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Daily roadkill monitoring and long-term population census reveal female-biased mortality for a small mammal along a wildland-urban interface

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ABSTRACT

Expanding road networks in the wildland-urban interface may increase wildlife mortality from vehicle collisions. However, our knowledge of long-term roadkill rates and impacts on vertebrate populations is poor. We capitalized on a 31-year study to determine how roadkill rates varied with demography and traffic volume in a population of golden-mantled ground squirrels (*Callospermophilus lateralis*; GMGS) along 1 km of rural road in Colorado, USA. Despite low annual numbers of roadkill events (0–7 GMGS), adult female mortality was high (10.9 %) and increased with female cohort size. Adult roadkill rates increased with our traffic volume index. We estimate 71 % of roadkill events would have been undetected if we performed weekly instead of daily surveys. Hence, population-level impacts of road mortalities are likely underestimated in short-term studies that lack paired demographic data. Understanding true rates of roadkill in wildland and developing areas will help inform conservation strategies.

1. Introduction

Two decades ago, Forman and Alexander (1998) called roads "the sleeping giant of conservation ecology." Today, there are over six million km of public roads in the United States; 70 % of these are roads through rural areas, equaling 4.2 million km of road that bisects non-urban wildlife habitat (U.S. Dept. of Transportation, 2018). In an age of increasing development along the wildland-urban interface (Radeloff et al., 2005) and increasing travel to outdoor spaces for recreation (Cordell, 2012), it is vital to understand how roads affect wildlife populations, especially as a direct source of mortality. In the U.S., vehicle collision is a major anthropogenic source of mortality for many vertebrate species (Forman and Alexander, 1998). As road networks continue to expand into new habitats, wildlife is increasingly at risk of road mortality (Radeloff et al., 2005).

Many roadkill studies focus on large mammals, whose numbers are often reduced by roads (Fahrig and Rytwinski, 2009). However, the effects of roads may be especially negative for small mammals that use roadsides to move (Coffin, 2007), disperse (Saeki, 2001), and detect predators (Bakker and Van Vuren, 2004). Previous roadkill studies have reported neutral effects of roads on some small mammals, whose high reproductive rates may offset road mortality rates, or even positive effects due to a release from predation near roads (Galantinho et al., 2017; Fahrig and Rytwinski, 2009; Garland and Bradley, 1984). However, this is not the case for all small mammal species, as high densities of roads have also been associated with population declines (Roedenbeck and Voser, 2008). Notably, many studies find that small and medium-sized mammals account for the majority of their recorded roadkills (Canova and Balestrieri, 2019; Smith-Patten and Patten, 2008); yet without data on population size, numbers alone do not reveal the impact of road

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mortality.

Literature about the effects of roads on small mammals is incomplete for several reasons: (1) most public transportation databases do not report vehicle-small mammal collisions (Roedenbeck and Voser, 2008); (2) small mammals may be difficult to detect in surveys because of their size and shorter persistence time of carcasses due to scavengers (Santos et al., 2011); and (3) few studies have used paired demographic data (i.e. age, sex) and population data (i.e. number, density) to determine roadkill rates within a population (e.g. Ruiz-Capillas et al., 2015). Small mammals vary in ecology and behavior, and some species may be especially vulnerable to road mortality if their home ranges include a highly trafficked road and if they do not adopt road or traffic avoidance behavior (Fahrig and Rytwinski, 2009). Ground squirrels in particular have been observed to cross roads more frequently than other small rodents (Oxley et al., 1974; Garland and Bradley, 1984).

We investigated road mortality in a censused small mammal population over 31 years to determine roadkill rates, and whether those rates are influenced by demography and traffic patterns. The golden-mantled ground squirrel (*Callospermophilus lateralis*; GMGS) is a common hibernating small mammal (150-300 g) of the mountainous western United States (Bartels and Thompson, 1993). GMGS are diurnal and exhibit site fidelity, facilitating consistent daily surveys of roadkill events for known individuals. We expected that different demographic groups of this species may be impacted by roads in unique ways: as a consequence of male-biased juvenile dispersal (Mabry et al., 2013) and adult female territoriality (Jesmer et al., 2011), we predicted that juvenile squirrels would be more susceptible to vehicle collision than adults, and males would be more susceptible than females in both age classes. Understanding true rates and impacts of roadkill on small mammals under increasing development and use of wildland areas will help inform conservation strategies.

2. Methods

2.1. Study area and species

We studied GMGS in the East River Valley of Gunnison County, Colorado (38°58′N, 106°59′W) at the Rocky Mountain Biological Laboratory (RMBL; 2900 m elevation) from 1990 to 2020 (Fig. 1). Vegetation at RMBL consisted mostly of subalpine meadow, interspersed with stands of aspen (*Populus tremuloides*), willow (*Salix* spp.), and spruce (*Picea engelmannii*). Snowpack lasted for 8–9 months each year (barr, 2021). County Road 317 (CR 317, speed limit 25mph), which runs north from the town of Mount Crested Butte and does not connect to other towns or roads, extended 1-km through our 13 ha study site (Fig. 2). This one-lane, unpaved road is used to access RMBL and nearby, popular outdoor recreation sites. It is closed for roughly half of the year, with opening and closing dates determined by snowpack. During our study, CR 317 first opened between April 12th (2012) and June 6th (1995), and closed between November 9th (1998,2002) and January 2nd (2000).

Adult GMGS (≥1 year old) were active above ground at our study site between late April and early September. The GMGS breeding season began in April or May, depending on snowmelt, after females emerged from hibernation and encountered scrotal males. Pups emerged from their natal burrows at weaning (~30 days after birth; Phillips, 1981), from mid-June through mid-July (Wells et al., 2017), and began dispersing several weeks later, from mid-July through September. Adults reduced aboveground activity beginning in August, juveniles in September, and all squirrels had entered hibernation by October, before closure of CR 317.

Annual population size fluctuated, ranging from 24 to 140 GMGS (Kneip et al., 2011), and the annual adult male to adult female ratio within the population was approximately 2:3. Adult female GMGS were solitary, though often lived in close proximity to conspecific neighbors

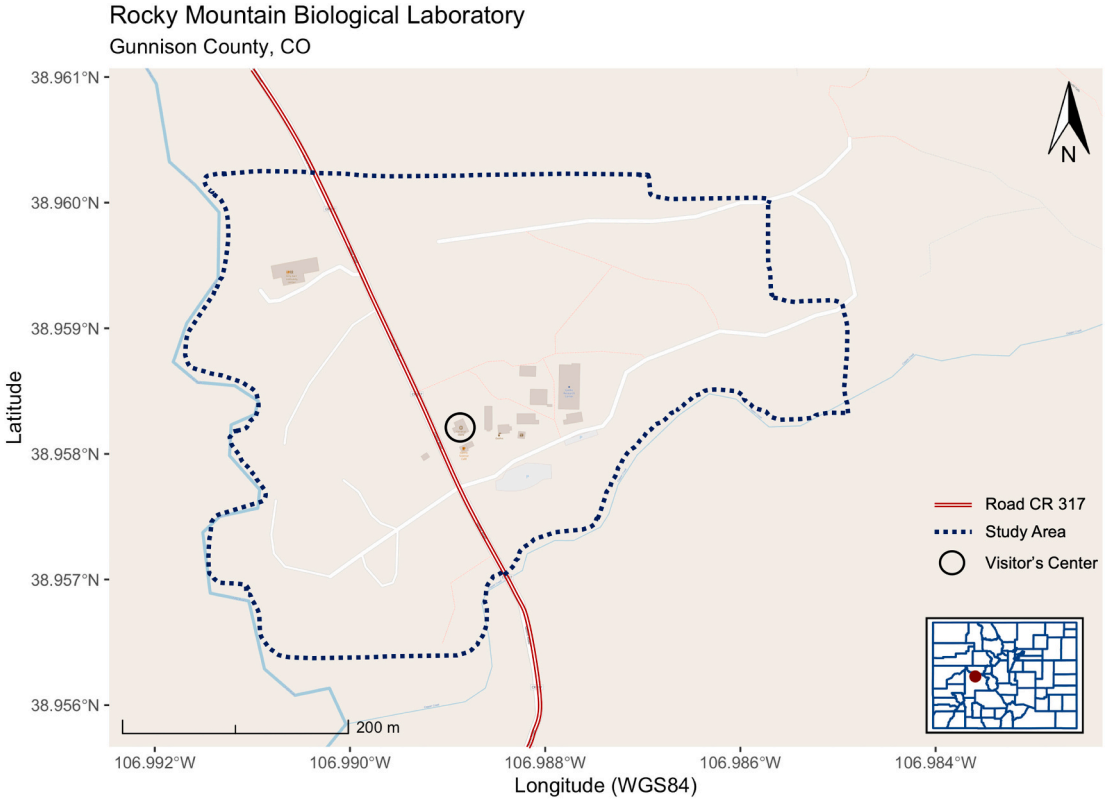


Fig. 1. Map of study site at the Rocky Mountain Biological Laboratory, in the East River Valley of Gunnison County, Colorado, USA. Dashed line indicates boundaries of the golden-mantled ground squirrel (GMGS) study area, and double-line indicates unpaved County Road 317. Shaded polygons indicate buildings (tan) or parking areas ("P"); Visitor's Center (circled) is where tourist traffic volume was recorded.



Fig. 2. Images of the Rocky Mountain Biological Laboratory and golden-mantled ground squirrel (GMGS). Clockwise from left: A. Fencing alongside County Road 317 (CR 317); B. Adult female GMGS in the lactation stage of reproduction perching on a fence post by CR 317; C. Large-scale view of CR 317 and study site.

and kin (Wells and Van Vuren, 2017). Adult males range widely during the breeding season, as mating with multiple territorial females increases their reproductive success (Wells et al., 2017). Male-biased juvenile dispersal typically began in July, when we observed juveniles born within the study site moving beyond the boundaries of their natal home ranges, and recorded juveniles born elsewhere immigrating into our study area. Adult females, especially post-breeding adult females, rarely immigrated, while adult male immigrants entered the study site in all months of the active season.

This GMGS population was censused during the active season. From late May through early September each year, there were four waves of live trapping (Tomahawk, Model 201) to obtain body mass and determine reproductive status of all individuals. Trapping procedures were approved by the Institutional Animal Care and Use Committees of University of California, Davis and RMBL, and met guidelines set by the American Society of Mammalogists (Sikes, 2016). We gave new squirrels numbered ear tags for permanent identification (Self-piercing fish tag, Style 1005-1, National Band & Tag Company, Newport, Kentucky, USA) and all squirrels unique dye marks on the dorsal pelage each season to identify them visually. We knew the age of individuals born at our study site, and we estimated an immigrant's age to be juvenile or adult based on body mass. We determined individual sex based on an ano-genital distance, and adult female reproductive status by nipple development throughout the season.

2.2. Roadkills

We observed behavior and spatial locations of squirrels by walking the study area multiple times per day; these observations included scanning CR 317 for roadkill, defined as a GMGS carcass on the road with visible injury from vehicle collision. Our daily scans were supplemented by community member roadkill observations that we identified by ear tag. Hence, we typically knew of a roadkill event within a few hours. At our site, persistence time of roadkill carcasses was typically short, from a few hours (Wells and Van Vuren, personal observation) to up to 2 days (b.barr and D. Inouye, pers. communication). Carcasses were observed being scavenged by crows (*Corvus brachyrhynchos*) and red foxes (*Vulpes vulpes*). Transient GMGS, defined as squirrels present in the study site for <14 days, and non-eartagged GMGS roadkill events within our study site were excluded from this study.

2.3. Traffic

Exact traffic counts on CR 317 were not available, so we used the weekly number of visitors at the RMBL Visitor Center -located in our study area on CR 317- from the 2018 and 2019 seasons as a traffic volume index (TVI). During both years, the Visitor Center opened in the second week of June and closed after the GMGS study period ended. To determine the relationship between weekly TVI and number of adult GMGS roadkill events for each week of the active season that we had tourist counts (June 5–September 3), we fit a generalized linear model with a quasiPoisson distribution (for roadkill count data, which were overdispersed) and log link (R version 3.6.2, R Core Team, 2019). We excluded juvenile GMGS from this analysis because they are only active beginning mid-summer after they emerge from their natal burrow.

2.4. Density

At high densities, adult female golden-mantled ground squirrels increase home range overlap in preferred habitat instead of spilling into unpreferred habitat (Aliperti et al., 2022). Hence, adult female density may increase the number of roadkill events because more female home ranges may be in preferred habitat adjacent to the road in high density years, or because more territorial chases in high density years (Van Vuren et al., *unpublished data*) may put females in the path of oncoming vehicles. We examined the effect of female density on the number of females roadkilled in two ways. First, we used *total female density*, defined as the number of adult females present in our 13 ha study area during the annual census; the study area is fixed from year to year, so increases in adult female population size represent increases in density. Next, we used *cohort size*, defined as the number of new adult females entering the study each spring, and tracked how many of each cohort

were eventually roadkilled. Most of the cohort consisted of resident yearling females who were newly adult, but some females were older immigrants and hence new to the study site; we combined these two groups because they both might vie with established females for new home ranges, and be involved in more chases with resident females. For the cohort size analysis we excluded the first year of the study (1990) because we could not distinguish new versus established resident females. Because total female density and cohort size were measured on different timescales (annual vs. cohort), we fit separate regressions for each of the two measurements. The density generalized linear model used annual total female density to predict the number of female roadkills per year, fit with a Poisson distribution and a log link. The cohort generalized linear model used starting cohort size to predict the number of female roadkills out of each cohort, again fit with a Poisson distribution and log link.

2.5. Roadkill survey frequency

From our daily roadkill surveys, we recorded which day of the week each GMGS was killed. Then, we calculated the percent of carcasses that would have been detected if only weekly instead of daily surveys had been conducted during 2005–2020. Records from before 2004 lack consistent dates of roadkill events and were excluded from this analysis. We used a carcass persistence time of 2 days (b.barr and D. Inouye, pers. communication) and calculated the percentage of carcasses that would have been observed in weekly surveys conducted on each day of the week. For example, Monday surveys would have recorded GMGS killed on Sunday and Monday. We simulated weekly surveys for each day of the week in case mortality patterns varied among days (e.g. weekdays versus weekends). We then averaged these percentages to obtain an overall estimate for weekly survey detections.

3. Results

Over the study period, 66 out of 1316 GMGS were roadkilled, ranging from 0.0 % to 9.5 % of the population each year (avg. 5.0 %). The proportion of adult females killed by vehicles (22/201 = 10.9 %) was nearly twice as large as that of adult males (11/189 = 5.8 %) (X^2 (1, $N = 390$) = 3.3, $p = 0.069$). Similar proportions of juvenile females (14/454 = 3.1 %) and juvenile males (19/472 = 4.0 %) were killed by vehicles over the study period (X^2 (1, $N = 926$) = 0.597, $p = 0.440$). Overall, adult GMGS had a significantly higher proportion of roadkill events (33/390 = 8.5 %) compared to juvenile GMGS (33/926 = 3.6 %) (X^2 (1, $N = 1316$) = 13.8, $p < 0.001$). While only a few adult females were killed by vehicles each year (0–3), this represented 0.0 %–20.0 % of the annual adult female population (Fig. 3).

Total traffic volume index was similar between years ($n = 15{,}966$ in 2018, $n = 18{,}954$ in 2019). Weekly TVI started low in the early season (week 6 TVI: $n = 373$ in 2018, $n = 387$ in 2019) and increased to a peak in the middle of July ($n = 1972$ in 2018, $n = 2501$ in 2019) before declining again (Fig. 4). Adult GMGS roadkill events also peaked in mid-July, whereas juvenile GMGS roadkills peaked later in the season (Fig. 4). There was a significant positive relationship between TVI and adult GMGS roadkill events ($\beta = 0.001 \pm 0.0005$, $t = 3.859$, $p = 0.0001$).

Adult female density did not have a significant effect on the number of female roadkill events each year ($\beta = 0.046 \pm 0.033$, $t = 1.407$, $p = 0.160$). By contrast, cohort size did have a positive effect on the number of female roadkill events from that cohort ($\beta = 0.110 \pm 0.0490$, $t = 2.257$, $p = 0.024$).

Based on a 2-day persistence time for GMGS carcasses, we calculated that the average weekly detection rate of roadkill events would have been only 28.6 % (range 17.1 %–36.6 %) of our daily detection rate (Fig. 3).

4. Discussion

Typical methods for estimating roadkill events and rates are conducted on a weekly (Barthelmess and Brooks, 2010) or monthly (Ruiz-Capillas et al., 2015) basis. This survey frequency likely underestimates true roadkill rates on a section of road (this paper; Henry et al., 2021). Additionally, there have been few studies assessing the impacts of road mortality on mammalian populations over a period >3–5 years (Canova and Balestrieri, 2019; Bartel et al., 2008). Daily roadkill monitoring revealed few roadkill events (0–7) of GMGS per year. Yet when paired with demographic and population data, we determined that those few events still accounted for up to 20 % of the annual population (avg. 5 %). Had we decreased our survey frequency from daily to weekly, approximately 71 % of those roadkill events would have been undetected.

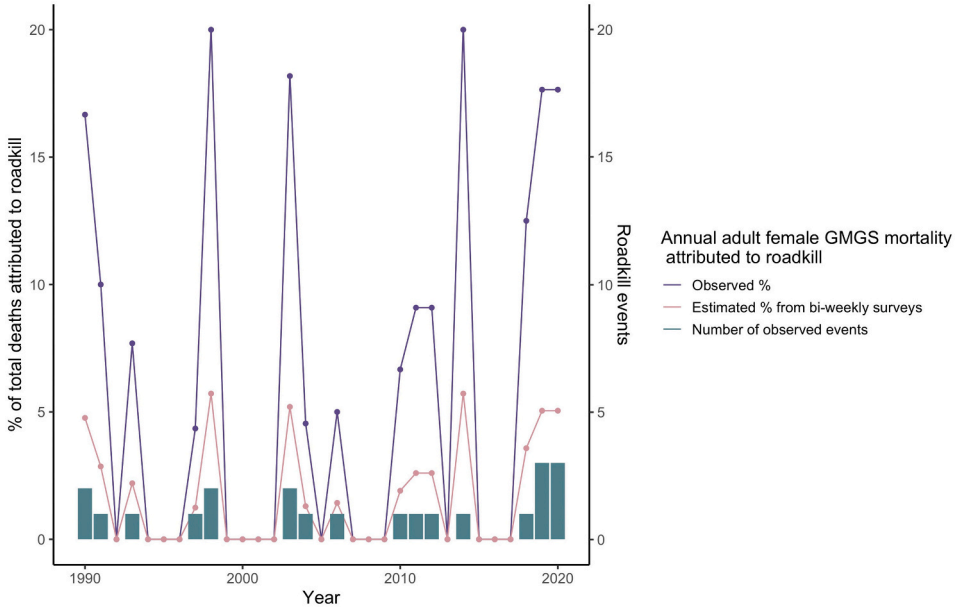


Fig. 3. Observed (purple line) and estimated (pink line) annual percent of adult female mortality caused by roadkill. Estimated mortality assumed a 28.6 % carcass retrieval rate from simulated weekly surveys. Number of individual adult females killed annually by vehicles are also shown (green bars). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

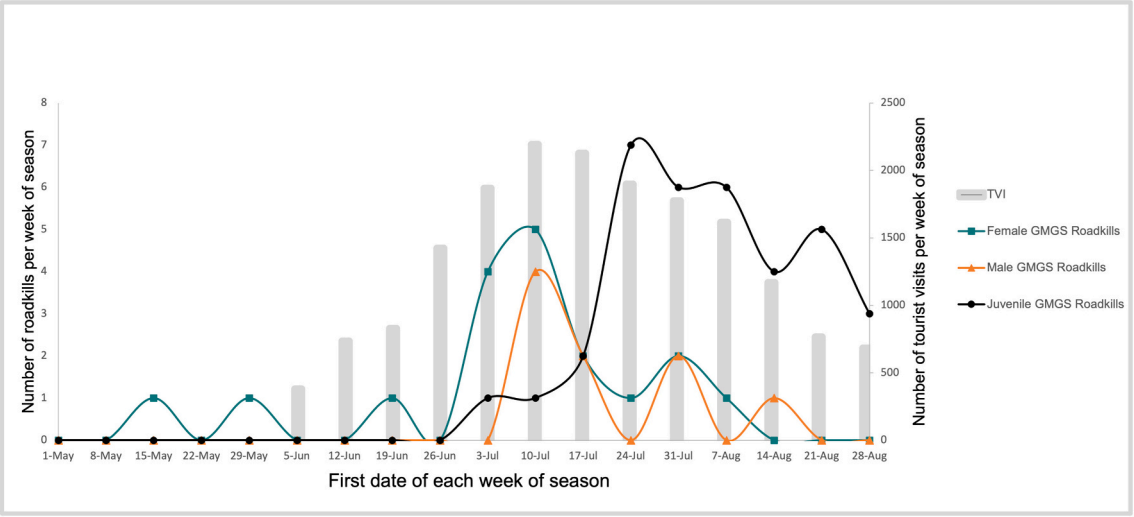


Fig. 4. Number of adult female (green squares), adult male (orange triangles) and juvenile (black circles) golden-mantled ground squirrels killed in each week of the active season in Gothic, CO, USA. Annual traffic patterns are also shown by using the number of tourist visits each week as a traffic volume index (grey bars). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Weekly surveys, though undercounting mortalities, can still provide important information about trends in roadkill events each season.

Contrary to prediction, adult females were the demographic group most affected: nearly twice the proportion of adult females versus adult males died in roadkill events. Though we predicted that males might be more at risk from their wide-ranging exploratory behavior, their road crossing may occur more during the mating season in April and May when traffic volume is absent or low. By contrast, adult female territorial chases peak during July (Van Vuren et al., unpublished data), at the same time traffic volume peaks. Territorial chases may not directly cause road mortality, but a July peak of both chases and vehicle collisions may be driven by wider female movements at that time.

In addition to the female-bias in mortality, absolute rates of female mortality were substantial: 1 in 10 females died in roadkill events. Substantial, female-biased mortality rates in this small mammal population are potentially significant because GMGS are longer lived than other rodents with similar road mortality rates (e.g. wood mouse, *Apodemus sylvaticus*; Ruiz-Capillas et al., 2015) and are constrained by their life history to reproduce only once per year (Phillips, 1981). In other longer-lived taxa with annual breeding, high female-biased roadkill rates have been associated with skewed adult sex ratios, altered age structures, and potential consequent population declines (Aresco, 2005; Desbiez et al., 2020; Ryu and Kim, 2020).

For GMGS, adult female survival is the primary driver of population dynamics (Hostetler et al., 2012). However, expected population declines from substantial female mortality may be masked by immigration from other populations and recruitment of philopatric yearlings. Given lower reproductive rates for yearling versus older female GMGS (Kneip et al., 2011), we might expect population growth to slow with a shift toward younger females replacing roadkilled older adults.

Despite substantial road mortality, further work is needed to assess if this is additive or compensatory with other sources of mortality in this population, which include predation (Kneip et al., 2011), additional anthropogenic impacts (e.g. drowning in outhouses, CPW *personal observation*), and potentially starvation over-winter (Bihr and Smith, 1998). For example, individual variation in exploratory or risk-taking behavior (e.g. Aliperti et al., 2021) could underlie compensatory mortality between road mortality and predator- or other anthropogenic mortality, if "bold" GMGS are both more likely to be killed by predators and by vehicles. Alternatively, if montane predators are likely to target roadsides for both prey and scavenging opportunities (e.g. red fox *Vulpes vulpes,* Rod-Eriksen et al., 2020), GMGS with home ranges adjacent to roads may be more likely to be either depredated or killed by a vehicle as compared to GMGS with home ranges distant from roads. However, the absence of clear links between road mortality risk and overwinter starvation – for example through food supply – suggests at least partial additive mortality.

Female territorial interactions may explain interannual variation in road mortality. While annual female GMGS roadkill rates do not increase with annual female density, they are positively affected by cohort size. Large cohort years reflect a combination of an increase in juvenile or yearling female immigration into the study area and an increase in survival rate of juveniles overwinter. The former may occur when other populations in the valley are large, and more female juveniles disperse from those populations into ours. The latter may occur after early springs, when juveniles emerge earlier in the summer from their natal burrows, and hence have more time to grow and accumulate body fat to increase their survival overwinter (Schlageter, 2022). Female home ranges generally overlap somewhat, but only female kin share more space at high densities (Aliperti, 2020). A larger starting cohort size likely increases competition for yearling and immigrant females establishing a home range, causing females to overlap more with kin or shift into less crowded areas (Aliperti, 2020). In this way, a larger cohort may push more female GMGS toward roads or increase their willingness to take risks crossing roads.

The spatial configurations of female home ranges could influence risk of road mortality in other ways. Ground squirrels seem to prefer habitat features that enhance visibility to detect predators (MacHutchon and Harestad, 1990), and in our study system, GMGS prefer patches of dry meadow that contain vision-enhancing features such as rocks and other perches (Aliperti et al., 2022). Fencing lines both sides of CR 317, and GMGS frequently used fence posts as perches to observe their surroundings (Fig. 2). Vision-enhancing perches could increase the quality of a female home range (Aliperti et al., 2022), signifying that habitat along the CR 317 roadside, including bordering fences, may function as an ecological trap (Coffin, 2007; Noonan et al., 2022). Attraction to road-adjacent habitat for nesting or foraging has also been implicated in high road mortality in other taxa, such as freshwater turtles (Aresco, 2005) and birds (Mumme et al., 2000). Unfortunately, we do not yet have adequate information to quantify the relationship between female home ranges' proximity to CR 317 and risk of road mortality.

Roadkill rates for adults varied strongly with our traffic volume index. Traffic has been shown to affect seasonal fluctuations in roadkill rates in other mammalian species (Seo et al., 2015). For mammals in

particular, reproductive cycles and dispersal patterns also correspond to increased roadkill rates (Seo et al., 2015; Canova and Balestrieri, 2019), but this is not the case for our study. Despite substantial GMGS movement during May breeding, August dispersal, and late summer pre-hibernation foraging, roadkill rates for the adult GMGS population during these periods were low. It appears that this is because tourist traffic during August and September was low and is typically low during May after the road opens for the season.

The East River Valley is a mountainous area that is increasingly popular for outdoor tourism during the summer. With warming temperatures and earlier snowmelt (barr, 2021), CR 317 is projected to open earlier in the coming years, increasing risk of vehicle collisions during the GMGS mating season. Additionally, earlier snowmelt may lead to earlier ground squirrel emergence dates (Goldberg and Conway, 2021; Tamian et al., 2022; Wells et al., 2022) and potentially a prolonged active season, leading to more days they are exposed to traffic. Female-biased roadkill rates suggest that female survival, which drives population dynamics in ground squirrel species (Sherman and Runge, 2002; Hostetler et al., 2012), may be increasingly strained in the coming years with warmer springs resulting in longer exposure to traffic and potentially longer seasons out of hibernation.

With demographic information collected by monitoring a population over several decades, we were able to calculate precise roadkill rates in a population of small mammals. Our site is a case study of human impacts along the wildland-urban interface and provides another example of substantial direct mortality along a relatively low-traffic road (e.g. Mumme et al., 2000). Mitigation strategies that could minimize roadkill events in rural recreational areas include the implementation of a public transit bus for trail access and the use of traffic calming measures, such as speedbumps (Olgun et al., 2021), dynamic signage (Hardy et al., 2006), and spatio-temporally flexible warning systems (Mayer et al., 2021). Roads are having dramatic impacts on ecosystem structures, processes, and components (Galantinho et al., 2017; Lowry et al., 2013; Coffin, 2007) and are a significant cause of biodiversity loss around the world (Ruiz-Capillas et al., 2015; Kioko et al., 2015; Galantinho et al., 2017). In areas where rural development and recreation are on the rise, it is crucial to document their impacts on resident wildlife populations.

CRediT authorship contribution statement

Katherine Burgstahler: Conceptualization, Data curation, Formal analysis, Writing – original draft, Writing – review & editing. **Jessica Isidro:** Conceptualization, Data curation, Formal analysis. **Dirk H. Van Vuren:** Data curation, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **Amy C. Collins:** Formal analysis, Visualization, Writing – review & editing. **Jaclyn R. Aliperti:** Investigation, Data curation, Visualization, Writing – review & editing. **Caitlin P. Wells:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing.

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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