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Non-bulrush Habitat Use by Amargosa Voles (*Microtus californicus scirpensis*)

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***Abstract*.—Understanding how sensitive species use their habitats is critical to conservation and management efforts. The Amargosa Vole (*Microtus californicus scirpensis*) is believed to be strictly reliant on Three-square Bulrush (*Schoenoplectus americanus*, hereafter Bulrush) dominated habitats, but has anecdotally been observed in non-Bulrush dominated habitats as well. Using range-wide camera-trapping and live-trapping survey data from 2015–2016 and 2019–2020, we summarized detections of voles in non-Bulrush dominated habitats. Through live-trapping data, we observed that up to 17% of trap locations that captured voles occurred in non-Bulrush dominated habitats, with a mean distance from Bulrush habitat of 16 m. Furthermore, voles were detected at multiple camera trap locations in non-Bulrush dominated habitats. Voles were most often detected in non-Bulrush dominated habitats containing Saltgrass (*Distichlis spicata*), rushes (*Juncus* spp.), Boraxweed (*Nitrophila occidentalis*), Yerba Mansa (*Anemopsis californica*), and Common Reed (*Phragmites australis*) dominated habitats. The relatively regular detection of voles in non-Bulrush dominated habitats may indicate that these areas are also important to the ecology and biology of the species. Incorporating non-bulrush vole habitat into conservation and management objectives is likely to have multiple benefits for the conservation of the Amargosa Vole.**

Key Words.—camera-trap; detection; live-trap; marsh; vegetation

Introduction

The Amargosa Vole (*Microtus californicus scirpensis*, hereafter vole) is a federally and California state-listed Endangered subspecies of the California Vole (*M. californicus*; U.S. Fish and Wildlife Service [USFWS] 2019; California Natural Diversity Database 2024). The species is only found in approximately 22 ha of disconnected marsh habitat in the Mojave Desert near Tecopa and Shoshone, California. Depending on the year, voles occur in 51–86% of available marsh sites (Deana Clifford et al., unpubl. report), with these marshes typically having low plant diversity and are dominated by Three-square Bulrush (*Schoenoplectus americanus*, hereafter bulrush), which has been positively associated with vole abundance and occupancy (Klinger et al. 2016; López-Pérez et al. 2019; Foley et al., unpubl. report). Bulrush has also been documented to comprise a dominant proportion of the diet of the vole, although bulrush cannot solely support voles, and voles must rely on a variety of different forage species (Castle et al. 2020a). As such, there has a been a misconception about the relative importance of other vegetation habitats for the vole and most management and conservation efforts have primarily focused on protecting and managing bulrush-dominated habitats. Other habitats, including bulrush-mixed habitats (López-Pérez et al. 2019), have been rarely evaluated for voles, resulting in little information on whether voles use these habitats or not. Without a comprehensive understanding of the habitat-use by the vole, we lack a complete understanding of the ecology of the species and are hindered in optimal management and conservation of it. Herein, we report on detections of voles within non-bulrush dominated habitats from various vole survey efforts.

Methods

We conducted vole surveys and vole reintroductions within the Amargosa River basin in the Mojave Desert near Shoshone (35.9797°, -116.2720°) and Tecopa (35.8824°, -116.235368°) in Inyo County, California, at elevations from 390–417 m (Fig. 1). The vole occupies wetlands fed by the Amargosa River as well as ephemeral and perennial spring-fed surface flows. The majority of marshes where voles have been studied are dominated by bulrush interspersed with other wetland plant species (e.g., graminoids, forbs) and surrounded by upland plant communities (e.g., graminoids, forbs, shrubs, and trees; Rado and Rowlands 1984).

Between 2015–2016, we live trapped small mammals using Sherman traps at 15 grid locations across the entirety of the known extant range of the vole (Janet Foley, unpubl. report). Trapping grid design followed

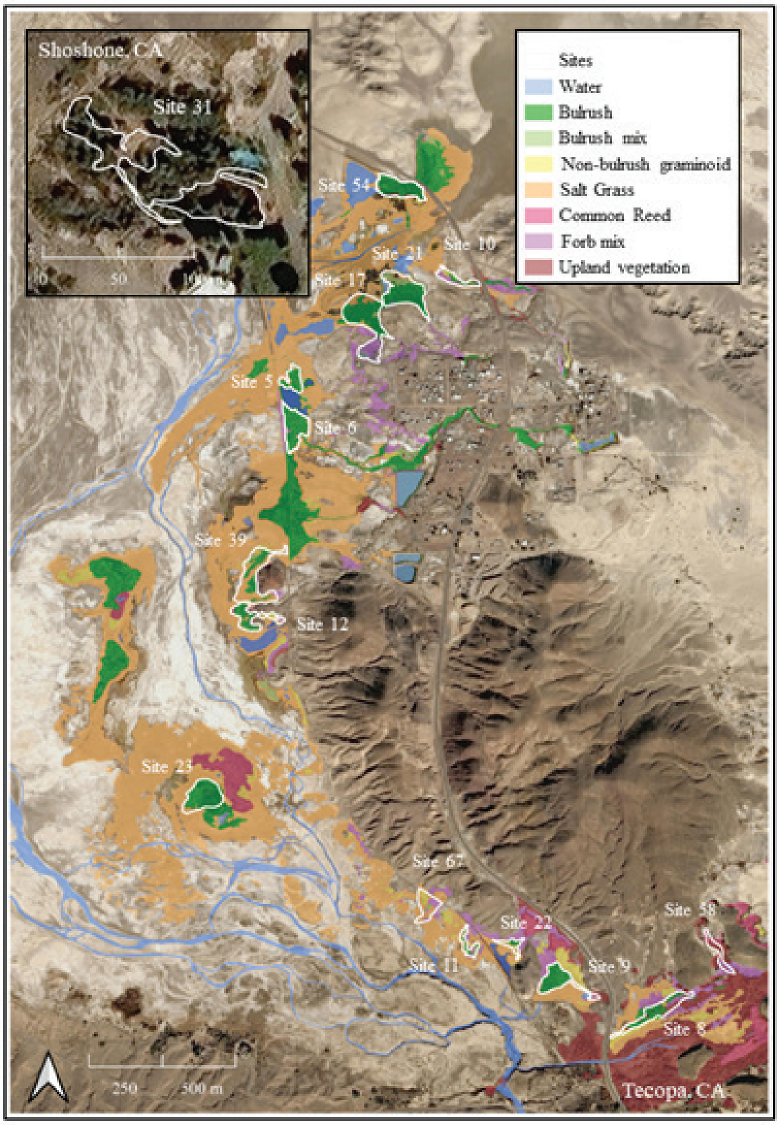

Figure 1. Map depicting major habitat types and sites surveyed for Amargosa Voles (*Microtus californicus scirpensis*) using live trapping, camera trapping, and sign surveys in 2015–2016 and 2019–2020, near Tecopa and Shoshone, Inyo County, California. Site 31 could not be included in the vegetation classification: see Site 31 description in text for details.

methodology established by Klinger et al. (2015) and each grid covered a 1-ha area, with a majority of trap locations located in bulrush-dominated habitat, but also with portions of each grid located in non-bulrush-dominated habitats. We trapped each grid for 5 d, approximately every six weeks for 12 mo. At least once during the 12-mo survey, we assessed the vegetation at each trapping location by identifying each species and quantifying the percentage cover using Daubenmire values (Daubenmire 1959; Janet Foley, unpubl. report) within a 1-m2 quadrat. To avoid sampling in areas trampled due to repeated surveys, we placed quadrats on the opposite side of the trail from each trap. Additionally, during this survey effort, we placed 1–3 baited camera traps in 21 sites, which we set to record data for approximately six weeks. We sampled most camera locations 2–3 times over the course of a year (Roy et al. 2023).

Between 2019–2020, we assessed sites for vole occupancy using un-baited camera traps at six sites and we surveyed for vole sign (feces, clipped vegetation, burrows, runways) at another seven sites. We set 14 camera traps in and on the periphery of each marsh, in areas which lacked dominant bulrush habitat. We placed camera traps in areas where sign consistent with voles was present or near burrow entrances that we suspected were occupied by voles (e.g., set at egress points from marshes to detect voles moving among marshes). The camera traps were active for 4–11 d and typically not baited, except for cameras in Site 8. We baited cameras in Site 8 with a mixture of oatmeal and peanut butter placed on the ground within the field of view of the camera. We performed sign surveys along the perimeter and areas surrounding each marsh and we recorded locations of presumptive vole sign using a GPS device. We assessed vegetation at each camera-trap location as described above.

Results

During the 2015–2016 range-wide assessment, approximately 17% of trap locations with captured voles (89/518) occurred in non-bulrush dominated habitats (< 5% cover of live bulrush or bulrush litter). At approximately half of these trap locations (53), bulrush was completely absent (0% cover) from the sampling quadrats; however, some quadrats may have been in proximity to bulrush sites (within 1 m). Across all non-bulrush dominated sites, vegetation communities consisted of > 25% cover of the following species (singly or in combination): Inland Saltgrass (hereafter saltgrass, *Distichlis spicata*, n = 35), rushes (*Juncus* spp., n = 21), Boraxweed (*Nitrophila occidentalis*, n = 6), Yerba Mansa (*Anemopsis californica*, n = 4), sedges (*Carex* spp., n = 3), Common Reed (*Phragmites australis*, n = 12), and Annual Sunflower (*Helianthus annuus*, n = 3). The distance of individual trap locations to the nearest bulrush habitat ranged from 0 m (immediately adjacent) to 61 m from bulrush, with 15.7% of these locations occurring along the edge (0 m distance) of bulrush habitat, 29.2% occurring near bulrush (1–10 m), and 31.5% occurring ≥ 20 m from bulrush (overall mean distance = 16 m; Fig. 2). The highest proportion of vole captures in non-bulrush dominated habitats occurred during summer and early fall (May-September). During the same survey period, the one baited camera trap in non-bulrush-dominated habitat was placed in a Common Reed patch (100% cover), located >10 m from bulrush habitats. This camera was active for one six-week period during which voles were detected during the summer and fall seasons.

During the 2019–2020 occupancy survey period, there were 99 camera trap nights during the sampling period across six marshes, with voles being detected in six of the 14 camera traps stations (Table 1). Voles were detected at sites dominated by bulrush, Yerba Mansa, Boraxweed, rushes, and Common Reed; including at three locations (within Sites 9 and 17) where bulrush was completely absent (Table 1). It is of note that these detections, via cameras, do not indicate the number of voles detected, but simply the occurrence of voles outside of bulrush dominated habitats. In addition to camera detections, we observed multiple instances of vole sign on the periphery of bulrush patches of six of the seven sites surveyed for sign. We found vole sign in habitats dominated by rushes, Common Reed, Yerba Mansa, and Boraxweed.

Site specific vegetation descriptions.—*Site 5*: This site consisted of a moderately sized bulrush marsh adjacent to open water (Fig. 1). This bulrush patch was surrounded by saltgrass with small amounts Boraxweed. Voles live trapped in non-bulrush-dominated trap locations (n = 6) were captured in areas of > 15% saltgrass and < 5% bulrush (live and/or litter) cover, including three locations where bulrush (live and litter) was absent.

Site 8: This site consisted of moderately sized bulrush and cattail (*Typha* spp.) patches, centered along a stream and fed by multiple sources (Fig. 1). The bulrush patch was surrounded by patches of Yerba Mansa, saltgrass, Common Reed, Alkali Sacaton (*Sporobolus airoides*), mesquite (*Prosopis* spp.), and salt cedar (*Tamarix* spp.). While voles were detected at two camera locations, only one location was co-dominated by non-bulrush (Common Reed; Table 1). We did not find vole sign in the peripheral area of this site.

Site 9: This site consisted of a bulrush marsh surrounded by a well-developed margin of rushes, Yerba Mansa, Boraxweed, and saltgrass (Fig. 1). The site also included two substantial patches of Common Reed,

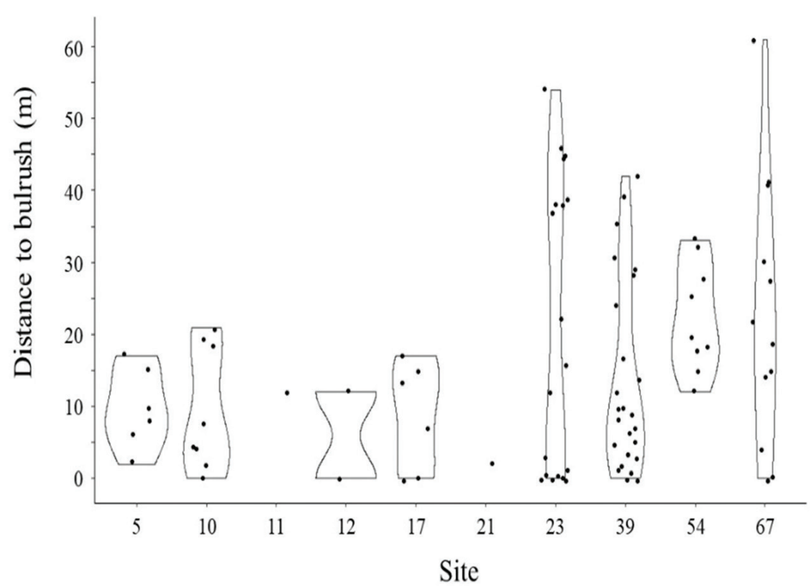

Figure 2. Violin plot showing the distance (m) of live trap locations that detected Amargosa Voles (*Microtus californicus scirpensis*) in non-bulrush dominated habitat to bulrush habitat within each sampled site during the 2015–2016 survey. Data collected from near Tecopa, Inyo County, California.

Table 1. Habitat notes for camera trap detections of Amargosa Voles (*Microtus californicus scirpensis*) in Sites 8, 9, 17, 22, and 58 in Tecopa, California, from 2019–2020. The abbreviation CN = camera identification number, SM/WD = soil moisture/water depth, and VD = voles detected (yes/no) with the number detected in parentheses.

Marsh	CN	Vegetation cover	SM/WD	VD	Notes
17	17.1	65% Yerba Mansa, 20% Boraxweed, litter depth 70cm	Moist soil	Yes (1)	10 trap/nights. A small patch of bulrush coming down hill. Vole sign, no burrow.
9	9.1	70% Boraxweed, 4% Common Reed, 2% Yerba Mansa, litter depth 40cm	Dry soil	Yes (3)	11 trap/nights. Vole sign present, burrow present; 20-25m from the edge of bulrush patch. Voles observed using the burrow a couple of times.
	9.2	40% rushes, 2% Boraxweed, other spp. 10%, litter depth~60cm	Dry soil	Yes (2)	9 trap/nights. Vole sign tunnel through the grass, burrow built in the Juncus.
	9.3	60% rushes, 5% Yerba Mansa, 5% Boraxweed, litter dept 70cm	Dry soil	No	5 trap/nights. bulrush edge at 40m to the camera trap. Poop signs and two burrows.
	9.4	70% rushes, 5% saltgrass, litter depth 55cm	Dry soil	No	5 trap/nights. ~30 pellets of poop vole. Burrow present.
	9.5	50% Common Reed, 5% Yerba Mansa, litter depth 20cm	Dry soil	No	5 trap/nights. Two burrows with vole signs.
22	22.1	75% Yerba Mansa, bulrush < 5%, woody debris 2%, litter depth 50cm	Dry soil	No	11 trap/nights; House mouse every day, no voles were recorded
8	8.1	60% Yerba Mansa, 30% rushes, 20% Boraxweed, litter depth ~55cm	Dry soil	No	9 trap/nights. No standing water. No vole signs observed.
8a	8a.1	85% Common Reed, 25% bulrush, litter depth ~65cm	Moist soil, near small stream	Yes (12)	4 trap/nights. Voles observed every day, up to 3 voles observed in single frame, one aggression event.
	8a.2	85% bulrush, 15% Common Reed, litter depth 75-100cm	25cm	No	4 trap/nights. No images captured
	8a.3	90% bulrush, 7% Common Reed, 3% cattail, litter depth up to 150cm	Litter too deep to determine	Yes (1)	4 trap/nights. One vole individual captured on 1/20 @ 9:30pm. One *Peromyscus* individual observed same day.
	8a.4	80% Common Reed, 15% bulrush, 10% cattail, litter 65-70cm deep	13cm	No	4 trap/nights. One possible observation of house mouse.
58	58.1	60% rushes, litter depth 50cm	Dry soil	No	9 trap/nights; Harvest mouse every day, no voles were recorded
	58.2	40% bulrush, 40% Yerba Mansa, 5% Boraxweed, litter depth ~60cm	Dry soil	Yes (3)	9 trap/nights. Burrow-like tunnel. Woody debris in the area. Vole signs.

uphill of the bulrush marsh. Outside of the bulrush marsh, voles were detected on camera at two locations dominated by Boraxweed and rushes, respectively (Table 1). Additionally, we found vole burrows into the soil layer and vole feces in non-bulrush habitats along the periphery of Site 9.

Site 10: This site consisted of a strip of bulrush following a stream that flowed from a culvert under a road (Fig. 1). The bulrush area was surrounded by Yerba Mansa, saltgrass, Boraxweed, sedges, rushes, Alkali Sacaton, Almutaster (*Aster pauciflorus*), and Goldenweed. We trapped voles in eight locations where no bulrush was present but at sedge (n = 1 site), Yerba Mansa-sedge co-dominant (n = 1), Yerba Mansa, (n = 1), Yerba Mansa-rush co-dominant (n = 1), saltgrass-Boraxweed co-dominant (n = 1), Rush (n = 2), rush-Boraxweed (n = 1) dominated trap locations.

Site 11: This site consisted of a relatively small to moderately sized bulrush area surrounded by saltgrass, Boraxweed, rushes, Annual Sunflower, and Common Reed (Fig. 1). The site had no apparent water source other than seasonal upwelling of groundwater or perhaps a diffuse spring discharge. We trapped voles at one location outside of the bulrush area in Boraxweed dominated habitat.

Site 12: This site consisted of a moderately sized bulrush area adjacent to a seasonal pond and was surrounded by areas of Common Reed, saltgrass, Boraxweed, rushes, and upland vegetation (Fig. 1). We trapped voles at two non-bulrush dominated locations; one location completely lacked bulrush (live and litter) and the second location had minimal (< 0.5%) bulrush litter present. One location was dominated by saltgrass and the other by a Boraxweed-saltgrass mix.

Sites 17 and 21: These sites consisted of a large bulrush marsh surrounded by saltgrass wetlands on the north and west and upland habitat with some rushes and Boraxweed on the south and east side of the site (Fig.

1). Camera trapping detected a vole in a Yerba Mansa dominated habitat patch located adjacent to a stream on the hillslope above the site. We found vole sign (feces, clippings, burrows) along the entire waterway flowing from residences and a recreational vehicle park on the hill above Site 21. While some bulrush occurred in these uphill locations, they were often dominated by rushes and saltgrass with a few patches of Yerba Mansa. We trapped voles in these sites at seven locations where bulrush was not dominant, including four locations where bulrush was not present. These locations were dominated by saltgrass (n =5) or a saltgrass-rush mix (n = 2).

Site 22: This site consisted of a relatively small patch of bulrush mixed with Annual Sunflower and surrounded by Yerba Mansa, saltgrass, and Alkali Sacaton (Fig. 1). We found vole sign along the periphery of the bulrush area; however live-trapping and camera trapping did not detect voles outside of bulrush habitat at this site.

Site 23: This site was disconnected from other potential vole habitat patches by alkali desert playa and consisted of large bulrush patches adjacent to spring sources surrounded by a large Common Reed patch to the northeast and saltgrass and rushes along other portions of the site (Fig. 1). A camera trap detected voles within a 100% Common Reed patch. We captured voles at 19 trap locations located in non-bulrush dominated habitats, including 11 locations where bulrush was absent. These locations were dominated by saltgrass (n = 9), Boraxweed (n = 1), and Common Reed (n = 12) communities. Within the Common Reed patch, 10 locations lacked any bulrush presence.

Site 31: This site occurred in the extreme northern portion of the range of the species where voles had been translocated into restored desert wetland habitat (Fig. 1). The site consisted of bulrush areas along spring-fed streams and ponds, goldenrod (*Solidago* spp.) meadows, Common Reed patches, and upland areas dominated by mesquite and shrubs. Voles were only detected on camera in bulrush dominated habitat. While we observed most vole sign in bulrush areas, we found vole feces in mesic, marginal habitat around the periphery of bulrush areas.

Site 39: This site consisted of a central bulrush dominated area and was surrounded by saltgrass, rushes, and Yerba Mansa (Fig. 1). We trapped voles at 25 non-bulrush dominated trap locations, including 13 locations where bulrush was absent. These trap locations were in Rush (n = 7), saltgrass (n = 12), saltgrass-rush (n = 1), saltgrass-Boraxweed (n = 1), saltgrass-Goldenweed (n =1), rush-sunflower (n = 1), saltgrass-rush-Goldenweed (n = 1), saltgrass-rush-bulrush (n =1), and Seaside Arrowgrass (*Triglochin concinna*, n = 1) dominated habitats.

Site 54: This site consisted of a large bulrush dominated area and was fed via a culvert by hot-spring water that originates at the head of Site 1 (Fig. 1). The bulrush area was surrounded by rushes and saltgrass. We captured voles at nine non-bulrush dominated trap locations, including three where bulrush was completely absent. These trap locations were located in saltgrass (n = 4), Rush (n = 3), and saltgrass-rush (n = 2) dominated habitats.

Site 58: This site consisted mostly of cattail dominated vegetation which followed a small stream flowing from a spring before entering a larger marsh area consisting of bulrush-cattail mixed habitat and which connected to other sites (Fig. 1). The site was surrounded by areas of relatively high plant diversity, with areas dominated by Yerba Mansa, rushes, Boraxweed and interspersed with mesquite and cottonwood (*Populus* spp.). Camera traps at this site detected voles at a location co-dominated by Yerba Mansa and relatively young bulrush (Table 1).

Site 67: This site consisted of two very small bulrush patches that were surrounded by patches of Yerba Mansa, Boraxweed, saltgrass, rushes, Alkali Sacaton, and Annual Sunflower (Fig. 1). We trapped voles at 12 trap locations where non-bulrush dominated trap locations, including 10 where bulrush was absent. These areas were in Rush (n = 2), Boraxweed (n = 2), Annual Sunflower (n = 2), saltgrass (n = 1), sedge (n = 1), rush-sunflower (n = 1), rush-Yerba Mansa (n = 1), Boraxweed-rush (n = 1), and saltgrass-Yerba Mansa-sunflower (n = 1) dominated areas.

Discussion

While it is clear from previous works examining Amargosa Vole habitat use that voles are dependent on bulrush for their ecology (e.g., Klinger et al. 2016), we have shown non-bulrush dominated habitats are also used by the species, with up to 17% of trap locations in which we captured voles being located in non-bulrush dominated locations, especially habitats in Common Reed, rushes, sedges, and Boraxweed dominated communities. Vole habitat use and selection is complex may be driven by a variety of factors (Ostfeld et al. 1985; Lin and Batzli 2001; Yletyinen and Norrdahl 2008), and while outside the scope of this paper, we believe that the detection of Amargosa Voles in non-bulrush habitats is likely associated with interactions of local biological and ecological drivers. First, the use of non-bulrush habitats may be associated with dietary needs, as bulrush has low nutritional values and Amargosa Voles must consume other plant species, particularly species with higher protein content than bulrush, to meet basal metabolic and nutritional requirements (Castle et al. 2020a). These resources are most abundant in non-bulrush areas (Janet Foley et al., unpubl. report). With approximately 45% of trapping detections occurring within 10 m of bulrush, these detections may represent short distance excursions of voles into non-bulrush dominated habitats in search of needed forage resources. Castle et al. (2020a) noted that sedges, Beaked Spikerush (*Eleocharis rostrellata*), rushes, grasses (Poaceae), Yerba Mansa, Annual Sunflower, and saltgrass are important components of vole diets, and most of these plant species were documented at our vole-detection locations. Beaked Spikerush and non-saltgrass grasses (e.g., Alkali Sacaton, *Sporobolus airoides*) were not dominant species at our vole-detection sites but have been detected within vole-occupied marshes and are often associated with the periphery of bulrush patches in this system (Rado and Rowlands 1984; Janet Foley et al., unpubl. report). Second, because Amargosa Voles are reliant on standing water in this system (Janet Foley et al., unpubl. report), and this likely partially explains their dependence on water-associated bulrush, voles may only be able to use non-bulrush areas when standing water is seasonally available (e.g., more standing water in summer; pers. obs.). Third, the use of non-bulrush areas may also be influenced by the population dynamics of the species. The majority of vole detections in non-bulrush habitat occurred in summer months, when the vole population is reaching the peak of its yearly cycle (McClenaghan and Montgomery 1998; López-Pérez et al. 2023), and our detections may indicate that carrying capacity has been reached within a site and voles are dispersing in search of adequate habitat (Lin and Batzli 2001) or due to factors such as competition, inbreeding avoidance, and mate searching (Le Galliard et al. 2012). These non-bulrush areas may represent important dispersal corridors between habitat patches. Whether Amargosa Voles can persist in these non-bulrush areas is unclear. We observed voles using burrows outside of bulrush habitats in Site 9 (Fig. 3), which may indicate continued use of non-bulrush habitat in this site, but no persistent populations of voles have previously been detected in non-bulrush habitats at other sites (Klinger et al. 2016; López-Pérez et al. 2019; Janet Foley et al., unpubl. report). Amargosa Voles most likely require bulrush patches for survival (Klinger et al. 2015, 2016), due to the insulative litter layer of bulrush providing protection against extreme temperatures and cover against predators, but further studies are needed to understand the complexity of range-wide habitat selection and subpopulation persistence for the species.

We detected more voles in non-bulrush habitat and generally at greater distances from bulrush habitat in the southern portion of the range of the species than the north. While this trend may have been caused by our sampling effort, there are also possible ecological explanations for this pattern. Sites in the north generally have larger bulrush patches and may allow for higher densities of voles to persist, lessening the need for dispersal to non-preferred habitats (Andreassen and Ims 2001). Southern sites tend to be more florally diverse and have more gradual transitions between vegetation communities, thus they may provide more opportunity for voles to use non-bulrush habitat. More research into specific causes of differences in habitat use between marshes may lead to greater insight into species biology and aid in the management of the species.

Despite its importance to vole survival, bulrush alone is not sufficient to support the species (Castle et al. 2020a) and non-bulrush habitats seem to also be important to vole ecology even though these areas have been underrepresented in the literature and management concern. We suggest that managers should manage both bulrush and non-bulrush areas as vole habitat. In particular, non-bulrush areas adjacent to or connecting bulrush habitats should be managed for their forage and as corridors for dispersal between core habitat patches. By ensuring adequate forage resources surrounding bulrush patches, managers may be able to positively influence vole biology and population viability (Jones 1990; Turchin and Batzli 2001; Forbes et al. 2014). By promoting non-bulrush vole habitat between bulrush patches, where bulrush is not adapted to local conditions (e.g., soil salinity, water availability), managers may be able create corridors between source populations in larger bulrush areas (Janet Foley et al., unpubl. report) and safeguard populations against deleterious effects associated with isolated populations. This could aid in populations re-establishing in sites following local extirpation. Doing so would support a functional

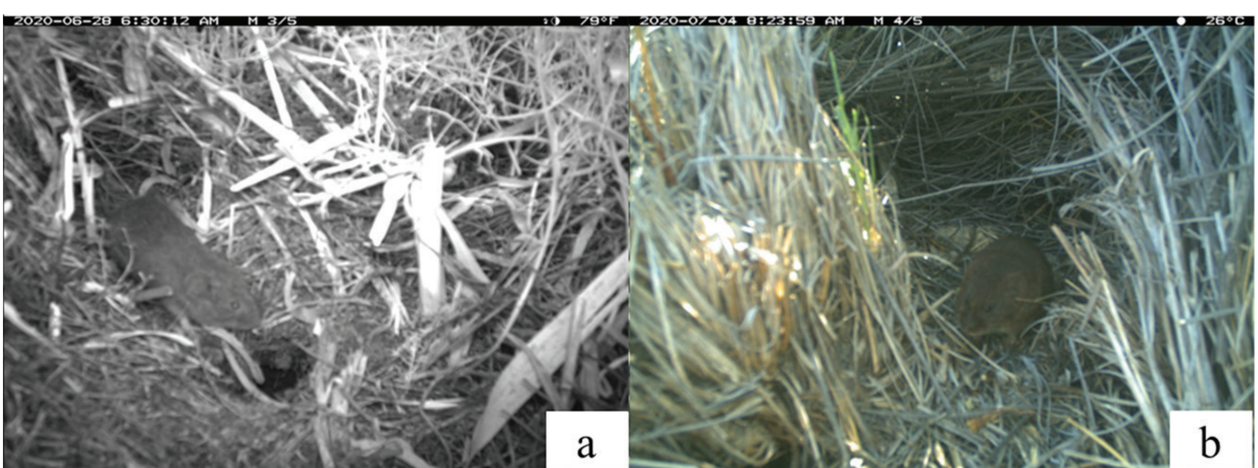

Figure 3. Images of Amargosa Voles (*Microtus californicus scirpensis*) captured using remote camera trapping techniques in 2019–2020 at Site 9 near Tecopa, Inyo County, California. Images depict (a) voles using below-ground burrows in Boraxweed (*Nitrophila occidentalis*) dominated habitat and (b) in Common Reed (*Phragmites australis*) dominated habitat.

metapopulation (Reed 2004; Molofsky and Ferdy 2005), which has been identified as necessary to the survival and recovery of the species (USFWS 2019; Castle et al. 2020b). Incorporating non-bulrush vole habitat into management objectives is likely to have multiple beneficial effects for the conservation of the vole as well as other rare and protected species in the area.

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