



Roads as dynamic stressors: physiological response of mule deer to roads differs during range residency and migration

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Abstract

Context Wildlife responses to disturbance may include physiological stress responses that are often difficult to observe yet important for wildlife health. Coupling physiological biologgers with tracking data can identify anthropogenic features associated with stress responses. Diagnosing when, where, and the response to stressors, along with how species may

habituate or sensitize to stressors over time, is crucial for conservation efforts.

Objectives We examined if mule deer (*Odocoileus hemionus*) exhibited acute stress responses to road crossings, identified the road features and contexts associated with the size of response, and determined factors that influence the response through repeated exposures over time.

Methods We used GPS locations paired with cardiac monitors across three regions of Utah, USA to measure fine-scale changes in deer heart rates during road crossings. We measured dynamic traffic patterns

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using human mobility data (HMD) to characterize associated traffic volumes during crossing events.

Results Road crossing events were associated with detectable heart rate spike (30.6 bpm) and elevated mean heart rate (8.3%) in deer. Road crossings with higher HMD derived traffic volume resulted in greater heart rate spikes during migration (46%) and summer (24%) seasons. Habituation among deer correlated with higher frequency of crossings and better body condition, while sensitization correlated with higher traffic presence and higher road density.

Conclusions Our findings highlight the stress response to roads and the factors driving the magnitude of the response. Integrating fine-scale physiological data with animal movement and human mobility data offers a means to diagnose dynamic stressors on the landscape at both broad and fine spatial and temporal scales for wildlife.

Keywords Heart rate · Human mobility data · Stress response · GPS tracking · Biologging · Road ecology · *Odocoileus hemionus*

Introduction

Habitat fragmentation and the resulting barriers to movement have long been concerns of wildlife habitat management in the rapidly developing western United States, which contains many of the continent's remaining terrestrial migratory species (Theobald and Romme 2007; Polfus and Krausman 2012). In addition to disrupted movement and habitat connectivity, human development and presence introduce novel stressors that may exceed adaptive capacity, thus leading to loss of resiliency to repeated disturbance (Lowry et al. 2013). Repeated exposure to human disturbance has been shown in some instances to negatively affect energy expenditure through behavioral changes and increased stress (Creel et al. 2002; Wilson et al. 2020). As a result, this persistent 'wear-and-tear,' or allostatic response, has the potential to decrease survivorship and recruitment, thus negatively affecting long-term persistence of populations (Wingfield and Sapolsky 2003; Wahl et al. 2011). Nevertheless, the exact role that repeated disturbances play in causing acute stress events remains underexplored.

Roads can have acute demographic impacts on wildlife via vehicle strikes (Coffin 2007; Beckmann and Lackey 2008). Roads can also alter behavior and movement (Shepard et al. 2008; LaPoint et al. 2013) and are a potential source of acute (e.g., minutes to hours; Ditmer et al. 2018) and chronic physiological stress (e.g., days to weeks; Arregi et al. 2024). Vehicles represent an unpredictable disturbance to wildlife that can result in an anticipatory stress response, one which requires cognitive processing rather than a direct physiological challenge to homeostasis (Boonstra 2013). These acute stress responses can occur in close proximity to a road, during a crossing event, or possibly after crossing (Ditmer et al. 2018; Brieger et al. 2022). Repeated exposure to stressors can result in either habituation, a decrease in response through time, or sensitization, an increase in response through time (Bejder et al. 2009).

Diagnosing whether a response is habituation or sensitization requires sequential measurements from the same individual through time (Bejder et al. 2009). Most studies aiming to quantify stress associated with roadways use glucocorticoids from fecal sampling (Lunde et al. 2016; Karaer et al. 2023), which introduces a large amount of temporal and spatial uncertainty in the relationship due to the coarse temporal nature of hormone sampling (but see Ditmer et al. 2018). However, biologging technology permits the use of additional near-real time physiological biomarkers (e.g., heart rate) to identify and quantify stressful events and responses in wildlife (Ditmer et al. 2018). The result is that studies can quantify stress caused by specific features, rather than aggregate measures, through the course of monitoring.

Recently, the use of anonymous human mobility data (HMD) has enhanced the resolution at which we can measure and compare exposure of wildlife to humans across the landscape (Abernathy et al. 2025a, b), thus permitting insight into direct effects of human presence on stress in animals. Traditional approaches for quantifying wildlife responses to roadways are static (e.g., distance to road, road density) and fail to capture the dynamic impact of vehicles – although some studies have used temporally aggregated metrics for traffic data (e.g., Frank et al. 2023). HMD offers much finer temporal resolution estimates of traffic compared with previous approaches because it is based on mobile phone applications transmitting locations on any roadway

rather than monitoring specific road segments for metrics like annual average daily traffic (Wang et al. 2013; Hu et al. 2021). Therefore, the use of biologists, GPS tracking, and HMD in tandem can offer unparalleled insight into the dynamics of stress responses relative to human activity levels at very fine temporal resolution.

Mule deer (*Odocoileus hemionus*; hereafter ‘deer’), an ungulate found throughout western North American ecosystems, often conduct seasonal migrations between summer and winter ranges. Many deer populations inhabiting snow-dominated systems have declined in abundance in response to increasing residential and energy development (Johnson et al. 2017) and associated increase in vehicle strikes (Olson 2013). The migratory routes that individuals take between ranges can also put them at risk of mortality through direct (e.g., vehicular collisions) or indirect (e.g., resource fragmentation) impacts (Coe et al. 2015). The selection of migratory routes and summer range has been shown to reduce survivorship in mule deer inhabiting areas close to residential development and roads (Sawyer et al. 2019). Consequently, as deer navigate changing anthropogenic landscapes, individuals may be more prone to an accumulation of external stressors that can negatively affect individual health and ultimately fitness (Cooke et al. 2024). Determining the explicit stressors for deer is a priority given concern over their economic value and population trajectories.

We complemented traditional GPS tracking with physiological biologists to monitor the heart rates of mule deer within three distinct regions in Utah, USA, and relate their physiology with fine-scale traffic data collected through anonymous HMD locations. We tested the hypothesis that road crossings would elicit a stress response in deer as identified by an elevated heart rate and/or heart rate spike compared to non-road crossing events. We addressed three questions: 1) What is the magnitude of change in heart rate parameters during road crossings? 2) When and where do the most acute physiological responses to roads occur, and what other aspects of a road segment (e.g., traffic volume, building density, vegetative cover) influence the magnitude of the physiological responses? 3) Do deer exhibit signs of habituation or sensitization with repeated road crossings? We discuss the implications of our results for landscape conservation efforts for deer.

Methods

Study area

We selected three sites across the state of Utah that reflected a climatic gradient. Sites also varied with respect to topographic features, snowpack, and human development intensity (Fig. 1).

The northernmost site, (1) Bear River Mountains (latitude: 41°N, hereafter ‘Cache’), and the middle site, (2) Mount Nebo (latitude: 39.5°N, hereafter ‘Nebo’), are predominately continental climate with hot summers, along with dry, hot semi-arid steppe precipitation (low humidity, low rainfall) (Beck et al. 2023). Both northern sites are characterized by a mix of highly developed valleys and adjacent, low-development mountains (1350 – 3100 m). The southernmost site, (3) Pine Valley Mountains (latitude: 37.3°N, hereafter ‘Pine Valley’), is a dry climate with hot summers and arid to semi-arid steppe precipitation (Beck et al. 2023).

Animal handling and collaring

Mule Deer used in this study were part of a larger monitoring program by the Utah Division of Wildlife Resources (UT DWR) in Utah, USA. Between November 2021 and March 2024, adult (1+year) female mule deer were captured via a net gun fired from a helicopter, physically restrained, and brought to staging areas where they were processed (Van de Kerk et al. 2020; Brigham Young University IACUC protocol: #150110). Deer were fitted with GPS radio-collars (Model G5-2DH, Advanced Telemetry Systems Inc., Isanti, MN, USA, 700 g) that were programmed to record location fixes every 2-h. We collected data on animal weight (kg), measured maximum rump fat (Stephenson et al. 1998), assessed body condition (Cook et al. 2010), and aged all deer using tooth wear and eruption patterns (Robinette et al. 1957; Hinton et al. 2023). We released all deer at the processing site immediately following data collection.

Biologging implantation

Mule deer were implanted with modified cardiac event recorders (Medtronic Inc., Reveal LINQ™, 1.2 cc; 4.0 mm×7.2 mm×44.8 mm; 2.4 g;

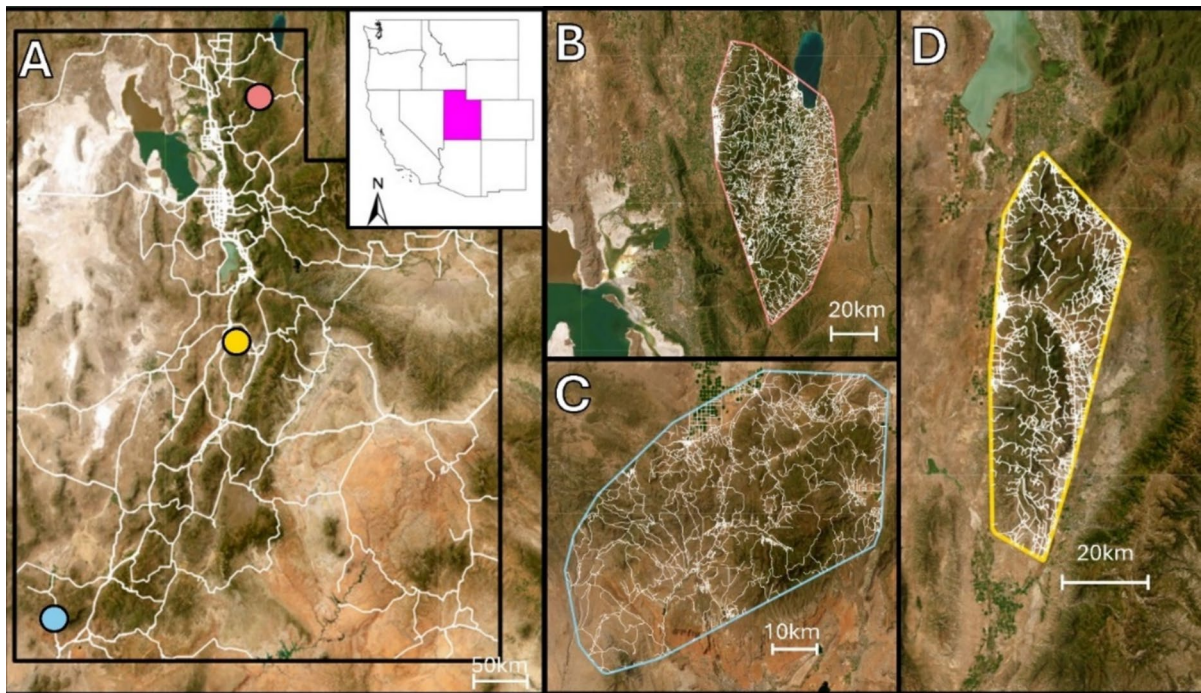


Fig. 1 Field sites in Utah, USA for (A) Bear River Mountains (Cache, Red), Mount Nebo (Nebo, yellow), and Pine Valley mountains (Pine Valley, blue) with white lines showing major highways throughout the sites. Inset shows Utah (purple) in the Western United States. Side panels show the 100% convex hull

around all mule deer locations along with roads (white) from the US Census TIGER/Line Files for (B) Cache (road density = 1.39 km/km²), (C) Pine Valley (road density = 0.95 km/km²), and (D) Nebo (road density = 1.27 km/km²). All images are oriented north with appropriate scale bars

lifespan: ~2–3 years; B-Ware custom software). Devices were inserted subcutaneously on the left side of the midthoracic region above the heart using an aseptic technique by a field veterinarian (Utah State University IACUC protocol: #13,045). Each recorder monitored cardiac (ECG) events continuously to provide mean heart rate at 2-min intervals. Data were downloaded via transcutaneous telemetry (CareLink™ Model 2090 Programmer with software Model SW007, Medtronic Inc., Minneapolis, MN; Laske et al. 2018) in spring (late-February/March) or winter (late-November/December) during subsequent recapture of animals.

Integrating physiological and ecological parameters

Question 1: identifying physiological responses to road crossings

To identify the magnitude of change in heart rate parameters during road crossings, we compared two

heart rate metrics during crossing and non-crossing events for all recorded deer locations. GPS locations from collared deer were used to identify crossing events based on intersections between a road (USGS 2021) and the line derived from two consecutive GPS points. The 2-h sampling of GPS locations from the collars served as a window for obtaining two metrics of acute stress response: mean heart rate and heart rate spike. For each individual, we calculated the mean heart rate (in beats per minute), derived from the average of all 60 2-min interval measures that occurred during the 2-h movement step (i.e., two consecutive GPS points from a deer). In addition, we calculated the maximum heart rate spike as the largest increase in heart rate between consecutive 2-min interval measures. While the exact timing of road crossings is unknown, our conservative (mean heart rate) and liberal (heart rate spike) metrics of acute stress response during the 2-h window provide underlying physiological insight at two different time scales during a road crossing. For instance, rapid increases

in heart rate, a metric captured at the 2-min resolution, indicate an acute stress response to a disturbance (Chabot et al. 1990; Dittmer et al. 2015), whereas the mean heart rate, a more conservative metric that covers the entire 2 h duration, captures a sustained response of elevated heart rate to a disturbance (Moen et al. 1982; Reimoser 2012).

Mule deer often migrate between summer and winter ranges depending on available forage resources (Schuyler et al. 2021), and as a result cross roads during different times of the year. Therefore, we identified migration, summer range residency, winter range residency, and year-round residents using a methodology similar to van de Kerk et al. (2021) (Fig. S1). For each mule deer, we calculated the net squared displacement (NSD) starting from the first location occurring four days after capture (Northrup et al. 2014) within the winter range in December using the *adehabitatLT* R package (Calenge 2006). The NSD was treated as a time-series, and we used the *strucchange* R package (Zeileis et al. 2003) to identify breakpoints. To determine whether a breakpoint indicated a range shift (e.g., winter to summer range), we used the *overlapping* R package (Pastore 2018) to identify overlap between the density distribution of NSD values between consecutive segments. For each unique breakpoint, we assigned the preceding and subsequent seven days to characterize migration, whereas winter and summer ranges were defined as where the largest proportion of time was spent during summer months (May–October) or winter months (November–April). If we did not identify unique summer or winter ranges, we classified those deer as year-round residents. All three sites had migratory deer ($n_{\text{Cache}}=9$; $n_{\text{Nebo}}=9$; $n_{\text{Pine Valley}}=11$) that had been monitored for a total of 10,644 deer days (Cache=3625 days; Nebo=2395 days; Pine Valley=4624 days), ranging from 54 to 813 days per individual. This resulted in a total of 105 deer seasons across the three sites (migration: $n_{\text{Cache}}=10$, $n_{\text{Nebo}}=5$, $n_{\text{Pine Valley}}=12$; summer range residency: $n_{\text{Cache}}=9$, $n_{\text{Nebo}}=4$, $n_{\text{Pine Valley}}=10$; winter range residency: $n_{\text{Cache}}=18$, $n_{\text{Nebo}}=15$, $n_{\text{Pine Valley}}=22$). Only the two northern sites had year-round residents ($n_{\text{Cache}}=2$; $n_{\text{Nebo}}=1$) and these individuals were removed from subsequent analyses.

We created models for both heart rate metrics, mean heart rate and heart rate spike (log-transformed), using generalized additive mixed models

(GAMM) with Gaussian distributions to compare movement steps that intersected roads (i.e., crossing event) and all other movement steps where roads were not crossed (i.e., non-crossing event). Fixed effects included road crossing events (binary; crossing=1), whether deer were occupying summer range residency, winter range residency, or migrating, and movement rate (km/hr). Movement rates during a crossing event ranged from 0–1.52 km/hr, and 0–1.58 km/hr during non-road crossing events. We included an interaction between movement rate and crossing to account for changes in physiological markers with activity level. We also included a cyclic cubic regression spline for month to capture annual temporal variation. Each model had a random effect for deer ID and random slope for month to capture individual variability. Our dataset consisted of over 100,000 movement steps, with over 7000 being classified as crossing events.

Question 2: ecological drivers of acute physiological responses during road crossings

To determine the factors associated with when and where the most acute physiological responses to roads occur, we focused explicitly on road crossing events within the deer dataset. We quantified forest cover for each movement step using data from the U.S. National Land Cover Database (NLCD) at a 30 m resolution for 2021 (Dewitz 2021). We calculated the percentage of forest cover raster cells that intersected each movement step. We only quantified forest because it was the only significant land cover type in our study area besides shrub/scrub, which otherwise dominated the region and served as the reference category against forest cover. We used the *prism* R package (Hart and Bell 2015) to define average daily temperature at each location with a spatial resolution of ~4 km×4 km. We mapped aboveground biomass at 30 m, annual resolution across the study region from 2021 to 2024 using a machine learning model (gradient-boosted regression tree; (Prokhorenkova et al. 2018)). The model was trained on Global Ecosystem Dynamics Investigation (GEDI) L4A footprint level biomass data (Dubayah et al. 2022) with Landsat-based tree cover (Sexton et al. 2013), Normalized Difference Vegetation Index, stand age, and other covariates for spatially continuous predictions of aboveground biomass (Mg/ha).

To account for the level of anthropogenic development around each crossing, we calculated building density along each road crossing segment. We buffered each road crossing intersection by 50 m and counted the number of building footprint centroids derived from Microsoft Building Footprints dataset (Microsoft 2018), then divided by the road segment length. Speed limits (miles per hour, mph) were based on the Utah Geospatial Resource Center roads (UGRC 2021). When speed limits were not associated with a road (e.g., dirt road, National Forest secondary roads), we assumed that the speed limit was 25 mph.

We developed an index of traffic volume using data from anonymized smartphone GPS locations (human mobility data, HMD). The HMD data were collected from software development kits that are integrated into mobile applications. The HMD were compiled and managed by Unacast, Inc. (formerly Gravy Analytics). These data represent approximately 10–15% of all smartphone users from undisclosed data providers who adhere to regulations of the California Consumer Privacy Act and the European General Data Protection Regulation.

HMD from each month that overlapped with our study temporally and spatially were filtered to remove low accuracy fixes, unrealistic movement speeds, and other potentially incorrect spatial information based on quality flags within the data. We removed any locations that occurred within 5 m of the building footprint data (Microsoft 2018) because we associated these fixes with smartphone users that may not be operating a vehicle. We then counted the remaining HMD locations within each 50-m buffered road segment that deer crossed by year, month, day of the week (to consider traffic volume on weekdays vs. weekends), and by time of day (i.e., night, crepuscular, day) using the *suncalc* R package (Thieurmél et al. 2019). As a result, we were able to associate each road crossing by our sampled deer with an average relative estimate of traffic volume during the time of day, week, and month of crossing (e.g., average traffic during daylight hours, on the weekend, during May). The corresponding HMD values for each road segment, assigned a season (migration, summer or winter range residency), weekday or weekend, and time of day. All crossing events were associated with the altitude of the sun, representing the amount of daylight, using the *suncalc* R package (Thieurmél

et al. 2019). Lastly, for each deer, we calculated the time since the last crossing (hours) from a specific crossing event as a measure of road exposure.

To identify external factors that influenced the magnitude of acute physiological responses to road crossings, we modeled the same heart rate metrics. We accounted for environmental, temporal, and other anthropogenic covariates associated with crossed road segments. Our models included covariates for vehicle speed limit (mph), building density (count/km), traffic volume (average vehicle count), forest cover (%), and biomass (Mg/ha). We also included variables for sun altitude (measuring amount of daylight), amount of time since last crossing (hours), deer movement rate (km/hr), and ambient temperature (°C) during the movement step associated with each crossing. We ran a separate GAMM model for each season (migration, summer range residency, or winter range residency). Similar to the first set of models, we included a cyclic cubic regression spline for Julian date, and we included deer ID as a random effect. All covariates were centered and scaled per individual within each model. All GAMMs were run using the *mcgv* R package (Wood and Wood 2015) in R v4.4.3 (R Core Team, 2025).

Question 3: modeling responsiveness to road crossings over time

We determined whether deer exhibited signs of habituation or sensitization to repeated road crossings by assessing responsiveness of deer throughout the time monitored. We (1) evaluated whether individuals' physiological responses as heart rate spikes increased (sensitization) or decreased (habituation) over time, and (2) identified factors influencing these patterns. First, we modeled the heart rate spike during each crossing through time by including a covariate representing the length of time from the first road crossing event to each subsequent crossing event, which we centered and scaled per individual. We included a random intercept for deer ID and a random slope for length of time from the individual's first road crossing event. We obtained individual slope coefficients from the main model and ran 10,000 bootstrap iterations to derive a 95% confidence interval (CI) per individual using the *boot* R package (Canty and Ripley 2017). We considered an individual slope coefficient to be statistically significant if its 95% bootstrap CI did

not include zero. Negative estimates would indicate a waning of response to repeated road crossing (i.e., habituation), while positive estimates would indicate increased responsiveness over time to repeated road crossing (i.e., sensitization).

Second, we obtained metrics associated with body condition (ordinal scale) and age (years) for each deer, measures of the built-surroundings within each deer's home range (road density [km/km^2], building density in home range [count/km^2]) and three indices of crossing experience (frequency of road crossing [crossing/day], proportion of roads crossed with traffic present [binary response], proportion of roads crossed by deer with speed limits greater than 40 mph [binary response], and proportion of road crossed during winter range residency) to identify possible covariates that could lead individuals to habituate or sensitize more to repeated road crossings.

Body condition (Cook et al. 2010) and estimated ages from dental wear (Hewison et al. 1999; Hamlin et al. 2000; Hinton et al. 2023) were taken during standard captures by UTDWR. Home range for subsequent road and building density estimates of covariates was determined using 95% MCP for the entire time deer were monitored to better understand exposure to modified landscapes (Calenge 2006). We determined road density using the USGS roads shapefile (USGS 2021) and building density from the centroids of the Microsoft Building Footprints dataset (Microsoft 2018), divided by the area of the home range, for each individual deer. The frequency of road crossing was calculated as the total number of crossings divided by the time in days that an individual deer was monitored. We developed metrics for the proportion of road crossings: (1) occurring within winter range (as a means of comparison to summer range and migration), (2) presence of traffic during road crossing, and (3) roads crossed where speed limits exceed 40 mph, by the total number of road crossings of each deer.

We then determined whether individual covariates had a better fit with the data as linear or non-linear functions (Fig. S2), which resulted in frequency of crossing and road density being included in subsequent linear regression models with a B-spline (ns() from *splines* R package, $\text{df}=2$; R Core Team 2025). Given our sample size of 28 individuals with significant slope coefficients, linear regression models had a maximum of three unique covariates, or two

unique covariates with an interaction. We compared all combinations of covariates and selected the most parsimonious models based on $\Delta\text{AICc} < 2$ for model averaging using the *MuMIn* R package (Bartoń 2022).

Results

Do road crossing events elicit acute stress responses?

Mule deer heart rates exhibited significant spikes during crossing events, with an average increase of 30.6 bpm ($\beta_{\text{crossing}} = 0.094 \pm 0.008$, $p < 0.001$) relative to movements without a road crossing, suggestive of a short-term acute stress response (Table S1; Fig. 2C). During road crossings, we found a decoupling of heart and movement rates where there was little effect of movement rate on heart rate spikes, indicating that short term acute stress responses were triggered by the crossing itself. In contrast, during non-crossing events heart rate spikes increased with accelerated movement rates (Fig. 2A).

Seasonal ranges and migration also influenced short-term acute stress responses. The magnitude of short-term acute stress response was most pronounced during winter range residency (27.9 bpm), followed by migration (26.8 bpm average spike; $\beta_{\text{migration}} = -0.036 \pm 0.006$, $p < 0.001$) and summer range residency (25.6 bpm average spike; $\beta_{\text{summer range}} = -0.084 \pm 0.006$, $p < 0.001$) (Table S1). Mule deer heart rate spikes varied significantly across the year (month, smoother, $p < 0.001$; Fig. S3A).

Mule deer mean heart rates were elevated by an average 8.3% when crossing a road relative to non-crossing events ($\beta_{\text{crossing}} = 6.7 \pm 0.22$, $p < 0.001$) (Table S1), also indicating a sustained acute stress response during road crossing. The interaction between movement rate and mean heart rate during crossing showed a more muted response where mean heart rate increased less with movement speed during crossing than during non-crossing events (Fig. 2B). Although crossing events during migration ($\beta_{\text{migration}} = -1.85 \pm 0.17$ bpm, $p < 0.001$) and summer range residency ($\beta_{\text{summer range}} = -1.08 \pm 0.19$ bpm, $p < 0.001$) showed slightly lower heart rate increases compared to during winter range residency, the road crossing effect remained consistently elevated across all three seasons (Table S1). Mean heart rate showed

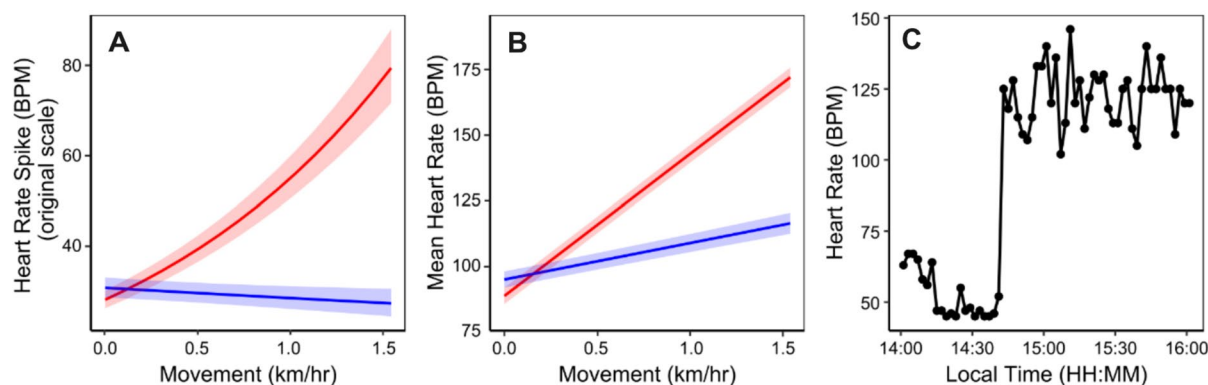


Fig. 2 The decoupling of movement rate and heart rate parameters during crossings (blue=cross; red=non-crossing) provides evidence that roads function as landscape-level stressors that trigger stress responses largely independent of physical exertion. **(A)** Effect plot of heart rate spike across gradient of movement rates showing that during road crossing (blue), spikes remain relatively constant across increasing movement rates. **(B)** Effect plot of mean heart rate during a step length

during road crossing (blue) does not increase to the same degree as non-crossing events (red). Non-crossing step lengths in both metrics display a positive association between movement rate and heart rate parameter. **(C)** Example of 2-min heart rate (black dots) during a road crossing step showing the rapid spike, and sustained elevated heart rate. Movement rates during a crossing event ranged from 0–1.52 km/hr, and 0–1.58 km/hr during non-road crossing events

significant cyclic variation throughout the year (month, smoother $p < 0.001$; Fig. S3B).

What factors influenced the magnitude of acute stress responses during road crossing events? Heart rate spikes in mule deer were most strongly influenced by traffic volume during migration road crossings ($\beta_{\text{traffic volume}} = 0.037 \pm 0.016$, $p = 0.017$), summer range residency road crossings ($\beta_{\text{traffic volume}} = 0.017 \pm 0.0076$, $p = 0.025$), and by time since last crossing ($\beta_{\text{last cross}} = 0.012 \pm 0.005$, $p = 0.024$) during winter range residency (Fig. 3A).

During migration, the magnitude of a heart rate spike during road crossings increased by 46.3% [95% CI: 15.8, 84.9%] over the observed range of scaled traffic volume compared to a 24.1% [95% CI: 10.8, 38.9%] increase during summer range residency crossings (Fig. 4).

During the winter range residency, heart rate spikes increased 12.0% [95% CI: 10.2, 13.8%] across time since previous crossing, indicating a seasonal shift in the primary driver of short-term acute stress response. Other external factors were correlated with the heart rate spike during crossing, such as crossing at night during migration (27.7% [95% CI: 27.6, 27.9%]; $\beta_{\text{sun altitude}} = -0.066 \pm 0.013$, $p < 0.001$) and summer range residency (9.6% [95% CI: 9.0, 10.2%]; $\beta_{\text{sun altitude}} = -0.017 \pm 0.007$, $p = 0.021$). During summer range residency, heart

rate spikes increased with forest cover (18.9% [95% CI: 14.8, 23.2%]; $\beta_{\text{forest}} = 0.020 \pm 0.008$, $p = 0.012$) and temperature (16.3% [11.8, 21.0%]; $\beta_{\text{average temperature}} = 0.023 \pm 0.011$, $p = 0.026$). In winter, spikes declined with warmer temperatures (−9.9% [8.1, 11.7%]; $\beta_{\text{average temperature}} = -0.016 \pm 0.007$, $p = 0.018$) and faster movement (−11.1% [9.0, 13.3%]; $\beta_{\text{movement rate}} = -0.012 \pm 0.006$, $p < 0.001$), indicating less acute stress responses during periods of higher temperatures and faster movements. Seasonal smoothers were significant in summer and winter (Julian date: $p < 0.001$) but not during migration ($p = 0.37$; Fig. S4A).

Mule deer mean heart rates during the entire movement step crossing a roadway had similar influence of sun altitude increasing heart rate but contrasting effects of building density on heart rate during migration and winter range residency. Higher building density was associated with increased heart rates during migration ($\beta_{\text{building density}} = 1.71 \pm 0.66$, $p = 0.010$), but decreased heart rates during winter range residency ($\beta_{\text{building density}} = -0.47 \pm 0.22$, $p = 0.034$; Figs. 3B, 5) during crossing.

Other external factors also affected mean heart rate (Fig. 3B). For instance, time since last crossing had a similar effect of higher mean heart rates the longer it had been since crossing a road. Mean heart rate increased at night during crossings;

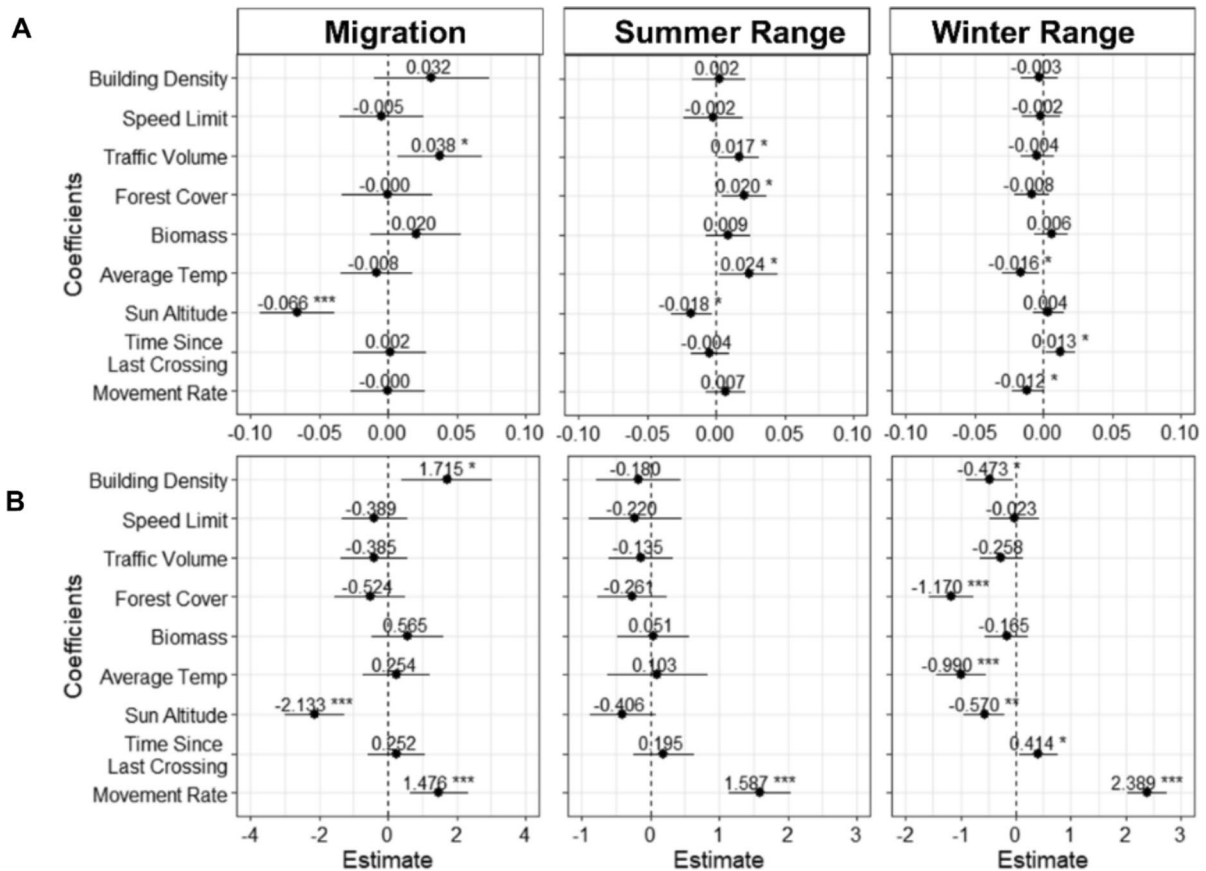


Fig. 3 When and where external conditions affected (A) heart rate spike and (B) mean heart rate during road crossings during migration and in summer and winter range residency. All coefficients are scaled within individuals and per season model. Numbers indicate the estimate, and the significance is indicated with an asterisk. Stress response during migration and

summer range residency were affected by higher traffic volume and at night, while winter range residency was affected by longer time since last crossing. Mean heart rate during crossing was elevated more at night during migration and in the winter range residency, and building density elevated heart rate more during migration than during winter range residency

more so during migration (+10.5% [10.2, 10.8%]; $\beta_{\text{sun altitude}} = -2.13 \pm 0.44$, $p < 0.001$) than winter (+3.6% [3.5, 3.7%]; $\beta_{\text{sun altitude}} = -0.57 \pm 0.18$, $p = 0.0026$). In winter, higher temperatures reduced mean heart rate (-6.7% [-6.9, -6.5%]; $\beta_{\text{average temperature}} = -0.99 \pm 0.23$, $p < 0.001$) while longer intervals since the last crossing increased it (+4.2% [4.0, 4.4%]; $\beta_{\text{last cross}} = 0.41 \pm 0.18$, $p = 0.021$). Greater forest cover lowered mean heart rate (-16.4% [13.4, 19.6%]; $\beta_{\text{forest}} = -1.16 \pm 0.21$, $p < 0.001$). Movement rate strongly elevated mean heart rate, most in winter (+28.6%), then summer (+13.9%), and migration (+10.9%) (all $p < 0.001$). Temporal smoothers were significant for all seasons (Julian date: $p < 0.001$; Fig. S4B).

Responsiveness of deer to repeated road crossings

The 29 individual mule deer had more than 7,000 road crossing events combined throughout the duration of monitoring. Overall, 51% (15 out of 29) had a sensitization to road crossing, with an increasing response to the stimuli of road crossing, whereas 45% (13 out of 29) had a habituation response, or decrease in response to the stimulus of road crossing. Only one deer had no effect of repeated road crossings on the heart rate spike.

The most parsimonious models ($\Delta\text{AICc} < 2$; Akaike's weights: 0.17–0.42) exploring habituation and sensitization included frequency of crossing, road density, mean body condition score, and

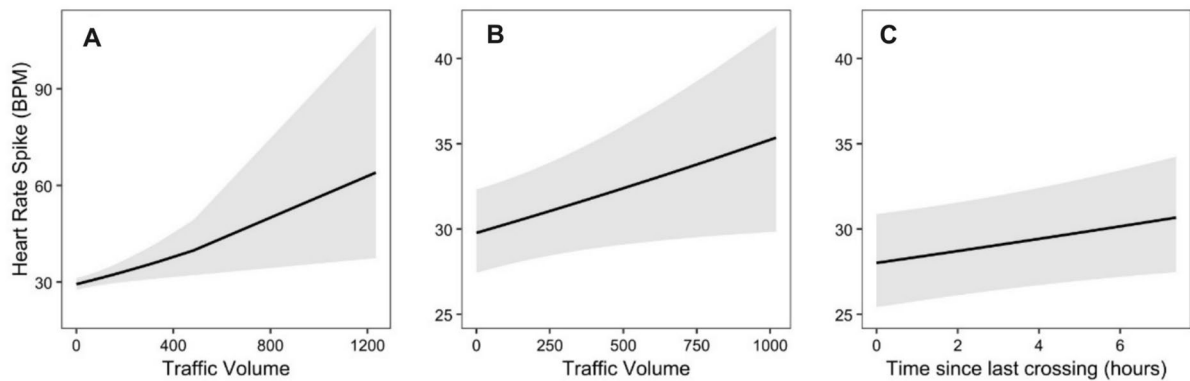


Fig. 4 Effect plots for other aspects of road segments that influence the magnitude of physiological response (heart rate spike) that have the greatest percent change along the observed range of the covariate during (A) migration, (B) summer range residency, and (C) winter range residency. Traffic volume had the greatest increase across the observed range during migra-

tion and in summer range residency indicating that traffic volume modulated the magnitude of stress response during crossings. In contrast, winter range residency had the greatest increase with time since last crossing, highlighting the importance of temporal exposure for stress response. The current plots were modeled using original data for interpretability

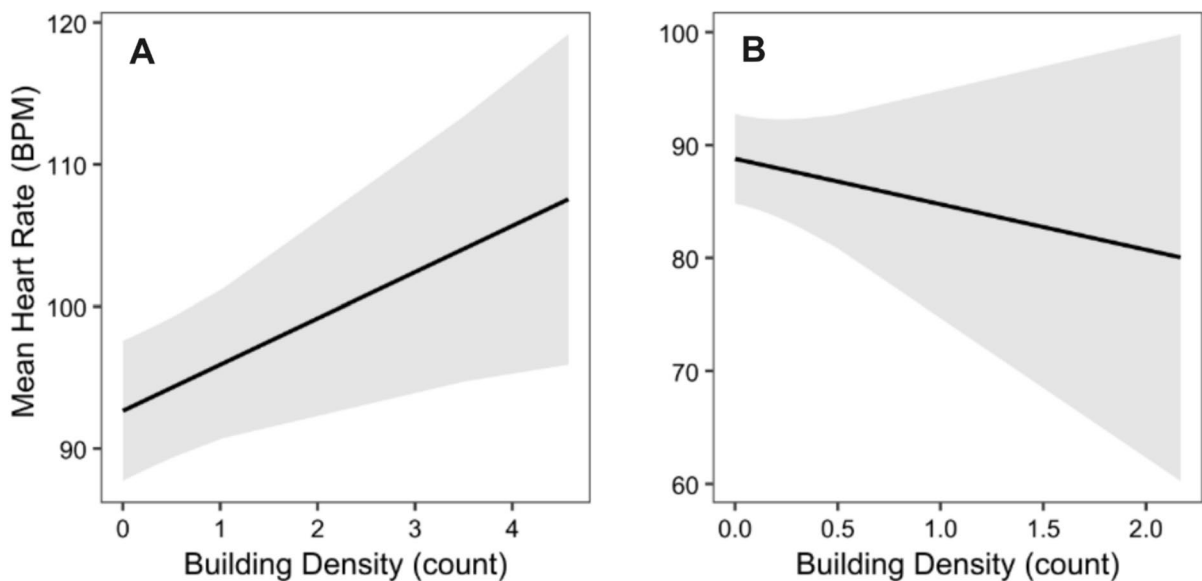


Fig. 5 Contrasting effects of building density on mean heart rate during road-crossing steps during (A) migration and (B) winter range residency. During migration, mean heart rate increased significantly across the observed gradient of building densities, suggesting heightened physiological arousal

in response to built environments. In contrast, during winter range residency, mean heart rate decreased across the observed count of buildings, possibly reflecting familiarity with anthropogenic features in the local landscape. The current plots were modeled using original data for interpretability

proportion of roads crossed with traffic (Table S2). Frequency of road crossing and road density had strong support as they were in all three models ($AIC_w = 1.00$), while mean body condition score ($AIC_w = 0.42$) and proportion of roads crossed with traffic ($AIC_w = 0.41$) were present in one of

the top models and significant in the conditional model average (Table S3). Deer that crossed roads more frequently and had a higher body condition score tended to habituate to repeated road crossings, while individuals who occupied areas with dense road networks and crossed proportionally

more roads with traffic became more sensitized to repeated road crossings (Fig. 6).

Discussion

Roads are a widespread feature of human-dominated landscapes and are known to cause direct wildlife mortality, and there is increasing evidence that exposure to roads may also be a source of chronic stress (Arregi et al. 2024). We found support for our hypothesis that road crossings would elicit an acute stress response in mule deer using high resolution physiological biologgers coupled with GPS tracking. First, we found the magnitude of change in short-term and sustained acute stress response, as measured by heart rate spike and mean heart rate during road crossings, was higher relative to other steps unassociated with roads after accounting for movement rate, other environmental and anthropogenic factors, and season. This highlights roads as a landscape level trigger for

stress responses. Second, among crossing events we found variation in the response across seasonal range residency and migration. Heart rate spikes increased most with higher traffic volumes during migration and summer range residency, whereas in winter range residency, the heart rate spikes increased more after longer durations between road crossings. Building density around roads had contrasting effects across seasons on mean heart rate during road crossing. During migration, mean heart rates were more elevated with increasing building density but declined with increasing building density during winter range residency. This contrast may reflect greater familiarity with built environments in winter ranges compared to less familiar structures encountered during migration. Third, we found substantial variation in individual responses to repeated road crossings. Deer became habituated (i.e., reduced heart rate response over time) across repeated road crossings if they crossed roads more frequently and had a higher body condition. In contrast, individuals became sensitized to repeated road crossings.

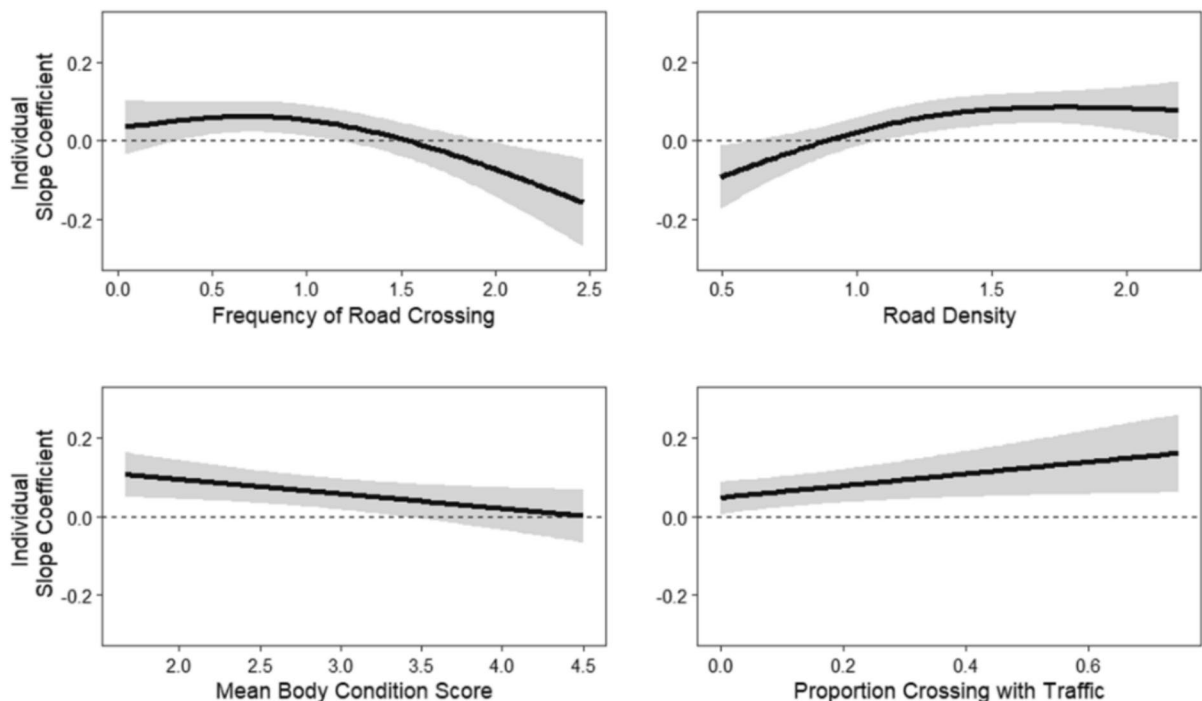


Fig. 6 Model averaged predictions of conditions affecting responsiveness (i.e., heart rate spike) of deer to repeated road crossings. Deer became habituated to repeated road crossings when they frequently crossed roads, whereas when they occupied areas with high road density, they became more

sensitized to repeated road crossings. Individuals with high body condition scores also habituated more to repeated road crossings while increasing proportion of roads with greater traffic volumes resulted in sensitization. The plots are based on the conditional model average of top models ($\Delta AIC_c < 2$)

to additional road crossings with traffic present and where they occupied areas with more dense road networks. This work highlights the dynamic effects that roads have on stress response in mule deer throughout important stages of their life history.

Long-term physiological monitoring highlights stress responses

Mule deer may not have a choice in avoiding roads, which are ubiquitous in all but the most remote landscapes (Coffin 2007). Traditional static methods of quantifying stress response in wildlife to road crossings (e.g., fecal glucocorticoid metabolites [FGM], Lunde et al. 2016; movement behavior, Dussault et al. 2007) fail to capture the dynamic stressor interactions that our sub-hourly resolution monitoring showed using heart rate. Our work highlights the explicit mechanisms and scenarios associated with single and multiple road crossings. For instance, we found a decoupling of movement rate from heart rate during road crossings, which provides evidence for roads triggering stress responses in deer irrespective of activity level. Short-term acute stress response during crossing, marked by a rapid spike in heart rate, was most pronounced on roads with greater traffic volume and at night during migration and on summer range residency. The pronounced spike at night may be related to how environmental visual cues are more homogenous at night compared to the dynamic illumination during the day (Newman et al. 2023). Many studies investigating responsiveness of wildlife to vehicles have focused on the behavioral reaction to a stimulus (Brieger et al. 2022). For instance, limited access to cover predicted a higher likelihood of a stronger behavioral reaction when crossing roads in roe deer (*Capreolus capreolus*), yet many of the observed road crossings in front of oncoming vehicles also had collisions that were narrowly avoided (Brieger et al. 2022). These prior exposures may alter the responsiveness of individuals before crossing roads, which may not be observed behaviorally but physiologically (Reimoser 2012). These differences in temporal, anthropogenic, and environmental sources affecting the stress response of deer show the multifaceted scenario that occurs during each road crossing and how our continuous monitoring captured the complexity of these events.

Responsiveness of deer to repeated road crossings

The continuous recording of heart rate and location enabled us to identify the impact of an individual's history of road crossings across three populations of deer over time. The two most important predictors of habituation or sensitization included the frequency of road crossings and the road density within the home range of individual mule deer. The habituation response (i.e., decreased heart rate and spikes) to increased frequency of road crossings is likely explained by cumulative road crossing experience. For instance, the proportion of roads crossed with traffic shows a direct link between exposure to vehicles and responsiveness to repeated road crossings leading to a sensitization response. The sensitization (i.e., increased heart rate and spikes) to increasing road density indicates that there may be indirect effects of roads on stress response. Distance to roads has clear impacts on time spent foraging, stress (measured via FGM), and time spent walking (Smith et al. 2023), and noise can alter behavior and responsiveness in wildlife (e.g., prairie dogs, *Cynomys ludovicianus*; Shannon et al. 2014). While it is plausible the proximity of deer to roads, while not always crossing, may also be contributing to the sensitization response observed in individuals occupying home ranges with higher road densities. Future work integrating sensory ecology and considering physiological traits (Dominoni et al. 2020; Ditmer et al. 2021) along with measuring the soundscape and the associated behavioral responses via accelerometry would elucidate these fine-scale encounters (Enari et al. 2025).

Interestingly, mean body condition was also an important predictor of habituation or sensitization to repeated road crossings, where increasing body condition correlated with more of a habituation response. Previous work has found correlations between higher hair cortisol concentrations, a proxy of stress, and low body condition of urban white-tailed deer (Potratz et al. 2019). Our finding that individuals with lower body condition are more likely to become sensitized with repeated road crossings raises the question of whether body condition can buffer against stress, or if the consequences of stress reduce body condition. The effects of repeated exposure to an anthropogenic stressor affecting body condition and responsiveness have been observed in other species. For instance,

while yellow-bellied marmots (*Marmota flaviventris*) tolerated closer approaches from humans over a 15-year period, individuals with already high flight initiation distances that were repeatedly approached became sensitized and increased their flight initiation distance. Furthermore, marmots that occupied highly disturbed areas gained less body mass, a proxy of fitness, than those in less disturbed areas (Uchida and Blumstein 2021). The relationship between body condition and responsiveness to repeated road crossings may be affected, in part, by aspects of built surroundings that we were unable to model, such as noise exposure near roads. Further research is necessary to determine whether fluctuations in body condition throughout the year affect the habituation or sensitization of individuals to repeated road crossings, or vice versa.

Integration of human mobility data with physiological response

The use of human mobility data added a unique layer of wildlife-road interactions that is otherwise limited by spatiotemporal constraints, such as monitoring road segments to determine annual average daily traffic (Wang et al. 2013). We identified two seasons where higher traffic volume affected the short-term acute stress response in deer: migration and summer range residency. During summer range residency, access to high-quality forage is crucial because it influences pregnancy, lactation, and overwinter survival (Hurley et al. 2014), while the migratory route can affect the survival of individuals by modulating their mortality risk (Sawyer et al. 2019). While both seasons are critical to locating and accessing higher quality forage (Schuyler et al. 2019), traveling through unfamiliar habitats with higher levels of traffic volume could increase the likelihood of a wildlife-vehicular collision. We noted that deer had a greater magnitude of short-term acute stress response with greater traffic volumes during migration relative to summer range residency, highlighting the potential for familiarity with sites modulating stress response. Interestingly, the lack of short-term acute stress response to traffic during the winter range residency could be a side effect of attempting to minimize energy expenditure during winter to promote survival (Hobbs 1989). We also identified a role of traffic volume on the responsiveness of deer to repeated

road crossing – insights that may be otherwise difficult to obtain without near real time physiological monitoring.

Roads as dynamic sources of stress to wildlife

Roads fundamentally reshape the landscapes by hindering movement, increasing mortality, and fragmenting habitats, all of which have well-documented negative effects on wildlife populations (Kauffman et al. 2021). Crossing roads has been shown to interfere with movement and behavior (Dussault et al. 2007). Although direct mortality can come from vehicular collisions, roads are also linked to increased predation risk (Whittington et al. 2011; Dickie et al. 2020). We show that, beyond being a modified landscape feature that interferes with movement and a risk of direct mortality, roads also serve as a dynamic source of stress through acute stress responses with road crossings. Many wildlife management decisions to facilitate road crossings for mule deer rely on game-proof fencing and wildlife crossings to reduce vehicular collisions, and this technique has been shown to benefit deer (Sawyer et al. 2012). However, deer cross roads without these game proof fences. It is possible that the continuous stress exposure could lead to significant physiological consequences that extend beyond immediate behavioral responses, including compromised immune function, altered reproductive success, and reduced survival that collectively impact population viability (Martin et al. 2011; Hing et al. 2016; Karaer et al. 2023). As humans continue to dominate the landscape, roads will continue to be an omnipresent threat for wildlife affecting management and health of populations, especially in the rapidly expanding western United States (Theobald and Romme 2007; Polfus and Krausman 2012). Although the dynamic interactions between deer and humans are context dependent (Abernathy et al. 2025b), improving our understanding of how different sources of stress affect the health of individuals, and by extension populations, allows us to better manage and help wildlife under changing landscape conditions.

Conclusions

Wildlife responses to anthropogenic disturbance are complex and influenced by a suite of external and

internal factors (Bejder et al. 2009). Integrating fine-scale physiological data with landscape and human mobility data provides a more comprehensive understanding of how dynamic anthropogenic features can shape wildlife health, behavior, and movement. We revealed that road crossings trigger significant spikes in heart rate, with responses varying across seasons, traffic volumes, and landscape characteristics. Notably, deer can become either habituated or sensitized to repeated crossings, depending on factors such as crossing frequency, road density, traffic, and body condition. Given the established links between chronic stress, immune suppression, and reproductive impairment (Martin et al. 2011; Hing et al. 2016; Karaer et al. 2023), it is plausible that increasing road density and traffic could contribute to declines in mule deer populations by reducing reproductive output and increasing mortality risk. These findings underscore the multifaceted impacts of roads on wildlife and highlight the importance of considering both direct and indirect effects in conservation. Our work contributes to the growing knowledge that roads are dynamic barriers for wildlife, which contributes to mortality, impact behavior, alter movement, and influence stress response.

Competing interests

The authors declare no competing interests.

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Author contributions M.A.D and G.W conceptualized the research goals. M.A.D, G.W, K.A.Z, D.C.S supported project administration. M.A.D, G.W, N.H.C acquired funding. V.S, K.R.H, B.R.M and R.T.L facilitated field collection of biometrics. N.H.C., J.O.S, P.W generated environmental variables,

T.G.L facilitated collection of physiological data, and H.N.A collected HMD data used in analyses. M.P.L curated data. A.F.P analyzed the data. M.A.D, G.W, and A.F.P wrote and edited the original draft. All authors contributed to the review of the final manuscript.

Data availability Data for conducting the analyses are uploaded to the dryad repository: <https://doi.org/10.5061/dryad.02v6wwqgk>.

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