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ACTIVITY PATTERNS OF THE ENDANGERED AMARGOSA VOLE (*MICROTUS CALIFORNICUS SCRIPENSIS*)

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***Abstract*.—Examining the activity patterns of wildlife is an important aspect of understanding the ecology of a species and may be especially important for species of conservation concern. We used remotely triggered cameras to describe the daily and seasonal activity patterns and examine ecological factors that influence the activity of the Amargosa Vole (*Microtus californicus scirpensis*), a California endemic listed federally and by the state as Endangered, and is a marsh habitat-specialist in the Mojave Desert. We found that vole activity was greatest during crepuscular periods, followed by nocturnal and diurnal periods. We saw strong seasonal effects, with the highest activity occurring in spring (March-May). Daily activity patterns varied at different times of the year, with lower activity during periods of seasonal temperature extremes. Daily high temperatures, however, were only weakly related to activity, and precipitation was not associated with changes in activity patterns. Of the factors we examined, marsh area was the most important factor in predicting vole activity, with larger marshes having higher vole activity than smaller marshes. Predation seemed to be strong driver of vole activity, with higher activity during periods of lower potential predation risk (crepuscular and new-moon periods), suggesting that voles may decrease their activity to avoid predators during periods when predators may more easily detect them (e.g., full moon). By highlighting factors that influence vole activity, we show the importance of understanding activity patterns relative to the ecology and conservation of this species.**

Key Words.—Camera trap; ecological interactions; Mojave Desert; seasonal

INTRODUCTION

The daily and seasonal activity patterns of a wildlife species reveal critical information about their ecology and behavior, with implications for their population dynamics (Sutherland and Singleton 2003), evolution (Kronfeld-Schor and Dayan 2008; Gerkema et al. 2013), energetics (Kenagy 1973; Tachinardi et al. 2017), and habitat use (Kenagy 1973; Brown et al. 1994). Activity patterns may also affect how a particular species interacts with other species, such as through competition and predation (O'Farrell 1974; Arias-Del Razo et al. 2011; Harrison 2019). Knowledge of activity patterns is particularly important to inform conservation actions for species at risk of decline or extinction without management intervention.

The Amargosa Vole (*Microtus californicus scirpensis*) is a federally and California state-listed Endangered rodent that is found within a small range of extremely isolated spring-fed marshes in the Mojave Desert (U.S. Fish and Wildlife Service [USFWS] 1997). The species is threatened by anthropogentic and climate change induced loss and degradation of habitat, alterations in hydrology, and the impacts from non-native species (USFWS 1997; Haswell et al. 2022). Studies on the ecology of the vole, including its distribution (Janet Foley et al., unpubl. report), demography and habitat use (Klinger et al. 2013; Klinger et al. 2015; Janet Foley et al., unpubl. report), predators (Roy et al. 2019), survival (Klinger et al. 2013), and general biology and behavior (Allan et al. 2018; Pesapane et al. 2018) have proven useful in understanding and managing this species. Understanding how activity of these voles varies seasonally and is affected by various factors will be important to their conservation. Moreover, previous studies of Amargosa Voles have relied upon live-trapping data (Klinger et al. 2013), which provides a snapshot of activity around set time intervals (e.g., day-time trapping vs night-time trapping), but is limited by both the timing of trap checks (every 6–8 h) and the need to avoid trapping during extreme temperature and weather events.

A better understanding of vole activity and behavior can aid in species management by targeting times of day or year to conduct surveys or limit disruptive human-use or the impacts of conservation activites on the species. Here we describe the activity patterns of Amargosa Voles using camera traps, which allow for continuous monitoring of animal activity. Our specific goals were to define the daily and seasonal activity patterns across the geographic range of the Amargosa Vole and to explore how ecological factors (time of day, temperature, precipitation, marsh location and size, and potential intra- and interspecific interactions) influence these patterns.

METHODS

***Study site*.**—We studied voles in marshes in the Mojave Desert near Tecopa, California (35.8481° -116.2267°; Fig. 1). The climate is characterized by wide daily and annual fluctuations in temperature, from a mean winter

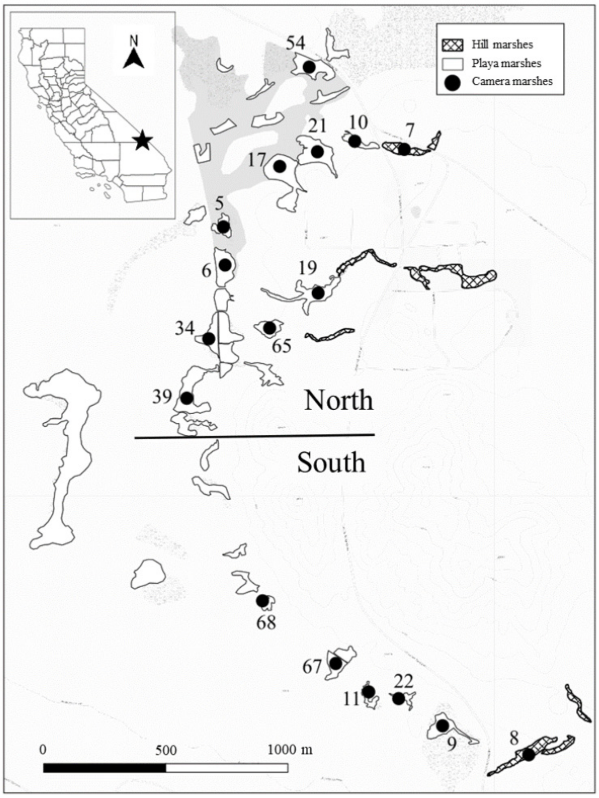

Figure 1. Locations of marshes near Tecopa, Inyo County, California (35.871°, -116.233°), where monthly camera trapping surveys of Amargosa Vole (*Microtus californicus scirpensis*) activity were conducted during 2015–2016. The black star represents the approximate location of the study area within California. Shaded areas in the base map represent ephemeral wetland habitats. Additional marshes are included in the map; however, only numbered marshes were included in this study.

Table 1. Sample marsh characteristics and total number of independent activity events of Amargosa Voles (*Microtus californicus scirpensis*) recorded by remote cameras in 17 marshes in Tecopa, Inyo County, California. Activity data were collected over approximately bi-monthly, five-day periods during 2015–2016. All marshes were located in Playa habitat except for marshes 7 and 8, which were located in Hill habitat (see Fig. 1).

Marsh ID #	Marsh size	Habitat	Marsh area (ha)	Activity events
North				
6	Large	Playa	1.20	17
17		Playa	2.21	161
19		Playa	1.44	163
21		Playa	1.61	181
39		Playa	1.75	132
54		Playa	1.28	145
5	Small	Playa	0.52	91
10		Playa	0.47	61
34		Playa	0.87	82
65		Playa	0.64	46
7		Hill	0.64	114
South				
9	Large	Playa	1.00	92
8		Hill	1.10	83
11	Small	Playa	0.32	5
22		Playa	0.25	22
67		Playa	0.66	98
68		Playa	0.24	1

low of 3.2° C to a mean summer high of 41.0° C, with a mean annual rainfall of 12.3 cm (www.ncdc.noaa.gov). Elevation of the marshes range from 290–420 m (Roy et al. 2019). Vole habitat is dominated by Olney's Bulrush (*Schoenoplectus americanus*), with additional common species including rushes (*Juncus* spp.), Common Reed (*Phragmites australis*), Southern Cattail (*Typha dominguensis*), Salt Grass (*Distichlis spicata*), Yerba Mansa (*Anemopsis californica*), Boraxweed (*Nitrophila occidentalis*), Slender Arrowgrass (*Triglochin concinna*), Alkali Sacaton (*Sporobolus airodes*), mesquite (*Prosopis* spp.), and other wetland and desert plants (Rado and Rowlands 1984).

Activity methods.—From December 2015 through November 2016, we placed cameras in 17 marshes (Fig. 1, Table 1) as part of Amargosa Vole range-wide surveys (Janet Foley et al., unpubl. report). Because the presence of voles is highly associated with Olney's Bulrush (Klinger et al. 2013), all marshes used in this study contained bulrush, except for Marsh 68, which was dominated by rushes. Eleven of the marshes studied were in the northern part of the range of the vole, which is considered to have more stable subpopulations (Castle et al. 2020a), and six marshes were in the southern portion of the range (Fig. 1, Table 1). Fifteen of the marshes were located along the Amargosa River floodplain (playa), and two were located above the floodplain (hills; Fig. 1, Table 1). We calculated the area of each marsh using Google Earth (earth.google.com/web), and we categorized marshes into large (≥ 1 ha) and small (< 1 ha) sizes (Table 1).

We deployed three NatureView CAMHD (Bushnell Overland Park, Kansas) or Reconyx PC900 (Holmen, Wisconsin) cameras at each marsh. We attached each camera using wire to a metal U-post (approximately 0.5 m above the ground surface), which we angled downward at approximately 45°. To minimize overexposure, we modified Bushnell cameras by placing black duct tape over half of the LED lights, and we attached a 600 mm lens for close-range photographs. We baited areas in front of cameras by distributing approximately 200 g of oats, peanut butter, alfalfa, and 4-way horse feed (oats, corn, barley, molasses) in a pile on the day we deployed each camera. To minimize false triggers, we trimmed vegetation within the field of view of each camera as needed. Vegetation trimming was minimal and only occurred in a small area (< 400 cm^2) to avoid substantially altering vole habitat use. We programmed cameras to take five photographs when triggered, with no delay between images. The cameras remained active for approximately six weeks, although at some sites, memory cards were filled with digital images sooner than six weeks. Due to limited numbers of cameras, we rotated cameras between half of the marshes every six weeks so that activity was recorded in marshes at least once per season (seasons defined below).

Experineced biologists reviewed images to identify small mammals to species. When voles were observed on an image, the date, time, and the number of voles in the image were recorded. We used Sanderson's AllPictures Method (Sanderson and Harris 2013) to calculate the number of activity events per hour. We considered images taken 15 min or more apart independent activity events (Rendall et al. 2014). At a few cameras, all bait was consumed within 5 d. Therefore, we analyzed only the first 5 d of camera images from each sampling period for all cameras.

We collected data on ecological variables such as time of sunrise and sunset, mean daily temperature, total precipitation, and moon phase (new moon and full moon) for the 5 d of data per sample period from National Oceanic and Atmospheric Administration (www.ncdc.noaa.gov) and Weather Underground (www.weatherunderground.com/history). For moon phase analysis, we only used nocturnal vole activity events that occurred during nocturnal periods within 3 d of the full moon or new moon periods. We assigned independent activity events to time of day categories based on sunrise and sunset times: crepuscular (one hour before and after both sunrise and sunset), diurnal (one hour after sunrise to one hour before sunset), and nocturnal (one hour after sunset to one hour before sunrise). We also assigned data to seasonal categories following Roy et al. (2019): (1) winter (December-February); (2) spring (March-May); (3) summer (June-August); and (4) fall (September-November). We also compiled vole demographic data from a range-wide study that occurred concurrently with this study (Janet Foley et al., unpubl. report), including monthly range-wide vole abundance. We assumed that vole population cycles were synchronous among marshes.

Statistical analyses.—We performed analyses with R (R v4.1.2, www.r-project.org) using an alpha of 0.05 for inferring statistical significance. We report all metrics as mean (± standard error). We used non-parametric tests whenever data could not be normalized using data transformations (e.g., log transformations for right-skewed data). We evaluated differences in the number of independent vole events among nightly and seasonal categories using a Two-way Analysis of Variance (ANOVA) followed by Tukey's Post-hoc Multiple Comparisons tests. We used Pearson's Product Moment Correlations to examine relationships between the number of monthly independent vole events and mean daily high and between daily low temperatures and mean precipitation during the first 5 d of each camera trapping period. Using a Wilcoxon Rank-sum Test, we compared the number of nocturnal independent vole events between full- and new-moon periods. Using a Pearson's Product Moment Correlation, we examined the correlation between vole activity (mean monthly independent activity events across all marshes) and monthly range-wide abundance estimates for the species. Finally, we compared the number of activity events between large and small marshes, between marsh regions (northern and southern), and between marsh locations (Playa and Hill) using Student's *t*-tests or Wilcoxon Rank-sum Tests. We then constructed Random Forest (RF) Models (Prasad et al. 2006) to determine which factors influenced the number of monthly independent vole events. Only predictor variables deemed significant in earlier tests were used in the model. We built RF models using bootstrapped subsamples of the original data and aggregated the results (Segal and Xiao 2011). The RF models were constructed in R using the randomForest package (Liaw and Wiener 2022), and variable importance was then estimated and plotted using the varImpPlot function.

RESULTS

Cameras were active for 815 camera days across all 17 marshes, resulting in 1,494 independent vole events (Table 1). Voles were detected in every month sampled (December 2015-November 2016) in 13 marshes (Marshes 5, 6, 7, 9, 10, 17, 19, 21, 22, 34, 39, 54, 67), but were only detected during spring and summer (i.e., not in fall or winter) in Marshes 8 and 11, and only during summer in Marshes 65 and 68. Mean hourly activity (number of of independent events/h) was highest in the spring (2.17 ± 0.34 independent events/h, n = 835), followed by summer (1.02 ± 0.17 independent events/h, n = 416), winter (0.90 ± 0.33 independent events/h, n = 194), and fall (0.68 ± 0.66 independent events/h, n = 49; Fig. 2). Furthermore, mean hourly activity was highest during crepuscular hours (1.95 ± 0.25 independent events/h, n = 343), followed by nocturnal hours (1.44 ± 0.24 independent events/h, n = 610) and diurnal hours (1.14 ± 0.18 independent events/h, n = 541; Fig. 2). Daily patterns of activity varied throughout the year with a significant Season and Time of Day interaction ($F_{6,1068} = 10.23$, $P < 0.001$). Diurnal activity in summer was 4.5 times lower than both summer crepuscular and summer nocturnal activity (Tukey's HSD, $P < 0.001$), and in winter, crepuscular activity was 2.9 times higher than winter nocturnal activity (Tukey's HSD, $P = 0.011$;

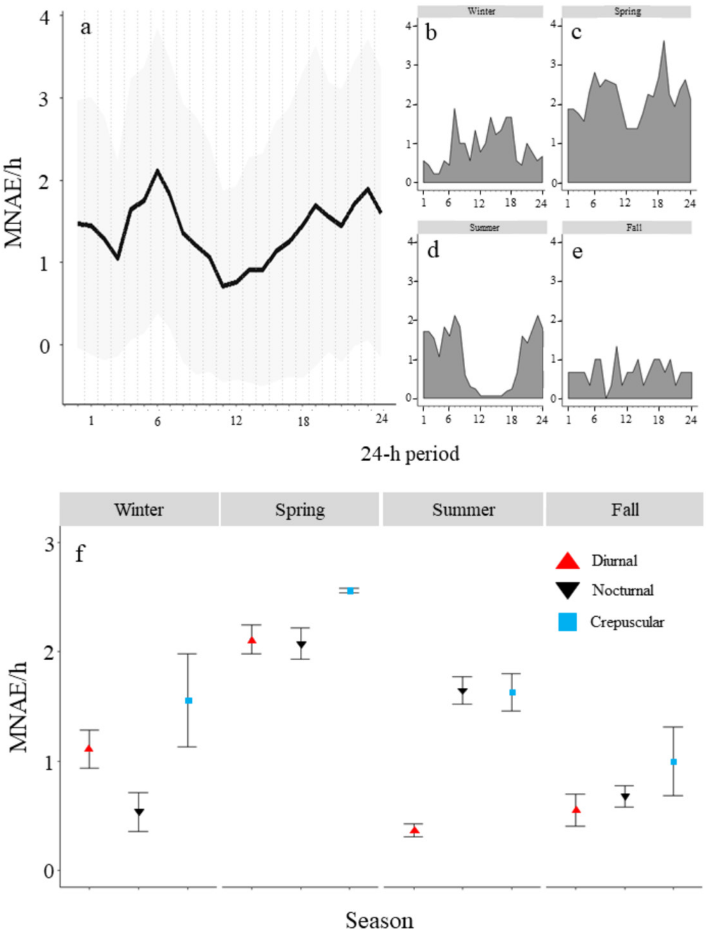

Figure 2. Daily activity patterns (mean number of activity events [MNAE]/h) of Amargosa Voles (*Microtus californicus scirpensis*) across the entire study period (a) and separately by season, during winter (b), spring (c), summer (d), fall (e), and (f) MNAE/h (± standard deviation) of Amargosa Voles during diurnal, nocturnal, and crepuscular periods for each season: winter (n = 194), spring (n = 835), summer (n = 416), and fall (n = 49). The shaded area of subgraph a represents the standard deviation around the mean. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Fig. 2). There was no significant difference in activity between winter diurnal periods and other winter periods (Tukey's HSD, $P > 0.050$) nor in daily activity patterns in the spring or fall seasons (Tukey's HSD, $P > 0.050$; Fig. 2).

Six marshes (21, 19, 17, 54, 39, 7) had high total activity over the course of the study (> 100 events per marsh; Fig. 1, Table 1). Activity was very low (< 50 independent events per marsh) at five marshes (68, 11, 6, 22, 65; Fig. 1, Table 1). On average, large marshes (> 1 ha) had 1.6 times more activity events than smaller marshes ($t = 6.989$, df = 1075.6, $P < 0.001$), and we observed a positive correlation between marsh area and the number of activity events within a marsh ($r = 0.33$, $t = 11.43$, df = 1,078, $P < 0.001$, Fig. 3). Northern marshes had significantly more vole activity (2.2 times) than southern marshes ($t = 10.06$, df = 919.6, $P < 0.001$; Fig. 3). There was no significant difference in mean vole activity between marshes in Playa habitat and marshes in Hill habitat ($W = 51674$, $P = 0.052$), but only two marshes were in Hill habitat and statistical power was low.

Lunar phase influenced vole activity, with 2.3 times more mean hourly events occurring during the new moon than the full moon ($W = 11425$, $P < 0.001$). We found a weak negative correlation between mean daily high temperatures and the number of activity events ($r = -0.09$, $t = -2.83$, df = 1,078, $P = 0.005$) but no significant correlation between vole activity and mean daily low temperature ($t = -0.13$, df = 1,078, $P = 0.898$) or mean precipitation ($t = -0.18$, df = 1,078, $P = 0.858$). Monthly vole activity was negatively correlated with range-wide vole abundance, but this relatioship was also weak ($r = -0.09$, $t = -2.89$, df = 1,078, $P = 0.004$; Fig. 4).

Due to statistically insignificant effects, we did not retain mean daily low temperature, mean precipitation, and habitat type in the RF model. The RF model ultimately included marsh area, marsh region (North, South), Season, Time of Day, Moon Phase, mean daily high temperature, and range-wide vole abundance. The RF model with these factors accounted for 60.7% of the variance in the number of monthly vole activity events, with marsh area being the most important predictor of vole activity (Fig. 5).

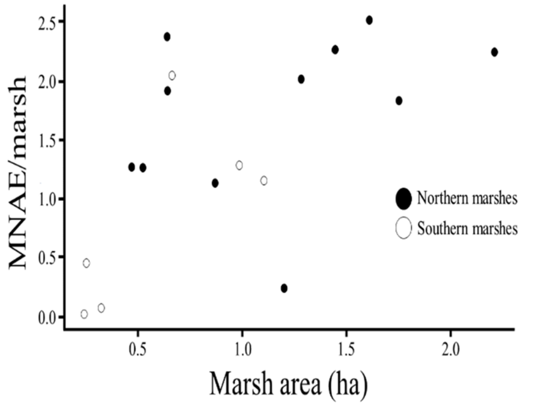

Figure 3. Correlation between the mean number of activity events (MNAE)/marsh of Amargosa Voles (*Microtus californicus scirpensis*) within each sampled marsh to the sample marsh area (ha) within northern marshes (closed circles) and southern marshes (open circles). Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California using remote camera traps.

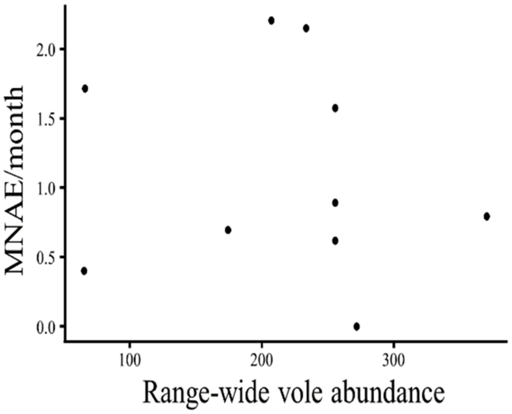

Figure 4. Correlation between the mean number of activity events (MNAE)/month of Amarogsa Voles (*Microtus californicus scirpensis*) to the range-wide abundance of voles during sampling periods. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Discussion

Our remote camera research fills previous data gaps and reveals new insights in the behavior and ecology of the Amargosa Vole by providing fine temporal-scale data that could not be inferred using other methods. We revealed differences in both daily and seasonal activity patterns of voles. Activity was highest during crepuscular periods and in the spring. We also found that activity changed seasonally, with higher diurnal vole activity than nocturnal activity in winter, and a reversed pattern in summer. Finally, we identified multiple factors that have important influences on Amargosa Vole activity.

Marsh area was identified as the most important factor in predicting vole activity. It is intuitive that in this system where larger marshes generally have higher abundances and densities of voles (Janet Foley et al., unpubl. report), there was also more vole activity. As such, the increased activity we observed in these marshes can likely be attributed to both higher vole numbers and more interactions between individual voles. These larger marshes generally have higher Olney's Bulrush cover and lower plant diversity compared to smaller marshes (Janet Foley et al., unpubl. report), and these differences in resources can also account for difference in activity (Abrams 1991; Fortier and Tamarin 1998; Blake and Loiselle 2018). The northern marshes are also mainly comprised of larger marshes, and any regional effects we observed are likely correlated with marsh area effects. That there was higher vole activity in the more demographically stable portion of the range of the vole highlights the importance of larger marshes in the biology of the species, metapopulation dynamics, and conservation (Foley and Foley 2016; Castle et al. 2020a). By conserving and managing for larger marshes, species managers can both maintain population dynamics and promote increased vole activity, which may provide beneficial intraspecific interactions (e.g., mating) and aid in recovering the species.

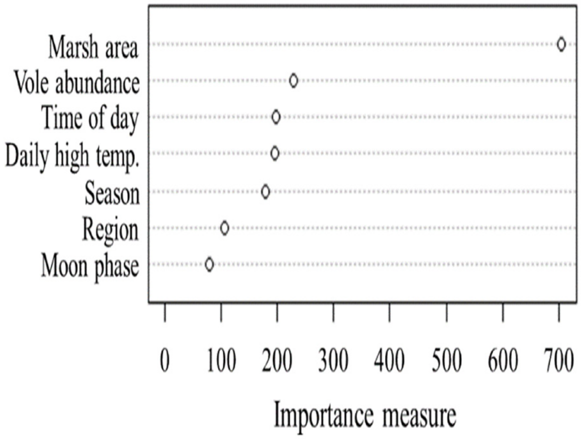

Figure 5. Variable importance plot depicting the importance measure (mean decrease in node impurity) of factors used in the Random Forest Model in predicting Amargosa Vole (*Microtus californicus scirpensis*) activity. Data were collected during 2015–2016 in marshes near Tecopa, Inyo County, California, using remote camera traps.

Several other factors also had important effects on vole activity and inform the biology of the species. Temperature factors have a strong role in shaping vole activity patterns as voles seem to avoid hot diurnal hours during the summer and cold nocturnal hours in winter, allowing them to optimize temperature and energy balance (Vieira et al. 2010; Tachinardi et al. 2017). This helps to explain how a wetland-dependent species can survive in extreme Mojave Desert envirornmental conditions (Körtner and Geiser. 2009). Predation risk also seems to have a strong influence on vole activity, with Amarogsa Voles being more active during periods of potentially lower predation risk (e.g., crepuscular periods, new moon nights; Daly et al. 1992). As the vole population is very small, fewer than 500 individuals on average (Janet Foley et al., unpubl. report), and predators have been identified as a key regulator of population abundance (Klinger et al. 2013), these predator avoidance strategies (Halle and Lehmann 1987; Halle 2000; Hoffmann et al. 2018; Monterroso et al. 2013) help to understand how the species can maintain viable population levels. Furthermore, in a system where marsh patches are relatively disconnected (Castle et al. 2020a), periods of heightened vole activity when predator pressure is low may allow for voles to safely disperse between marsh patches (Jacob and Brown 2000) and allow for the species to maintain metapopulation dynamics. Finally, our data suggest that vole activity seems to be influenced by population abundance. Although the inverse relationship between range-wide vole abundance and activity was weak, it may suggest that voles decrease their activity during periods of high density to avoid negative intraspecific interactions, such as aggression events between Amarogsa Voles during periods of high density (Pesapane et al. 2018). Intraspecific interactions may also explain some of the seasonal trends we observed, such as the the increase in activity in the spring potentially being related to mating or competition for resources. Increases in intraspecific interactions in summer may also explain why we observed voles in all marshes during periods of peak activity (summer) and not during periods of low activity (winter, fall). This suggests that animals are dispersing between habitat patches due to intraspecific competition in the larger marshes. The activity data collected here can aid to inform multiple aspects of vole biology and ecology.

For cryptic and rare species such as Amargosa Voles, remote camera studies such as ours complement traditional methods of studying occupancy, abundance, activity, and interactions between individuals but provide unique information that could not be collected otherwise. The vole activity data we have provided can be used to inform Amargosa Vole research and conservation. The data we provide can be used to make vole surveys more efficient by targeting research events to when voles are most active and therefore detectable, both seasonally and daily. Also, managers may use identified active periods to inform timing of management actions to maximize success (e.g., translocations) or reduce impacts to voles (e.g, habitat restoration activities). While predator management is not feasible in this system, by understanding that predator pressure impacts vole activity and potentially vole dispersal, managers can conduct conservation activities to limit predation pressure on the species (e.g., construct dispersal corridors between marshes, promote greater cover of Bulrush litter in marshes). Our survey occurred in bulrush-dominated habitats, but the data we provide can also be used to detect and monitor vole populations in other habitat types that may be used for foraging and dispersal (López-Pérez et al. 2019; Castle et al. 2020b). Finally, our results provide baseline ecological data for assessing the ecological interactions of Amargosa Voles, in support of the conservation needs of this species (USFWS 1997).

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