed traps, and strict fines to speed limit infractions—would decrease the human disturbances associated with traffic and likely increase highway permeability for tigers. Limiting disturbance from traffic at night is especially important, as tigers and other animals cross frequently at nighttime and collisions with vehicles are more likely. Ensuring that the highway expansion does not disturb forests in the Terai should be top priorities for tiger conservation efforts.

CRediT authorship contribution statement

N.H.C., N.M.B.P., N.S., B.R.L., K.D.H conceived of the idea. N.H.C. wrote the paper and contributed to the analysis. A.Z. performed the analysis. All authors contributed to the drafts of the paper.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02388.

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