



Rodent Diversity and Population Dynamics in an Off-highway Vehicle Area



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Introduction

Off-highway motor vehicle recreation is a common and growing form of outdoor activity on public lands in the United States. Off-highway vehicles (OHV) include 4-wheel drive vehicles, motorcycles, all-terrain vehicles (ATV), and other specially designed or modified motor vehicles used in a wide variety of ways. On public lands, off-highway vehicle recreation often occurs on trails in natural areas, where vehicle use can result in a loss of biodiversity and degradation of ecosystem health (Webb et al. 1983; Brooks & Lair 2005; Ouren et al. 2007). Indeed, the use of off-road vehicles in the United States is linked to population declines for approximately 13% of endangered species (Wilcove et al. 1998). Public agencies are often tasked with simultaneously managing legal off-highway vehicle recreation use and preserving habitat health and wildlife diversity. Given the growing popularity of off-highway vehicle recreation and the concerns with the effects of this use on ecosystem health, including biodiversity, detailed study of the environmental impacts of OHV recreation is warranted.

Studies of the effects of OHV recreation on animal species have previously been conducted, including effects on reptiles (Busack & Bury 1974; Beauchamp et al. 1998; Tull & Brussard 2007), avian species (Burger & Gochfeld 1990; Patterson et al. 1991; Melvin et al. 1994; Barton & Holmes 2007; Steenhof et al. 2014), and species in desert biomes (Bury et al. 1977; Luckenbach & Bury 1983). Several studies that investigated the effects of OHV recreation on mammals focused only on a single species, or looked at the combined effects of anthropogenic activities, including OHV recreation (Brooks 1995; Zielinski et al. 2008; Naylor et al. 2009, Jones et al. 2017). One study investigated the effects of OHV recreation on rodents (Reid 2012).

Rodents are model species for understanding the ecological effects of anthropogenic activities, including OHV recreation, for a multitude of reasons. Rodents are influenced by changes in habitat heterogeneity, habitat fragmentation, and resource availability (Buckner & Shure 1985; Jones et al. 2003; Orland & Kelt 2007; Germano et al. 2012). They are often keystone species that significantly influence biological diversity and biogeochemical processes. Studies have shown that they are prey for vertebrate predators; they use of a variety of food sources, including seeds and invertebrates; they are ecosystem engineers that create habitat structures (such as burrows); they influence nutrient cycling and soil aeration, and they contribute to species and functional diversity of the animal community (Maser et al. 1978; Brown & Heske 1990; Dibello et al. 1990; Jones et al. 1994; Carey & Johnson 1995; Goldingay et al. 1997; Valone & Schutzenhofer 2007; Davidson et al. 2008; Flynn et al. 2009).

OHV recreation can affect rodent ecology by changing habitat structure. The changes to habitat structure may affect the population dynamics and habitat relationships of rodents, resulting in changes to rodent abundance. Demographic variables can also influence rodent abundance. Rodent abundance is primarily influenced by apparent survival and recruitment as well as sex ratio, which together can determine reproductive success, mortality, immigration/emigration from a population, and effective population size. Therefore, habitat quality can be inferred from demographic data and habitat structure (Van Horne, 1983). Community composition and diversity of rodents are also influenced by habitat structure (Grant & Birney 1979; Tews et al.

2004; Pardini et al. 2005), which suggest that changes to habitat structure associated with OHV recreation could also affect rodent diversity and abundance.

To better understand the effects of OHV recreation within oak woodland habitat on rodent community structure and population demographics, we compared population abundance and community diversity between blue oak woodland sites within OHV and non-OHV areas in Carnegie State Vehicular Recreation Area (SVRA) near Tracy, California over a three-year period. We hypothesized that rodent population abundance and community diversity is greater in areas where habitat heterogeneity is greater, therefore any activity that reduced habitat heterogeneity would also reduce rodent population abundance. This study is the first that we are aware of to examine the effects of OHV recreation on rodent communities and populations in a woodland community.

Methods

Study Area

The study area is within the approximately 20.25 km² (7.82 mi²) Carnegie SVRA, a unit of the California Department of Parks and Recreation, in southeast Alameda and southwest San Joaquin counties, California (Figure 1). The study was conducted from December 2016 to November 2019. Carnegie SVRA is an off-highway recreation area that is open to primarily motorcycle and all-terrain vehicles (ATVs). Carnegie SVRA is situated in a rural area, approximately 24.14 kilometers (15.00 miles) east of Livermore with a population of 90,000 and 9.65 kilometers (6.00 miles) south of Tracy with a population of 82,000. Surrounding land use is primarily open space ranch land used for cattle grazing; the 28.33 km² (10.94 mi²) Lawrence Livermore National Laboratory Experimental Test Site to the north, which is mostly open space; and the 1.97 km² (0.76 mi²) SRI International explosives testing facility to the southeast, which is also mostly open space. Prior to 1930, Carnegie was the site of a large cattle grazing operation and as early as the 1930s, the area was used for off-road motorcycle riding.

The study area consists of rolling hills with some areas of extremely steep terrain and it ranges in elevation from 183 meters to 671 meters North American Vertical Datum of 1988 (NAVD88) (Google Inc. 2020). Approximately 6.37 km² (2.46 mi²) of the study area is open to off-highway vehicular use (mainly motorcycle and ATVs) with the remaining area closed to the public since there is no off-highway vehicle trail system in this area of the SVRA. However, the area closed to the public is accessible by a network of maintained dirt roads. Corral Hollow Creek, a semi-perennial stream, which drains a portion of the Diablo Range east of Livermore into the San Joaquin River basin of the Central Valley, flows through the study area. Also, there are numerous stock ponds throughout the study area (Figure 2).

The region is classified as semi-arid with a Mediterranean climate, with most rain falling in the winter and spring. Mild cool temperatures are common in the winter. Hot to mild temperatures are common in the summer. The average daily maximum temperatures are 31.7°C (89°F) in summer and 3.3°C (38°F) in winter and mean annual precipitation is 32.3 centimeters (12.7 inches) (PRISM Climate Group 2020).

Habitats within the study area include blue oak (*Quercus douglasii*) woodland (709 hectares or 1,751 acres), California sagebrush-black sage (*Artemisia californica* – *Salvia mellifera*) scrub (223 hectares or 551 acres), Fremont cottonwood (*Populus fremontii*) forest (80 hectares or 198 acres), and wild oats and annual brome (*Avena* spp. – *Bromus* spp.) grassland (1,013 hectares or 2,503 acres).

Study Design

Within the study area, six sites within blue oak woodland (hereafter referred to as grids) were randomly selected from sites that are currently used for on-going habitat and species monitoring, three each in the non-OHV and OHV areas (Figure 2). The OHV grids are located in the eastern portion of the SVRA, which has an 80-year history of off-highway vehicle recreational use, mostly by off-highway motorcycles. The non-OHV grids are located in the western portion of the SVRA, which are in areas closed to all off-highway vehicle use and previously were part of a cattle ranch dating back over 100 years.

Rodent Live Trapping

Each grid consisted of 50 Sherman live traps (H.B. Sherman Traps, Tallahassee, FL) spaced 20 meters apart. We used a square 5 x 5 trap configuration for all six grids with two traps at each trap location. All six 6,400-square meter (68,889 square feet or 1.6 acres) grids were trapped simultaneously. We set traps at or just before sunset (1600–2130) and checked them starting at sunrise (0600–1100) for three consecutive nights (henceforth referred to as a secondary trapping period). We baited with a mixture of sunflower seeds, bird seed, rolled oats, and peanut butter.

We conducted nine trapping periods (henceforth referred to as a primary trapping period) from December 2016 to November 2019 (December 2016; March 2017; July 2017; December 2017; April 2018; May 2019; July 2019; August 2019; and November 2019). We did not trap during January and February due to the increased risk of mortality from hypothermia. Moon phase was waxing or waning crescent with 7% to 36% illumination and all trapping periods were conducted under zero precipitation conditions.

Upon first capture, we marked all rodents with a single, unique numbered ear-tag (Monel Numeric size 1005-1; National Band and Tag Co, Newport, Kentucky, USA) and recorded species, sex, age-class, reproductive condition, and mass (grams) with a Pesola spring scale (Pesola AG, Baar, Switzerland). We also recorded head-body length, tail length, hind foot length, and ear length with a metric ruler. Upon recapture of a marked rodent within a secondary trapping period, we recorded ear-tag number, species, and sex. When a rodent was re-encountered in a primary trapping period that was tagged in a previous primary trapping period, we recorded ear-tag number, species, sex, age-class, reproductive condition, and mass.

We distinguished species based on pelage, body mass, and other morphological characteristics. We considered *Peromyscus maniculatus* to be adults if they had completed their post-juvenile molt (Kirkland and Layne 1989). We based age classes of other species on a combination of body mass and pelage characteristics. All rodent trapping, marking, and handling techniques were approved by the California Department of Fish and Wildlife (Permit Numbers: SCP-13528 and SCP-13619).



Rodent Diversity and Population Dynamics in an Off-highway Vehicle Area

Legend

- Park Boundary
- Corral Hollow Ecological Reserve
- Tesla Road
- Corral Hollow Road

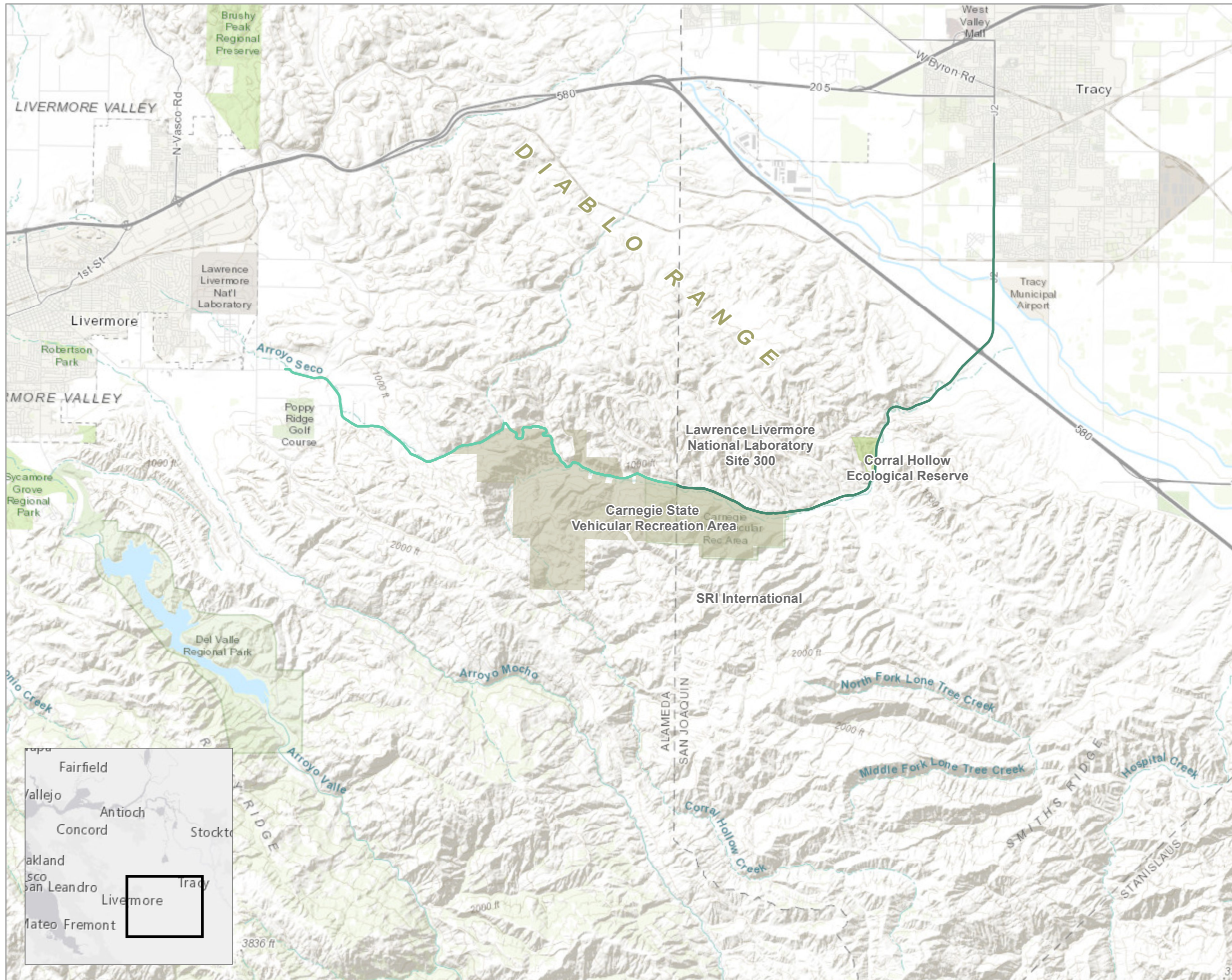


Figure 1:
Regional Location





Rodent Diversity and Population Dynamics in an Off-highway Vehicle Area



Legend

- Study Area
- Off Highway Vehicle Area
- Corral Hollow Ecological Reserve
- Corral Hollow/Tesla Road
- Grid Locations
- Streams
- Ponds

Figure 2:
Study Area



M I G Date: December 2020
Sources: ESRI, Carnegie SVRA,
TIGER, CDFW, USFWS

Precipitation

Rainfall records were compiled from monthly precipitation data at the Livermore Municipal Airport for 2013, approximately 15 miles northwest of Carnegie SVRA and from the station at Carnegie SVRA from 2014 to 2019 (Table 1).

Habitat Structure and Elevation

We assessed habitat structure using estimates for tree canopy coverage, trail and road density, area of woody debris piles, area of rocky outcrops, and areas covered by shrubs. Aerial imagery was used to estimate tree canopy coverage and trail density. We mapped the extent of the tree canopy and extent of trails and roads as discrete area polygons using Google Earth Pro within each grid, including a 20-meter (66 feet) buffer using aerial imagery from March 2017 (Google Inc. 2017). Trail width varied from approximately 0.6 meter to 1.8 meters (2.0 feet to 5.9 feet) and road width varied from approximately 2.5 meters to 5.0 meters (8.2 feet to 16.4 feet). The limit of the tree crowns was used to identify and map the extent of tree canopy cover.

Overlapping tree crowns were not double counted since we were only interested in area of the grid covered by the tree canopy and not canopy area contributed by each individual tree. Trails and roads were identified and mapped by areas that lacked vegetation and followed a linear arrangement. Additionally, trails were mapped under tree canopies by inferring their location by connecting the visible segments on either side of the tree crown(s) with an identical sized segment. Mean tree canopy coverage and mean trail density were calculated for the non-OHV and OHV areas by averaging the values for the three grids within each area.

Within each grid, we estimated the areas covered by woody debris, rocky outcrops, and shrubs in November 2017. Woody debris piles, rocky outcrops, and shrubby areas with a minimum area of one square meter (10.8 square feet) were measured. We created a habitat complexity variable (H_c) by summing the area of woody debris, the area of rocky outcrops, and the area covered by shrubs in each grid (Table 2). We determined the elevation and slope of each grid using Google Earth Pro (Google Inc. 2020). Slope was determined by subtracting the difference between the highest and lowest elevation in each grid and dividing by 80 meters (width of the grid) and converting the result to degrees. Aspect was determined in the field during the study period.

Demographic Analyses

We calculated community diversity at the grid scale and by OHV/non-OHV area with multiple metrics, including species richness (number of species captured) and the Shannon Diversity Index. We calculated Shannon Diversity Index as H' using number of unique individuals, for each species, captured in each primary trapping session. Species richness is the number of species present in a community or in the case of our study, the number of species captured. The Shannon Diversity Index is a widely used quantitative community diversity index that considers both species richness and relative abundance of species. Typical values are generally between 1.5 and 3.5 in most ecological studies, and the index is rarely greater than 4.

We calculated population abundance for all adults in the populations by OHV/non-OHV area using Program MARK (White & Burnham 1999). We could not estimate apparent survival, recruitment, and sex ratio due to insufficient number of recaptures between primary trapping

periods. Furthermore, we could not estimate population abundance for all species or for all trapping periods due to insufficient number of individuals captured. We used the full likelihood closed population capture-recapture models of Otis et al. (1978) to estimate population abundance during each trapping period. Data were grouped by species for analysis; the best model for each grouping was chosen based on AICc values.

Statistical Analyses

We used regression models (general linear model) to assess the relationship among OHV and non-OHV grids, primary trapping period, habitat complexity (H_c), elevation, precipitation, species richness, and Shannon Diversity Index (H'). We used an alpha level of 0.05 for all statistical tests, adjusted R^2 values, and we conducted analyses with the software R (version 4.0.3) (R Core Team 2020). We checked assumptions for regression using diagnostic plots for linearity and constant variance, independence, normality, and unusual observations. For time series regressions, we checked the independence assumption with the Durbin Watson Test. Since positive autocorrelation is common in time series data, we considered test statistic values from 1.5 to 2.5 as relatively normal.

Results

During the study, we trapped small mammals on 27 nights (7,800 trap nights), marking 603 unique individual rodents: 288 deer mouse (*Peromyscus maniculatus*), 88 pinyon mouse (*Peromyscus truei*), 66 California pocket mouse (*Chaetodipus californicus*), 58 California vole (*Microtus californicus*), 56 western harvest mouse (*Reithrodontomys megalotis*), 32 house mouse (*Mus musculus*), 10 desert woodrat (*Neotoma lepida*), and 5 San Joaquin pocket mouse (*Perognathus inornatus*) (Figure 3). See Table 3 and Table 4 in Appendix A for a complete list of species and number of unique individuals captured during the study at each grid location.

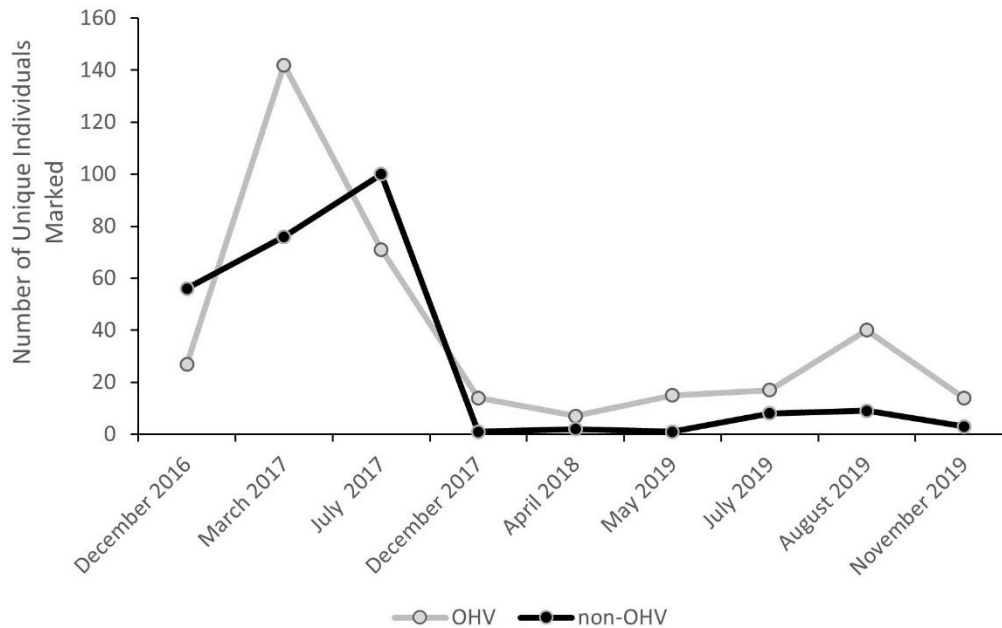


Figure 3. Number of unique individuals marked at each primary trapping period during the three-year study.

Precipitation. There was a significant relationship between the preceding 12-month precipitation totals preceding a primary trapping session and the number of unique individuals captured and marked in a primary trapping session ($F_{2,6} = 5.34$, $p = 0.046$; $R^2 = 0.52$) (Figure 4). The best model included grid location (OHV or non-OHV) as a predictor variable. The interaction term was not significant and therefore not included in the model. The Palmer Drought Severity Index (PDSI) estimated that the region was experiencing a severe to extreme drought from 2013 to 2015, a moderate drought to incipient wetness in 2016, normal to moderate drought in 2017, a moderate drought in 2018, and moderate wetness to incipient drought in 2019 (Dai et al. 2019).

Table 1. Precipitation Data for Carnegie SVRA. Precipitation data is in centimeters (inches).

Annual Precipitation (January-December)								
2013 ¹	2014 ²	2015 ²	2016 ²	2017 ²	2018 ²	2019 ²		
11.73 (4.62)	19.89 (7.83)	19.48 (7.67)	39.57 (15.58)	47.65 (18.76)	34.42 (13.55)	34.93 (13.75)		
12-month Period Preceding Primary Trapping Period ²								
December 2016	March 2017	July 2017	December 2017	April 2018	May 2019	July 2019	August 2019	November 2019
39.85 (15.69)	59.51 (23.43)	56.34 (22.18)	52.15 (20.53)	27.61 (10.87)	34.21 (13.47)	36.70 (14.45)	36.70 (14.45)	34.72 (13.67)

¹ data from Livermore Municipal Airport; ² data from Carnegie SVRA station

Habitat Structure. The habitat structure for each grid is summarized in Table 2.

Table 2. Summary of Habitat Structure in Each Grid.

Grid	Tree Canopy square meters (square feet)	Trail and Road Density square meters (square feet)	Habitat Complexity (H _c) square meters (square feet)	Elevation ² meters (feet)	Slope in degrees and Aspect
OHV					
Grid 11	2,616 (28,158)	4,151 (44,681)	528 (5,683)	471 (1,545)	24 northwest
Grid 15	3,811 (41,021)	3,690 (39,719)	139 (1,496)	322 (1,058)	23 northeast
Grid 108	1,697 (18,266)	245 (2,637)	110 (1,184)	329 (1,078)	19 northeast
Non-OHV					
Grid 34	3,247 (34,950)	0	328 (3,531)	591 (1,938)	19 southwest
Grid 46	4,505 (48,491)	0	700 (7,535)	546 (1,792)	24 northeast
Grid 49	1,581 (17,018)	467 ¹ (5,027)	102 (1,098)	641 (2,104)	9 west

¹ grid 49 was bisected by a dirt access road that is only used by maintenance staff and is not open to public use

² NAVD88

Species Richness: There was a significant negative relationship between species richness and trapping period ($F_{17,34} = 8.27$, $p < 0.001$; $R^2 = 0.71$) (Figure 5). The best model included OHV and non-OHV grids as predictor variables, and the interaction term between grid location (OHV or non-OHV) and trapping period. The interaction term explains how the relationship between species richness and primary trapping session depends on grid location (OHV or non-OHV).

There was also a significant relationship between species richness and precipitation ($F_{2,49} = 19.69$, $p < 0.0001$; $R^2 = 0.42$) (Figure 6). The best model included OHV and non-OHV grids as predictor variables. The interaction term was not significant and therefore not included in the model. There was a significant negative relationship between species richness and elevation ($F_{1,50} = 6.72$, $p = 0.012$; $R^2 = 0.10$) (Figure 7). Additionally, there were no significant relationships among species richness, trail density, tree canopy, H_c, and slope.

Shannon Diversity: There was a significant negative relationship between H' and trapping period ($F_{17,34} = 4.97$, $p < 0.001$; $R^2 = 0.57$) (Figure 8). The best fit model included OHV and non-OHV grids as predictor variables, and the interaction term between grid location (OHV or non-OHV) and trapping period. The interaction term explains how the relationship of H' and the primary trapping period depends on grid location (OHV or non-OHV).

There was also a significant relationship between H' and precipitation ($F_{2,49} = 17.85$, $p < 0.0001$; $R^2 = 0.40$) (Figure 9). The best model included OHV and non-OHV grids as predictor variables. The interaction term was not significant and therefore not included in the model. There was a significant negative relationship between Shannon Diversity (H') and elevation $F_{1,50} = 9.04$, $p =$

0.004; $R^2 = 0.14$) (Figure 10). Additionally, there were no significant relationships among species richness, H' , trail density, tree canopy, H_c , and slope.

Abundance Estimates. Due to small sample sizes, population abundance estimates were only computed for *P. maniculatus* and *P. truei* for the December 2016, March 2017, and July 2017 primary trapping periods (Figures 11 and 12). Because of non-overlapping confidence intervals, there were significant differences in abundance estimates for *P. maniculatus* between OHV and non-OHV grids in the March and July 2017 primary trapping periods (March 2017: non-OHV abundance estimate: 24.3, 95% CI [21.7, 36.9]; OHV abundance estimate: 45.4, 95 % CI [44.2, 52.8]; July 2017: non-OHV abundance estimate: 72.9, 95% CI [59.1, 105.3]; OHV abundance estimate: 26.4, 95% CI [22.3, 43.0]). There were no significant differences in abundance estimates for *P. truei* in the March and July 2017 primary trapping periods: non-OHV abundance estimate: 27.4, 95% CI [13.8, 93.4]; OHV abundance estimate: 16.2, 95 % CI [7.9, 59.8]; July 2017: non-OHV abundance estimate: 29.1, 95% CI [26.7, 40.0]; OHV abundance estimate: 19.5, 95% CI [11.7, 62.6]). For the December 2016 primary trapping period, the sample size was too small in the non-OHV grids to estimate abundance.

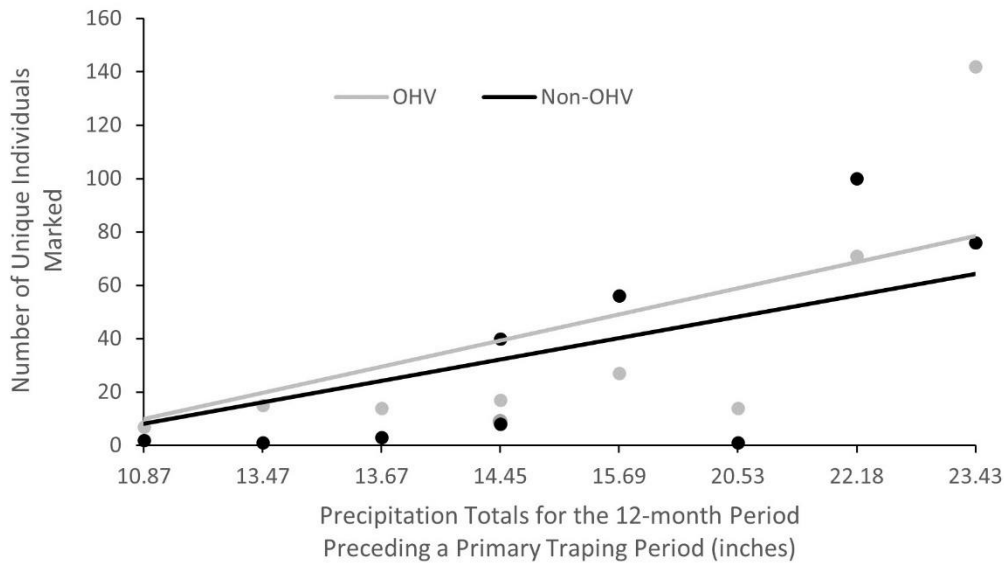


Figure 4. Number of unique individuals captured and marked in OHV and non-OHV grids and precipitation totals for the 12-month period preceding a primary trapping period. There was a significant relationship between number of unique individuals marked and precipitation and grid location (OHV or non-OHV) ($F_{2,6} = 5.34$, $p = 0.046$; $R^2 = 0.52$).

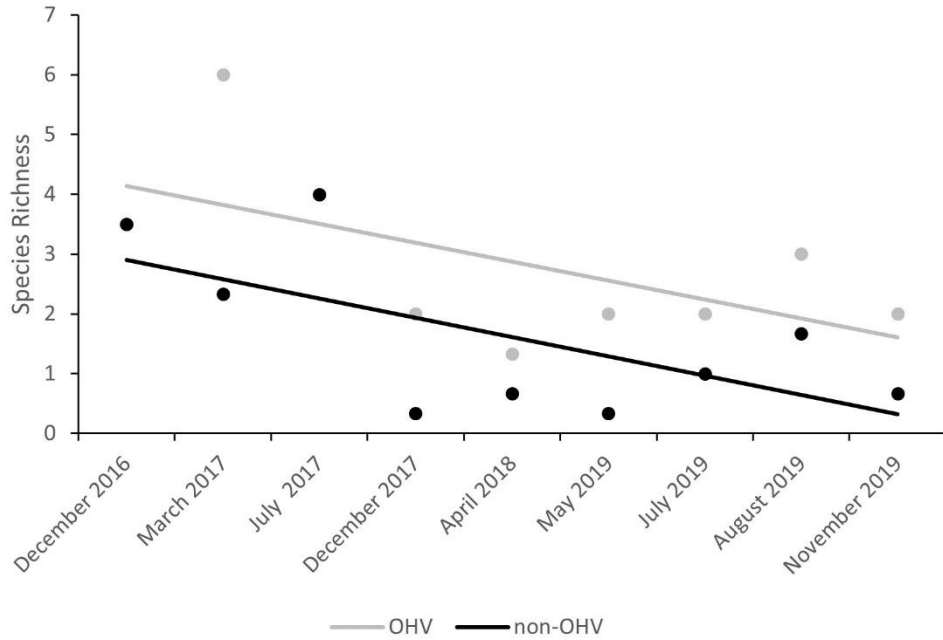


Figure 5. Species richness for OHV and non-OHV grids averaged for each primary trapping period. There was a significant relationship between species richness and grid location (OHV or non-OHV) and primary trapping period ($F_{17,34} = 8.27$, $p < 0.001$; $R^2 = 0.71$).

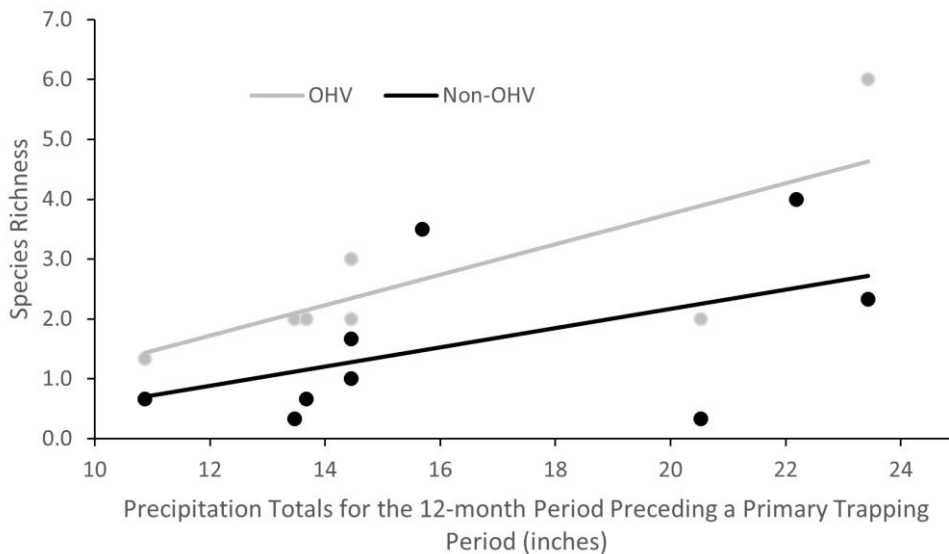


Figure 6. Species richness and precipitation totals for the 12-month period preceding a primary trapping period averaged across OHV and non-OHV grids. There was a significant relationship among species richness, precipitation totals, and grid location (OHV and non-OHV) ($F_{2,49} = 19.69$, $p < 0.0001$; $R^2 = 0.42$).

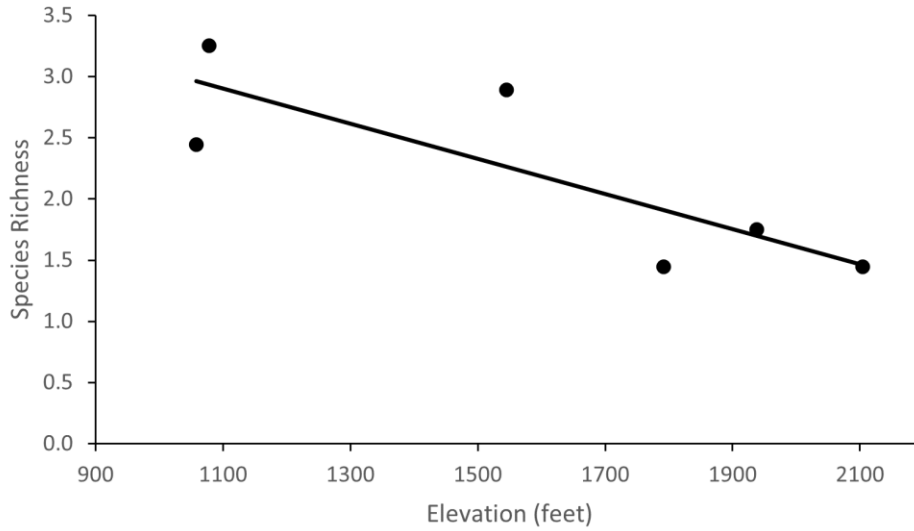


Figure 7. Species richness and elevation for each of the OHV and non-OHV grids averaged over the study period. There was a significant negative relationship between species richness and elevation ($F_{1,50} = 6.72$, $p = 0.012$; $R^2 = 0.10$).

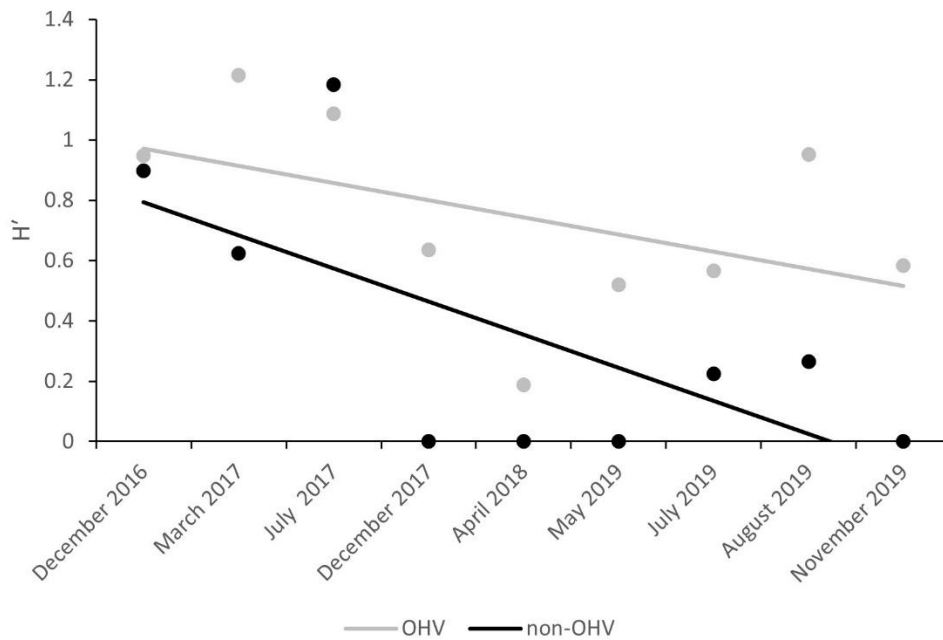


Figure 8. Shannon diversity (H') for OHV and non-OHV grids averaged for each primary trapping period. There was a significant relationship between H' and grid location (OHV and non-OHV) and primary trapping period ($F_{17,34} = 4.97$, $p < 0.001$; $R^2 = 0.57$).

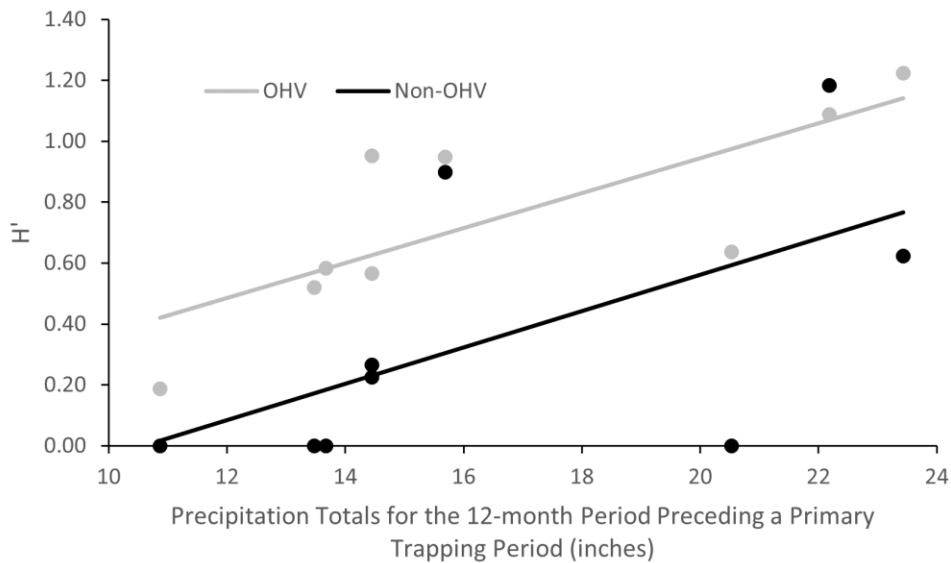


Figure 9. Shannon Diversity and precipitation totals for the 12-month period preceding a primary trapping period averaged across OHV and non-OHV grids. There was a significant relationship among Shannon Diversity, precipitation totals, and grid location (OHV and non-OHV) ($F_{2,49} = 17.85$, $p < 0.0001$; $R^2 = 0.40$).

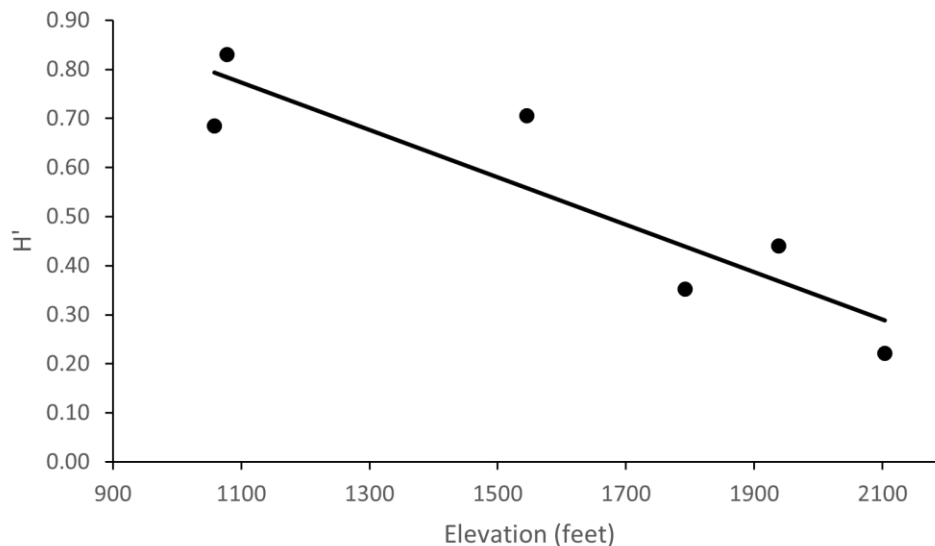


Figure 10. Shannon diversity (H') and elevation for each of the OHV and non-OHV grids averaged over the study period. There was a significant negative relationship between H' and elevation ($F_{1,50} = 9.04$, $p = 0.004$; $R^2 = 0.14$).

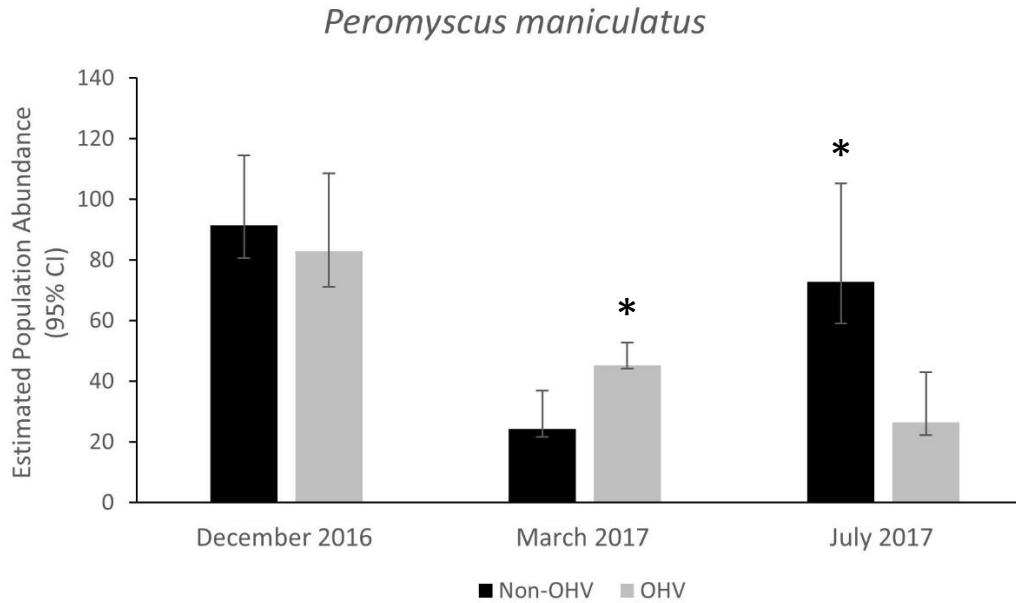


Figure 11. Population abundance estimates from Program MARK for *P. maniculatus* for three primary trapping periods (number of adult individuals in all the OHV or non-OHV grids, 95% CI); * indicates significance.

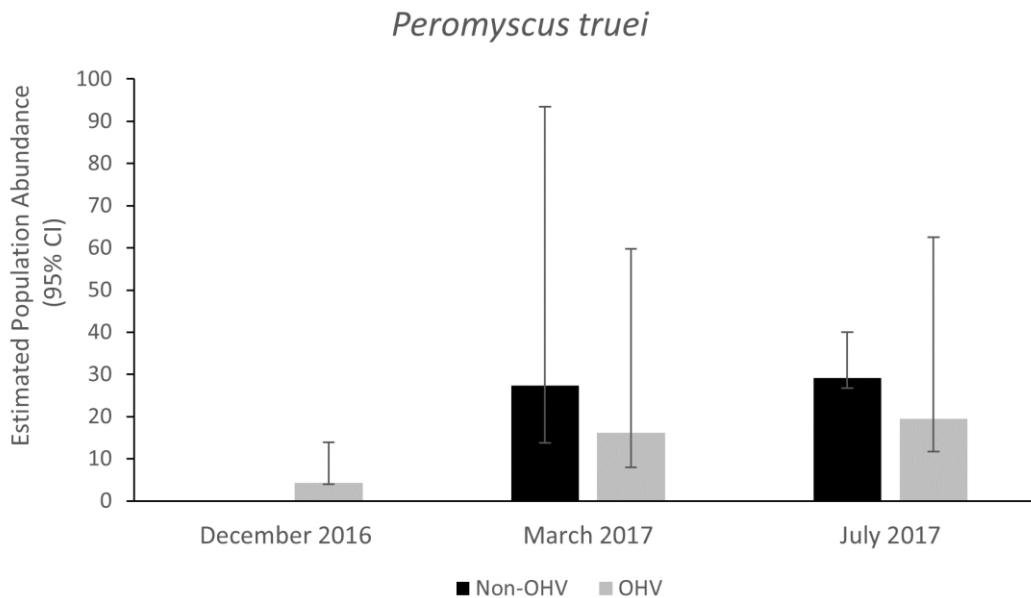


Figure 12. Population abundance estimates from Program MARK for *P. truei* for three primary trapping periods (number of adult individuals in all the OHV or non-OHV grids, 95% CI); * indicates significance. Due to a small sample size, an abundance estimate for non-OHV grids in the December 2016 primary trapping period could not be estimated.

Discussion

Precipitation and Small Mammal Population Growth

One of the most striking outcomes of the study was the pronounced decrease in the number of captures for both OHV and non-OHV grids after the July 2017 primary trapping period. For example, during July 2017, 171 unique individuals were captured and in December 2017, the number of unique individuals captured dropped to 15, a decrease of over 90% or 11 orders of magnitude. During the remainder of the study after July 2017, the number of captures never reached the capture levels of the three primary trapping periods from December 2016 to July 2017 (Figure 4).

Prior to the start of our study in 2016, annual precipitation totals at Carnegie SVRA were substantially below average from 2013 to 2015 and the region was in a severe to extreme drought (38% to 64% below average; Table 1). In 2016, annual precipitation was 23% above average and was experiencing incipient wetness at the beginning of the study. In desert regions, a direct positive relationship exists between drought-breaking precipitation and population growth rate. For example, Merriam's kangaroo rat (*Dipodomys merriami*) occupies the Sonoran Desert and lower elevations in the Mojave Desert in California and typically exhibit large fluctuations in abundance in response to temporal variability in plant productivity, which is dependent on the prevailing patterns of seasonal precipitation to stimulate growth of herbaceous plants (Ernest et al. 2000). The relationship between precipitation and population size is apparent in other mammals in arid environments, which often show pronounced fluctuations in population size and growth, oscillating from being almost absent to being very abundant (Beatley 1969; Previtali et al. 2009; Srivathsa et al. 2019). Boom-bust dynamics are well documented in small mammal populations in arid and semi-arid environments (Stapp 2010).

The results of our study show a similar relationship between precipitation and number of captures of unique individuals for a semi-arid environment. Due to small sample sizes, we could not determine if the same relationship exists between precipitation and abundance. However, since abundance estimates are derived from the number of unique individuals captured, it is likely that the relationship between precipitation and abundance would follow a similar pattern (Bennison et al. 2018). The best fit model also included grid location (OHV and non-OHV) as significant predictor variables, indicating that the relationship between precipitation and number of captures was the same regardless of the grid location, but that the number of captures was lower for the non-OHV area for a given precipitation total (Figure 5). However, the differences in the number of captures between OHV and non-OHV grids may not be significant due to the small sample sizes (see *Abundance Estimates* section below).

Because of the above average rainfall, the small mammal population at Carnegie SVRA may have experienced the start of a population "boom" in 2016, which coincided with the start of our study, since improved conditions in arid regions are brought about by above average precipitation that stimulates increased plant productivity, which increases food resources (Whitford 2002). Small mammals in arid environments often respond to an increase in plant productivity with elevated reproduction rates, increased survivorship, and increased abundance. (Newsome and Corbett 1975; D'Souza et al. 2013; Greenville et al. 2013). Furthermore, links

between rainfall and small mammal booms have been traced over periods exceeding 100 years (Plomley 1972; Greenville et al. 2012).

Population peaks, or “booms,” are often ephemeral, and may last less than a year if conditions deteriorate rapidly (Dickman et al. 2010). In our study, the small mammal population boom at Carnegie SVRA started in December 2016 or earlier, peaked by March 2017 and by December 2017, the small mammal population had entered a “bust” phase and dropped below the population size in December 2016. Generally, the low, or “bust,” phases of populations usually occur during prolonged periods when the environmental carrying capacity is low due to depressed food resources (Letnic et al. 2005; Yang et al. 2010). However, annual precipitation totals remained at above average levels for the remainder of the study period and the number of captures remained steady, with the exception of a sudden increase in the number of captures during the August 2019 primary trapping period. Such a pattern suggests that the small mammal population at Carnegie SVRA was not in a prolonged bust phase from 2018 to 2019, but rather the number of captures may be more representative of typical small mammal abundances in blue oak woodland communities. The population “boom” observed during the March 2017 primary trapping period was likely a response to a sudden increase in the availability of food resources after years of a severe to extreme drought in the region. Our study underscores the reality that small mammals are capable of rapid increases in abundance in response to resource pulses.

Abundance Estimates

Deer Mouse. In December 2016, *P. maniculatus* was equally abundant in the OHV and non-OHV grids, in March 2017 it was more abundant in the OHV grids, and in July 2017 it was more abundant in the non-OHV grids (Figure 9). Additionally, *P. maniculatus* was captured in all OHV and non-OHV grids during the study period. Despite the significant differences in abundance estimates for *P. maniculatus* between OHV and non-OHV grids in March 2017 and July 2017, the small sample sizes, variability in abundance estimates, and the limited number of primary trapping sessions for which abundance estimates were calculated precludes drawing conclusions in long-term trends in abundances in the OHV or non-OHV grids. Furthermore, *P. maniculatus* is the most widespread and common small mammal in North America and is found in large numbers in both disturbed and undisturbed habitats. They are habitat generalists that appear to utilize a wide variety of unoccupied niches in the landscape (Baker 1968; Morrison and Anthony 1988; Fitzgerald et al. 1994; Sullivan et al., 1999; Kaminski et al. 2007; Zwolak 2009).

Pinyon Mouse. In March 2017 and July 2017, *P. truei* was equally abundant in the OHV and non-OHV grids (Figure 10). Additionally, *P. truei* was captured in all OHV and non-OHV grids during the study period. However, the very small sample sizes, large variability in abundance estimates, and the limited number of primary trapping sessions for which abundance estimates were calculated precludes drawing conclusions long-term trends in abundances in the OHV or non-OHV grids. Furthermore, *P. truei* are common in the western U.S and can be found in a variety of habitats in California, including chaparral, desert scrub, coastal redwood belt, and oak woodlands (Hoffmeister 1981). There is evidence that *P. truei* is a habitat generalist and will colonize new areas if sufficient resources become available (Massey et al. 2018).

Since abundance estimates for both species were calculated only for the “boom phase” of the study period, it is unknown if grid location (OHV or non-OHV) would be significant factor in abundance of *P. truei* and *P. maniculatus* during the “bust phase” or periods of lower abundance.

Habitat Structure

Habitat structure and diversity have been correlated with species diversity of birds (MacArthur & MacArthur 1961; Terborgh 1977) and of small mammals (Rosenzweig & Winakur 1969). More specifically, species diversity and species richness of small mammals are influenced by changes in habitat structure, including anthropogenic modifications to the landscape, vegetation density, tree canopy cover, shrub density, and edaphic changes (Feldhamer 1979; Parmenter and MacMahon 1983; Loeb 1999; Kaufman et al. 2000; Davis et al. 2010; Sustaita et al. 2011; Marshall et al. 2012). Since all grids were located within blue oak woodland dominated by *Avena* spp. and *Bromus* spp. annual grassland understory, we assessed habitat structure using estimates for tree canopy coverage, trail and road density, area of woody debris piles, area of rocky outcrops, and areas covered by shrubs (Table 2).

While habitat structure gradients existed within the woodland grids, the differences in habitat structure among the sites were not a significant predictor of species richness and diversity. However, not all species were captured in each grid or in both OHV and non-OHV grids.

Desert Woodrat. *N. lepida* was only captured in two grids during the study period, grid 11 in the OHV area and grid 46 in the non-OHV area. Even though *N. lepida* occupy a wide range of habitats in California, the critical component of habitats occupied by *N. lepida* include features that afford protection from predators, including rockpiles, woody debris, and shrub cover (Verts and Carraway 2002). Both grids had up to boulder size rocks and the greatest habitat complexity (H_c), which includes area covered by rocky outcrops, downed logs, and shrubs, suggesting that *N. lepida* were present due to the habitat complexity in these two grids.

San Joaquin Pocket Mouse. *P. inornatus*, which was captured only in two of the OHV grids (Grid 15 and Grid 108) and only in low numbers. The hilly, woodland habitat with gravelly loam to clay soils in the OHV and non-OHV grids probably do not provide high-quality habitat for *P. inornatus* since this species is generally found in flat to low hills in open or scrub areas in the Central and Salinas Valleys. Also, *P. inornatus* will go into torpor in response to extreme heat or cold and stay in their burrows for extended periods of time (Ingles 1965).

Species Richness and Species Diversity

All species captured during the study were present in both OHV and non-OHV grids, except for *P. inornatus* (see *Habitat Structure* section above). Also, not all species were captured during each primary trapping session. See Table 3 and Table 4 in Appendix A for a complete list of species and number of unique individuals captured during the study. Our study showed that species richness and species diversity, as measured by the Shannon Diversity Index, was greater in the OHV grids and decreased at different rates in both the OHV and non-OHV grids during the three-year study (Figure 7 and Figure 8). In both OHV and non-OHV grids, species richness and diversity were the greatest, on average during the “boom phase” of the study and

then dropped off in both OHV and non-OHV grids, but a much greater rate for the non-OHV grids. The rate of decrease was much greater for species diversity than species richness.

Our hypothesis was that rodent population abundance and community diversity would be greater in areas where habitat heterogeneity was the greatest. The most pronounced difference between OHV grid and non-OHV grids was the presence of trails, which increases habitat heterogeneity, but was not a significant predictor of species richness and species diversity in our study. Other factors that influence habitat heterogeneity, including tree canopy density and habitat complexity (H_c) were also not significant predictors of species richness and species diversity (see *Habitat Structure* section above). However, our study showed that elevation and precipitation totals for the 12-month period preceding a primary trapping were significant predictors of species richness and species diversity (Figure 6 and Figure 7; and Figure 9 and Figure 10, respectively).

During our study, we did not collect long-term, fine-scale weather data at the grid locations; therefore, we were unable to determine if precipitation was influenced by elevation or if grid locations differed in precipitation totals, wind intensity, or temperature. Further confounding the relationship is the OHV and non-OHV grids fall along an elevational gradient with all the non-OHV grids at higher elevations than the OHV grids. In other words, differences between OHV and non-OHV grids may not be due to elevation since elevation and grid location are correlated. Although statistically significant, the amount of variance in species richness and diversity explained by elevation was low ($R^2 = 0.10, 0.14$, respectively), but the amount of variance explained by precipitation totals was moderate ($R^2 = 0.42, 0.40$, respectively), suggesting that the relationship between precipitation and species richness and diversity was stronger. The topography of the Park is characterized by a west to east decreasing elevational gradient, steeply sloping hillsides, long north-south ridgelines, and deep ravines. The topography combined with the direction of approaching winter storm systems, which typically approach the Park from the west or northwest, likely place the OHV grids in a rain shadow with the non-OHV grids receiving more rainfall. While species richness and diversity are significantly influenced by precipitation for both OHV and non-OHV grids, the OHV grids clearly have greater species richness and diversity, suggesting a more complex relationship.

One possibility is the influence of microclimates on species richness and diversity within the Park. Furthermore, microclimates could occur along an elevational component in the Park due to significant differences in temperature, winds, and precipitation patterns over relatively short distances due to the complex terrain of the Park. Even though grid location and elevation are correlated, elevation may still be an important component of understanding the relationship among species richness, species diversity, and grid location, especially in the context of microclimates. Indeed, species richness and diversity in rodent populations have shown to vary along elevational gradients and such relationships are generally associated with changes in vegetation communities, availability of food (productivity), microclimate, and topography (Patterson et al. 1989; Blaustein et al. 1996; Heaney 2001; Lomolino 2001; Sanchez-Cordero 2001; Grytnes and Vetaas 2002; Kluge et al. 2006; Agustina and Ojeda 2014).

There is also evidence that rodent population dynamics and community structure are affected by factors in addition to precipitation, microclimate, or food availability. For example, nearby habitats with nearly identical precipitation can differ markedly in rodent abundance and species

composition and these differences appear to reflect variation in risk of predation (Rosenzweig and Winakur 1969, Kotler 1984, Kotler and Brown 1988). Therefore, it is likely that rodent populations are regulated not only from the bottom up by resource availability but also from the top down by predation and the relationship is likely influenced by the interaction of both factors (Rosenzweig 1973, Brown 1989, Thibault 2010). During our study, it is possible that the risk of predation is greater in the non-OHV grids due to an increased abundance and/or diversity of predators. Small mammals in our study are primarily nocturnal, so predation is likely to occur at night. Even though the Park is closed at night, it is possibly that predators are less likely to frequent the OHV area due to daytime disturbance from OHV activities. This may be the case with avian predators since mammalian predators are regularly observed at night on cameras in the OHV area. Although we have no data from our study to support such an assertion, OHV recreation is known to negatively impact predators, including raptors and mammals (Steenhof et al. 2014, Jones et al. 2017). In conclusion, it is unclear what factor or combination of factors explain why OHV grids during the study period had greater species richness and diversity.

Appearance of Mus musculus

House Mouse. *M. musculus* is an introduced, invasive species that is widespread in North America and is often found in disturbed areas or marginal habitats and can increase in abundance rapidly and immigrate into new areas when required resources become available and intraspecific competition is minimal or non-existent (Caldwell 1964; Caldwell and Gentry 1965; De Long 1966; Lund 1996; Macdonald and Fenn 1996; Stenseth et al. 2003; Gomez et al. 2008).

A single *M. musculus* was first captured in May 2019 in the OHV area and the number of captures increased during subsequent trapping periods in the OHV area. The total number of captures peaked in the OHV area in August 2019 with *M. musculus* accounting for 52% of total captures and by November 2019, the number of captures declined with *M. Musculus* accounting for 28% of total captures in the OHV area. A single *M. musculus* was captured in the non-OHV area in August 2019 and accounted for 11% of the total captures in the non-OHV during the August primary trapping period.

Given the widespread distribution of *M. musculus* and the long history of human disturbance in the region, it is likely that *M. musculus* was present throughout the study area during the study period. During the “boom” phase in our study (December 2016 to July 2017), *M. musculus* was likely replaced by competitively superior native species in the grids or their abundance was so low that they were not detected. *M. musculus* is also known to migrate to other areas when faced with interspecific competition and low recapture rates have been observed for *M. musculus* in commensal habitats (Caldwell 1964; Caldwell and Gentry 1965; Pocock et al. 2004; Wu et al. 2006). After the bust phase in December 2017, *M. musculus* likely started to migrate into the OHV and non-OHV grids when interspecific competition was likely low, as evidenced by low capture numbers after December 2017, but food resources were likely still available due to the above average rainfall during the study period. Furthermore, boom-bust dynamics have been associated with biological invasions (Simberloff and Gibbons 2004; Lockwood et al. 2013).

The detection of *M. musculus* during the study was not likely due to a new invasion of a non-native species into previously unoccupied habitat, but rather the result of boom-bust population

dynamics and the return of a species already present in the study area that is adept at exploiting habitats where native species are present in low abundances.

Management Implications

It is possible that rodent populations in OHV areas are healthy and stable since species richness and species diversity were greater in the OHV area during our study; and precipitation patterns may play a dominant role in influencing population growth patterns in both OHV and non-OHV areas, as evidenced by the observed boom-bust dynamic. Indeed, Reid 2012 found species richness and species diversity for rodents was not correlated with off-road vehicle use in a desert ecosystem but found that some species declined in abundance in off-road vehicle areas while abundance of other species increased, likely due to reduced vegetation cover in off-road vehicle areas. Since additional population demographic parameters, including population abundance and survival were not estimated throughout the study period, the effects of OHV recreation on rodent populations are not completely clear, especially within the context of a boom-bust dynamic.

Given that trail density was not a significant predictor of species richness and species diversity, the presence of trails likely did not result in negative impacts on rodent populations. Our study suggests that the OHV grids contained sufficient undisturbed patches of vegetation and that any loss of vegetation coverage or reduction in habitat value from trails was not significant. However, there is likely a threshold trail density at which point there would be a significant enough change in vegetation cover that would impact rodent population dynamics. Therefore, existing trail density may be a useful guide for future trail development.

From a land use management perspective, the development of new trails should seek to limit disturbance by maintaining undisturbed patches of habitat within an area and by limiting OHV use to trails, which is a current trend at Carnegie SVRA. With increasing OHV use, it is likely that pressure on ecosystems to provide different and often conflicting services is going to increase. Therefore, the impacts and success of balancing off highway vehicle recreation with conservation will be enhanced if the needs of competing land uses are recognized at the planning stage.

Conclusion

Our study suggests that precipitation may be the best predictor of population growth patterns for rodents and that trail density was not a significant factor in rodent community dynamics at Carnegie SVRA during our study. While species richness and species diversity were greater in the OHV area during our study, it is unclear what factor or combination of factors are responsible for this observed pattern.

We were unable to estimate additional population demographic parameters including population abundance (except for two species at the beginning of the study), recruitment, and survival to characterize the rodent community dynamics at Carnegie SVRA due to the lack of data from the boom-bust dynamic observed during the study period. Determining these parameters would provide a more detailed understanding of potential ecological effects of OHV recreation on rodent populations. For this reason, future studies should consider increasing the number of grids in both the OHV and non-OHV grids to increase sample size.

To meet the challenge of sustaining ecological systems while also simultaneously providing recreational off highway vehicle use, land managers need indicators of habitat quality or ecosystem function that provide accurate assessments of underlying ecological conditions and long-term trends. Small mammal communities respond rapidly to change in habitat structure and occupy key positions in food webs, making them informative biological indicators of change.

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Appendix A

Table 3. Number of Unique Individuals Captured During the Study Period in the OHV Grids.

	<i>Peromyscus maniculatus</i>	<i>Peromyscus truei</i>	<i>Chaetodipus californicus</i>	<i>Microtus californicus</i>	<i>Reithrodontomys megalotis</i>	<i>Mus musculus</i>	<i>Neotoma lepida</i>	<i>Perognathus inornatus</i>			
Grid 11									Total	Species Richness	Shannon Diversity (H')
December 2016	15	2	0	0	3	0	1	0	21	4	0.89
March 2017	21	9	2	2	4	0	2	0	40	6	1.35
July 2017	14	7	6	16	3	0	3	0	49	6	1.60
December 2017	0	0	3	0	0	0	1	0	4	2	0.56
April 2018	0	3	1	0	0	0	0	0	4	2	0.56
May 2019	0	1	0	0	0	0	1	0	2	2	0.69
July 2019	0	3	0	0	0	0	0	0	3	1	0
August 2019	0	1	0	0	0	0	1	0	2	2	0.69
November 2019	0	5	0	0	0	0	0	0	5	1	0
Grid 15											
December 2016	1	2	0	0	3	0	0	0	6	3	1.01
March 2017	25	5	7	6	6	0	0	2	51	6	1.48
July 2017	0	0	5	0	0	0	0	1	6	2	0.67
December 2017	3	0	2	0	0	0	0	0	5	2	0.67
April 2018	2	0	0	0	0	0	0	0	2	1	0
May 2019	0	0	0	0	0	1	0	0	1	1	0
July 2019	1	0	0	0	0	1	0	0	2	2	0.69
August 2019	1	0	0	0	4	5	0	0	10	3	0.94
November 2019	0	0	2	0	0	2	0	0	4	2	0.69
Grid 108											
December 2016 ¹	-	-	-	-	-	-	-	-	-	-	-
March 2017	40	1	2	3	4	0	0	1	51	6	0.84
July 2017	4	0	10	0	1	0	0	1	16	4	0.99
December 2017	3	0	2	0	0	0	0	0	5	2	0.67
April 2018	1	0	0	0	0	0	0	0	1	1	0
May 2019	8	0	0	2	2	0	0	0	12	3	0.87
July 2019	3	0	1	0	3	5	0	0	12	3	1.00
August 2019	5	0	1	2	5	15	0	0	28	4	1.22
November 2019	2	0	0	0	1	2	0	0	5	3	1.05
Totals	149	39	44	31	39	31	9	5	347		

¹Grid 108 not trapped in December 2016

Table 4. Number of Unique Individuals Captured During the Study Period in the Non-OHV Grids.

	<i>Peromyscus maniculatus</i>	<i>Peromyscus truei</i>	<i>Chaetodipus californicus</i>	<i>Microtus californicus</i>	<i>Reithrodontomys megalotis</i>	<i>Mus musculus</i>	<i>Neotoma lepida</i>	<i>Perognathus inornatus</i>	Total	Species Richness	Shannon Diversity (H')
Grid 34											
December 2016 ¹	-	-	-	-	-	-	-	-	-	-	-
March 2017	9	11	0	0	0	0	0	0	20	2	0.69
July 2017	3	2	3	2	0	0	0	0	10	4	1.37
December 2017	0	0	0	0	0	0	0	0	0	0	0
April 2018	0	0	1	0	0	0	0	0	1	1	0
May 2019	0	1	0	0	0	0	0	0	1	1	0
July 2019	0	3	0	0	2	0	0	0	5	2	0.67
August 2019	1	5	0	0	0	1	0	0	7	3	0.80
November 2019	0	2	0	0	0	0	0	0	2	1	0
Grid 46											
December 2016	14	0	10	0	4	0	1	0	29	4	1.11
March 2017	18	9	0	0	0	0	0	0	27	2	0.64
July 2017	16	11	3	13	3	0	0	0	46	5	1.42
December 2017	0	0	0	0	0	0	0	0	0	0	0
April 2018	1	0	0	0	0	0	0	0	1	1	0
May 2019	0	0	0	0	0	0	0	0	0	0	0
July 2019	0	0	0	0	0	0	0	0	0	0	0
August 2019	0	0	0	0	1	0	0	0	1	1	0
November 2019	0	0	0	0	0	0	0	0	0	0	0
Grid 49											
December 2016	16	0	5	0	6	0	0	0	27	3	0.69
March 2017	24	1	0	4	0	0	0	0	29	3	0.55
July 2017	32	4	0	8	0	0	0	0	44	3	0.76
December 2017	1	0	0	0	0	0	0	0	1	1	0
April 2018	0	0	0	0	0	0	0	0	0	0	0
May 2019	0	0	0	0	0	0	0	0	0	0	0
July 2019	3	0	0	0	0	0	0	0	3	1	0
August 2019	1	0	0	0	0	0	0	0	1	1	0
November 2019	0	0	0	0	1	0	0	0	1	1	0
Totals	139	49	22	27	17	1	1	0	256		

¹Grid 34 not trapped in December 2016