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The Biology and Ecology of the Amargosa Vole (*Microtus californicus scirpensis*)

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***Abstract.*—Obtaining detailed biological data from field studies of small mammals is challenging, yet these data are crucial for management. We discuss data on sexual dimorphism, molt patterns, morphometrics, dietary habits, and behavior of the endangered Amargosa Vole (*Microtus californicus scirpensis*). These data are from our captive colony and field studies, but also include comparisons to data from other studies. Male voles had significantly larger body mass, longer total length, and longer tail length. Molt progression in 11 captive-reared individuals began at the dorsal mid-line, creating a strip of juvenile hair from head to rump that disappears around eight weeks of age. These traits allow for better characterization of age classes of voles captured in the wild. Captive voles initially rejected fresh cuttings of native Olney's Three-square Bulrush (*Schoenoplectus americanus*), the dominant plant in the wild Amargosa Vole diet, although they consumed all portions of the plant when it was provided erect in planted cups. We captured images of voles in the wild on camera twice consuming plants other than Olney's Three-square Bulrush. This information is essential to link management actions with species biology, including habitat management, disease work, and population biology.**

Key Words.—behavior; captive-breeding; conservation; food habits; Mojave Desert; natural history; recovery plan; species description

Introduction

Detailed biological data from field studies of small mammals are crucial for understanding the natural history of these animals and for developing management plans. Sources of such data may include published data, gray literature, museum field notes, and observations of captive breeding. The Amargosa Vole (*Microtus californicus scirpensis*) is a highly specialized desert rodent that is endemic to the Amargosa River valley and associated isolated springs near Tecopa in Inyo County, California (U.S. Fish and Wildlife Service [USFWS] 1997; Cudworth and Koprowski 2010). After Bailey (Bailey 1900) first described the vole over 100 y ago, few studied the vole until the State of California listed it as endangered in 1980 and the federal government listed it in 1984 (USFWS 1997). An early physical description of the animal indicated that whiskers of Amargosa Voles were white terminally and black basally, noses were black, tail was short and bicolored, dorsal pelage varied from bright brown to cinnamon-colored with neutral gray color ventrally, and that this vole was distinct from other voles in California by virtue of their small skull with comparatively wide zygomatic arch (Kellogg 1918).

After a status review (USFWS 1997), field studies focused on distribution, persistence, genetic status, and ecology (Neuwald 2010; Ott-Conn et al. 2014, 2015; Poulsen et al. 2017). The species is dependent on Olney's Three-square Bulrush (*Schoenoplectus americanus*) for both habitat and nutrition (Klinger et al. 2015). In 2016, the population estimate for all Amargosa Voles was just 66–425 individuals (unpubl. report). While the species was probably never abundant or widely distributed, it is now completely absent from its type locality in Shoshone, California. A railroad grade, roads, parks, and alkali flats separate remaining habitat patches in Tecopa but it is not known how important such barriers might be.

Despite an improved understanding of this species, empirical data needed to inform recovery planning were still lacking. In fact, the Recovery Plan for the Amargosa Vole stated that it could not establish criteria for delisting due to a lack of biological data specific for Amargosa Voles (USFWS 1997). In the absence of detailed information on key biological attributes, such as reproduction, behavior, and ontogeny, biologists surmised that biological characteristics of the Amargosa Vole were the same as more common and not desert-adapted subspecies of *Microtus californicus* (USFWS 1997). As part of recovery efforts, we established a captive breeding colony in 2014. In this paper, we present detailed biological data from our captive colony and summarize discoveries about the biology and ecology of the Amargosa Vole from a combination of colony and field data.

Methods

Study area.—We studied wild Amargosa Voles near Tecopa, California, in southeastern Inyo County. This area of the Mojave Desert experiences temperature fluctuations from a mean low of 3.2° C to high of 41° C and mean annual rainfall of 12.3 cm (National Oceanic

and Atmospheric Administration 2010). Amargosa Vole habitat is characteristically patchy with spring-fed marshes dominated by Olney's Three-square Bulrush (*Schoenoplectus americanus*; hereafter bulrush) separated by minimally vegetated alkaline playa and salt scrub.

Field sampling.—We collected data on wild Amargosa Voles as part of ongoing population assessments conducted by the California Department of Fish and Wildlife, the University of California, Davis, School of Veterinary Medicine, and the United States Geological Survey. We placed Sherman live traps (H.B. Sherman, Tallahassee, Florida, USA) in established grids near Tecopa Hot Springs, California, as previously described (Klinger et al. 2015; Foley et al., unpubl. report). Trap bait varied across trapping periods but included either peanut butter, four-way horse feed (corn, barley, oats, and wheat with molasses), and apples; or peanut butter and oats. We added apples for moisture. We handled Amargosa Voles when they were awake and typically recorded sex, body mass, age, reproductive status (males: position of the testes; females: condition of vaginal opening and size of mammae), body condition (Ullman-Cullere and Foltz 1999), and health, including trauma or evidence of ectoparasites. We tagged all voles with a uniquely numbered ear tag (1005-1 Monel, National Band and Tag Co., Newport, Kentucky, USA) and we secondarily tagged some individuals with subcutaneous passive integrated transponders (PIT).

To examine natural behavior in the wild, we deployed camera traps in 21 marshes. Typically, we placed three NatureView 11-9740 CAMHD (Bushnell Overland Park, Kansas, USA) or Reconyx PC900 (Holmen, Wisconsin, USA) cameras per marsh, which we fastened with bailing wire to metal U-posts and angled them downward in the direction of vole sign. We modified cameras by placing black duct tape over half of the LED lights to minimize overexposure and we attached a 600 mm lens for close-range photographs. We baited cameras by distributing approximately 200 g of oats, peanut butter, alfalfa, and four-way horse feed in a pile in front of each camera on the day the camera was armed, and we programmed these cameras to take five photographs when triggered with no delay between images. Cameras remained active for approximately six weeks, although full memory cards at some sites resulted in fewer than six weeks of data being collected; we considered this 4–6 week period a primary period.

Trained personnel reviewed images and when voles were observed on camera, the date, time, and number of voles were recorded. Events of aggression included biting, chasing, or fighting. Analysis of activity used a presumed number of independent observations of voles per hour based on Sanderson's AllPictures method (Sanderson and Harris 2013) assuming that events separated by at least 15 min were independent (Rendall et al. 2014). We analyzed the first five days from each primary period. The software summarized the number of events into four seasons: winter (December-February), spring (March-May), summer (June-August), and fall (September-November). Daytime was any hour after the time of sunrise and before sunset on the mid-day of the 5-d sampling period. Nighttime was any time after sunset but before sunrise as reported by the National Oceanic and Atmospheric Administration.

Museum data.—We reported descriptive characteristics and measurements of Amargosa Voles using specimens submitted to the Museum of Vertebrate Zoology at the University of California Berkeley from 2013-2016.

Captive colony sampling.—*Colony management:* A captive breeding colony of Amargosa Voles lived at the University of California, Davis, in both indoor and outdoor caging (Allan et al. 2018). Briefly, indoor environments consisted of 1–3 Amargosa Voles kept in polycarbonate cages (Bellmore, New York, USA) topped with wire lids with a thick layer (15 cm) of rice or wheat straw for bedding and fresh water daily. Technicians spot-cleaned bedding daily to remove wet or soiled straw, and transferred animals to sterilized cages with new straw monthly. We kept rooms at 18.3–23.9° C with a 12-h light cycle. Initially, we fed Amargosa Voles Harlan rodent chow #2018 (Teklad Diets, Madison, Wisconsin, USA) augmented with fresh bulrush grown in a greenhouse and occasionally fresh greens, fruits, seeds, root vegetables, or alfalfa, but we later transitioned them to a high-fiber, lower fat rabbit chow (LabDiet 5326-3, Stewart's Feed Service, Lawrenceville, Georgia, USA).

Outdoor environments consisted of 1–3 Amargosa Voles housed in mesocosms under a large, chain-link structure reinforced with 1.3 cm mesh hardware cloth to exclude small predators. Mesocosms were structural foam planters (139.7 × 100.0 × 63.5 cm) with potting soil and a bulrush clone from Tecopa. We provided water in large glass bowls and offered chow supplementary to bulrush. An irrigation system kept bulrush plants and soil moist.

Breeding: We established the vole colony with 20 wild-caught founder individuals. In 2016, we brought an additional 12 wild voles into captivity. When pups reached sexual maturity, we selected individuals for breed pairs based on an electronically maintained pedigree to minimize average relatedness. For each indoor pairing, we placed a male and a female vole together in a guinea pig cage with food, water, and bedding. Although we conducted breeding in outdoor housing when the colony was first established, we later discontinued this because monitoring births was infeasible in mesocosm burrows and there was an incident of parent-offspring inbreeding. If we only desired one litter from a breed pair, we removed the male from the breeding cage 20

d after pairing, before the first litter was born. This ensured that the post-partum estrus of a female was not consummated, preventing a second litter. If we desired more than one litter from a breed pair, we left the male in the breeding cage to assist with pup rearing and to allow for continued mating. If a pair did not produce a litter within approximately 60 d, we usually re-paired the male and female with new mates. Once pups were born, we left the breeding cage relatively undisturbed for the first 7–10 d except to provide fresh water and food. Twenty-one days after birth, we weaned pups, removed them from the parental cage, marked them with permanent ear tags, and housed them in groups of up to three same-sex litter-mates.

Ontogeny data collection: We based developmental progression on observations of 114 litters born in captivity. Although we checked pups daily, we rarely handled them prior to 10 d of age to avoid stressing the mother, which could result in offspring being abandoned or cannibalized. Following a molt study in California Voles (*Microtus californicus* ssp.; Ecke and Kinney 1956), we noted qualitative data on the coat color of live individual Amargosa Voles at least 10 d of age with a particular focus on the width and location of the dorsal stripe. Prior to weaning, we chose voles at random from each litter on each collection date because pups were too young to be ear-tagged and therefore could not be individually identified. After weaning, we randomly chose one individual from each litter and followed them for the duration of the study along with two additional voles that were litter mates of different sexes to improve sample size. In total, we assessed 11 individuals (six males, five females) for molt progression every 4 d from ages 10–56 d.

Statistical analyses.—We maintained data on every animal, including veterinary notes, birth dates, wean dates, death dates, and physical examination results, in an electronic spreadsheet in Excel (Microsoft, Redmond, Washington, USA) and the database FileMaker Pro Advanced 12.0v1 (FileMaker Incorporated, Santa Clara, California, USA). Initially, we managed colony lineages using the pedigree software PopLink 2.4, but these data were also moved to FileMaker. We conducted all analyses in R (Version 3.2.3; R Core Team 2017) and considered a P-value ≤ 0.05 to be significant. Where comparison of mean values was intended, we assessed differences using Welch's t-test. After assessing data for normality with a chi-square test, we used two-factor ANOVA to compare activity detected on cameras (as defined above) between day or night and season. We analyzed monthly distributions of aggression events with a chi-square and factors influencing breeding success using logistic regression. We defined breeding success as the birth of pups that were successfully weaned into the colony. An unsuccessful litter was one where we confirmed that pups were born but the dam did not successfully wean pups, either due to neonatal mortality, poor maternal care, or other reasons. We omitted attempted pairings from which pups were never born. We generated kinship coefficients to assess the impact of inbreeding on litter success from a kinship matrix of all pairs computed in the R package kinship2 (Therneau and Sinnwell 2015).

Results

Field observations.—Field observations tended to be limited to body measurements, assessment of coat color, records of longevity extremes, and observations of behavior inferred from camera traps. We assessed sexual dimorphism in mass using 2,343 (1,040 male, 1,303 female) adult wild voles captured between 2010 and 2017. Male mass ranged from 21–128 g (mean 81.4 g) and was significantly larger than female mass ($t = 6.89$, df = 1993.8, $P < 0.001$), which ranged from 23–109 g (mean 77.4 g; Table 1). Typically, voles in the

Table 1. Mean (± standard deviation: SD) body mass (g), total body length (mm), tail length (mm), and hind foot length (mm) of adult Amargosa Voles (*Microtus californicus scirpensis*) compared to body trait measurements of Sanhedrin Voles (*M. californicus eximius*). Sample sizes for traits are given parenthetically below mean values. Samples sizes for total length, tail length, and hind foot length are the same and given only for total length. Data for *M. californicus eximius* come from Cudworth and Koprowski 2010. Significant differences in trait means between males and females is indicated by superscript [a] and between captive and wild males with a superscript [b].

	M. californicus scirpensis		*M. californicus eximius*	
	Female	Male	Female	Male
Trait	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Body mass (g)				
wild	77.4 ± 12.6 (1,303)	81.4 ± 14.7[a] (1,016)	43.4 ± 1.8 (9)	47.1 ± NA (9)
captive	78.8 ± 17.5 (96)	89.7 ± 15.7[b] (113)		
Total length	200.6 ± 9.1 (13)	208.9 ± 10.3[a] (19)	167 ± 2.0 (21)	174 ± 2.9 (19)
Tail length	62.1 ± 3.8	66.3 ± 4.1[a]	45 ± 0.9	49 ± 1.2
Hind foot length	23.1 ± 1.6	23.1 ± 0.98	22 ± 0.3	22 ± 3.8

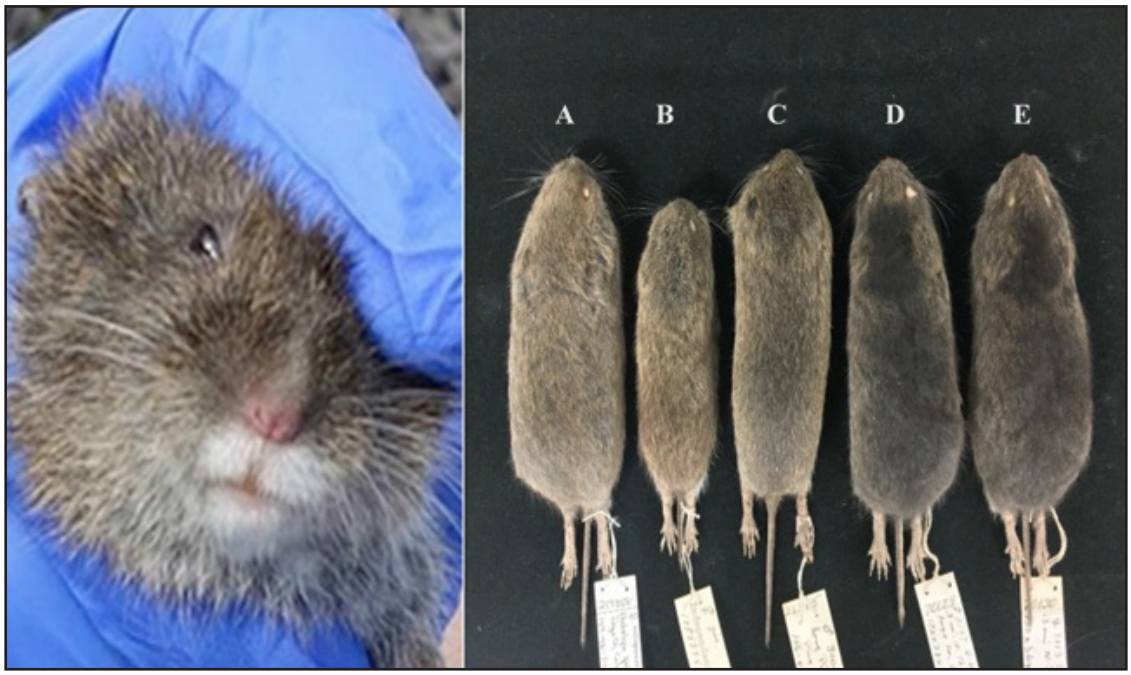

Figure 1. Characteristics that are unique to modern day Amargosa Voles (*Microtus californicus scirpensis*) include (left) white markings on the upper and/or lower lip, sometimes forming a "white beard" (Photographed by Eliška Rejmánková), and (right) extremely dark juvenile pelage of *M. californicus scirpensis* (D) compared to M. californicus vallicola (A-C) and *M. oregoni adocetus* (E; Photographed by Chris Conroy).

wild were a dark mouse brown and most had a distinct white circum-oral beard. It was common to recapture individual voles over several months, but recaptures diminished thereafter. Exceptions included four female voles that we occasionally recaptured and survived at least 16–20 mo.

Cameras recorded numerous instances of voles consuming bulrush, but there were also two cases of consumption of other plants: once on Yerba Mansa (*Anemopsis californica*) and the other on Clustered Goldenweed (*Pyrrocoma racemosa* var. *paniculata*). Camera evidence also confirmed agonistic behaviors. We examined 1,220 baited camera-days and there were 1,603 independent camera events: these featured a vole and 30 independent aggression events. Most events were non-specific, with two or three animals in the same proximity with evidence of chasing and subsequent absence of one of the animals. Seven images clearly showed a vole being bitten or rolled over by another vole. There were from one to 23 aggression events per primary period, with on average 0.02 aggression events per day (Table 2). Considerably more vole sightings and significantly more aggression events were observed in May than other months ($\chi^2 = 20.85$, df = 6, $P < 0.001$). All aggression events occurred when cameras were baited. Three aggression events between a vole and a Desert Woodrat (*Neotoma lepida*) were consistent with a vole possibly initiating the interactions but in the end, each vole left the scene to the woodrat. Hourly activity was highest in spring (2.2 vole sightings per hour) and lowest in fall (0.5 sightings per hour). Although nighttime activity was significantly higher than daytime (1.5 vole sightings per hour at night and 1.3 vole sightings per hour in day; $F_{1,1078} = 4.90$, $P = 0.030$), we observed numerous voles during the day.

Colony results.—We assessed length and body mass dimorphism using museum specimens including 15 adult females (one brought into the colony from the field, eight colony F_1 generation, and six F_2) and 20 adult males (one from the field, 10 F_1, and nine F_2). We also had body mass data from 209 captive-reared voles (113 male, 96 female). Overall, Amargosa Voles were relatively large (Table 1) and males had larger body mass ($t = 4.70$, df = 192.57, $P < 0.001$), longer total length ($t = 2.42$, df = 28.01, $P = 0.022$), and longer tail length ($t = 2.92$, df =

Table 2. Summary of independent aggression events among Amargosa Voles (*Microtus californicus scirpensis*) detected during the first 5 d of camera trap deployment between November 2015 and September 2016 near Tecopa, California. Abbreviations are TAE = total number of aggressive events, NIS = number of independent vole sightings, and PEA = proportion of events that were aggressive.

Month	Day 1	Day 2	Day 3	Day 4	Day 5	TAE	NIS	PEA
Nov./ Dec.	0	1	0	0	0	1	52	1.9%
Jan.	1	0	0	0	0	1	208	0.5%
March	0	1	0	0	0	1	413	0.2%
May	1	4	7	6	5	23	459	5.0%
June	0	1	0	0	1	2	248	0.8%
Aug.	0	0	0	1	1	2	223	0.9%

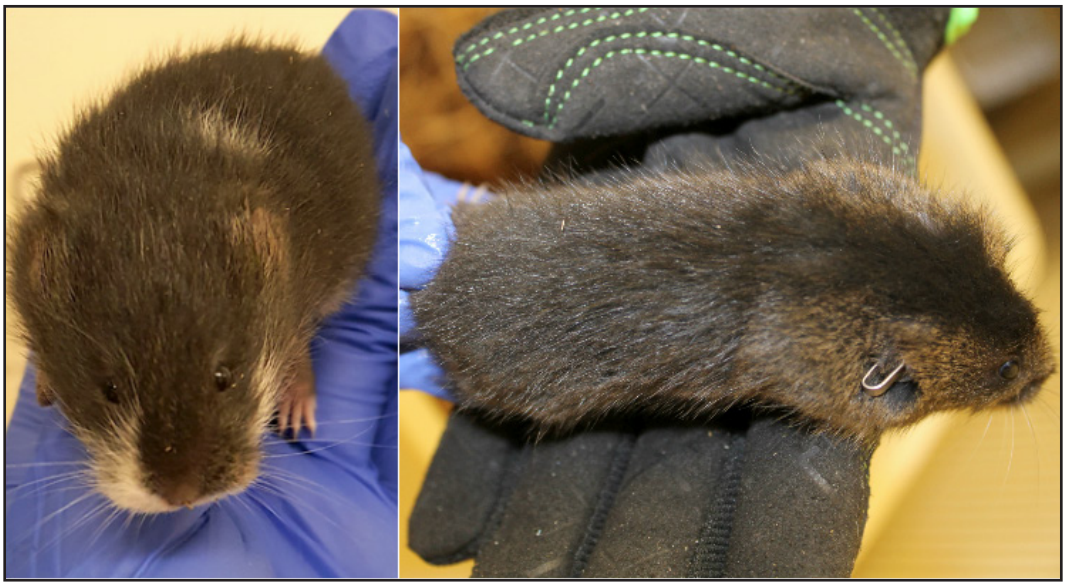

Figure 2. Left: Juvenile Amargosa Vole (*Microtus californicus scirpensis*) with irregular, exaggerated color markings consisting of sweeping white marks from nose to ear and a circular white patch behind the shoulder. (Photographed by Nora Allan). Right: Subadult Amargosa Vole exhibiting characteristic dorsal stripe of juvenile hair during molt. (Photographed by Risa Pesapane).

24.81, $P = 0.007$) than females, but hind foot length did not differ by sex (Table 1). Captive animals, particularly males, tended to be heavier than their wild counterparts ($t = 5.37$, df = 134.87, $P < 0.001$). Colony voles survived up to 34.5 mo in absence of medical conditions.

Whiskers were mostly white with a black base, tails were short and bicolored, and adult coat colors ranged from light to dark brown or cinnamon brown dorsally and gray ventrally. Amargosa Voles also occasionally had pink noses, typically exhibited areas of white above and/or below the mouth that sometimes formed a white beard and had extremely dark black juvenile pelage (Fig. 1). Additional markings commonly observed in the colony included white toes on one or more feet and white-tipped tails. One colony individual developed a large beard consisting of sweeping white marks from chin to ear and a circular white patch on the dorsal body (Fig. 2).

Newborn vole pups were hairless, blind, and pink in color (Fig. 3), turning gray to black on day two. Dark juvenile pelage was fully developed by day four and pups opened their eyes and became highly mobile on day nine (Fig. 3). White markings on the face were also present by day nine. Juvenile Amargosa Voles began to consume solid food between weeks two and three but continued to suckle milk from their dams until weaning at day 20–21. They were independent at three weeks of age, but retained portions of their juvenile pelage. Molting of fine, dark black juvenile hair to coarser, dark brown adult pelage began at the dorsal mid-line, creating a strip of juvenile hair (Fig. 2) from head to rump that extended down past the shoulder blades and hips. The dorsal stripe progressively narrowed, and molting continued in the posterior to anterior direction until about eight weeks of age at which point young voles were indistinguishable from adults.

The youngest female known to conceive in captivity was 25 d old. Males in captivity were not given an opportunity to breed before eight weeks of age. Both males and females continued to produce young after 12 mo of age with one female giving birth at 455 d old. Amargosa Vole gestation period was 20 d and litters could be born every 21 d, meaning females were receptive to copulation on the same day as parturition. Litter sizes ranged from 1–6 pups with a mean of 2.96 ± 1.32 (SD) pups per litter. Based on 37 pups from 10 litters and six breed pairs, the mean mass of each pup in a litter at weaning was 34.7 ± 7.5 g.

Among 78 litters in the colony, 64 (82.1%) were successful and 14 (17.9%) were unsuccessful. Differences in success among litters born to wild sires and dams (generation = Parental), F_1, F_2, and $F_{1.5}$ crosses (e.g., $F_1 \times F_2$) were not significant (coefficient = 0.65, $Z = 0.81$, $P = 0.400$), nor was there any trend towards reduced success after multiple generations in the colony. However, having a wild sire was marginally associated with failure to produce a successful litter, with an odds ratio of 3.1 (95% C.I. = 1.5–6.2, $P = 0.090$). Primiparous dams had 79% litter success compared to 85% success if the mother had a previous litter, alive or not. Dams of successful litters were on average 197.2 ± 74.9 d old compared with unsuccessful dams, which were 200.6 ±64.5 d old. There were significant differences in breeding success by month ($\chi^2 = 20.21$, df = 1, $P < 0.05$) ranging from 100% of litters successful in February, April, and November to just 20% in October.

Diet.—Captive Amargosa Voles housed indoors showed strong aversion to novel foods although adapting idiosyncratically to various foods. They were most willing to eat commercial rodent or rabbit chow, jicama,

Figure 3. Progression of Amargosa Vole (*Microtus californicus scirpensis*) pup development from day 1 (A) pups are born pink, hairless and blind, days 2-3; (B) skin of pup darkens as pigments deposit in the follicles, days 4–7; (C) juvenile pelage is present, and (D) days 9–11 eyes of pup are open and they are fully mobile. (Photographed by Risa Pesapane).

alfalfa hay, carrots, and sweet potatoes in spite of being offered fresh cuttings of native bulrush. They refused seeds of non-bulrush plants indefinitely. Initially, voles also rejected fresh cuttings of native bulrush although they consumed all portions of bulrush, including stalks, flowers, seeds, and rhizomes beneath the soil when bulrush was provided erect in planted cups. Amargosa Voles displayed a preference for upper stems over lower stems. To date, no captive voles have successfully maintained body mass on a diet of all bulrush. Voles engaged in allo- and autocoprophagia.

Behavior.—In cages with multiple individuals, we frequently observed mutual grooming. Both male and female parents groomed and retrieved pups and guarded the nest. Nest building efforts varied by individual and did not appear to be associated with sex, co-housing, age, or parental experience. Amargosa Voles regularly defecated, washed, and preened in the water bowls provided. Some individuals also clipped straw bedding and stacked clippings in water bowls.

In indoor housing, pairs of sibling males typically cohabitated indefinitely in rat cages without aggression with the exception of two cages where minor wounding was observed. In contrast, in outdoor housing, several pairs of sibling males demonstrated lethal aggression towards one another (so we discontinued cohabitation in outdoor pens). We only observed minor aggression between sibling females once in the colony. When provided with fresh soil, all voles, regardless of housing or sex, became more active and in some cases more aggressive towards handlers than those provided only with straw.

Captive Amargosa Voles engaged in tunneling, chewing on bulrush plants, shredding bulrush stalks, building nests with straw, climbing cage structures, and digging when soil was available. When clusters of bulrush were available, voles climbed the stalks to reach the tips, flowers, and seeds. Both indoor and outdoor voles in captivity readily cached chow that they did not immediately consume.

Discussion

For profoundly endangered species like the Amargosa Vole, biological details are critical for adequately linking species biology and ecology with management actions (Clark et al. 2002), and recovery plans that provide such linkage are more likely to improve population status (Boersma et al. 2001; Gerber and Hatch 2002). Our approach to Amargosa Vole conservation used both field and colony data to fill important gaps in knowledge. We report characteristics of Amargosa Vole biology and ecology that can now be included in recovery and captive release planning to more specifically address the needs of this subspecies.

Data from the field provided a snapshot of Amargosa Vole demography, behavior, and diet. Arguably, the

most important data collected were outcomes of vole-vole and vole-woodrat agonistic interactions, and the most important observations were that Amargosa voles consumed plants other than bulrush and wild individuals survived for nearly two years. The spike in aggression in May could have been due to changes in vole population size, breeding, changing food availability, or other factors. Amargosa Voles, like other microtine rodents, are locally important prey sources to a variety of predators and are *r*-selected to produce large numbers of offspring as long as resources support (Krebs 1966; Foley et al., unpubl. report). Investigations of the demography of the species are critical, but inference regarding population status is hindered by lack of ability to truly characterize age structure of the population because of lack of a series of individuals of known age with good data on size and coat color. Additionally, the Amargosa Vole has often been assumed to have a narrow niche breadth because of the extremely limited geographical range and obligate dependence on bulrush for food. However, even if unusual, consumption of other foodstuffs could provide flexibility for management and conservation of Amargosa Voles outside bulrush marshes of Tecopa.

Data from the captive colony served to fill in numerous answers to questions on the biology of the species that were previously only extrapolated from other California voles. This subspecies is considerably larger than most North American voles (Heske and Ostfeld 1990; Lidicker and Ostfeld 1991; Cudworth and Koprowski 2010), and we found that it has a molt progression and coloring of coat, whiskers, and tail similar to descriptions given previously (Kellogg 1918; Ecke and Kinney 1956). Categories of juvenile, subadult, and adult based on body mass can now be refined for Amargosa Voles. Our study suggests overlap among age categories in body mass, and that juveniles should be distinguished as individuals with a full pelage of dark, fine hair; subadults are individuals undergoing molt (i.e., with some portion of juvenile dorsal stripe present); and adults are individuals lacking all juvenile pelage. The white facial markings seen in field and colony, and larger swaths of white on some colony individuals, may be recently evolved characteristics given that earlier descriptions do not include these features. It is possible that the white beard was previously rare but during the period of the present study, it is present in almost all animals; this warrants further study to explore whether it is a result of a recent genetic bottleneck.

Colony data also informs the understanding of the reproductive strategy of this subspecies. Breeding as early as six weeks has been reported for California Voles (Hatfield 1935), whereas Amargosa Voles become sexually mature as early as one month of age and can continue producing successful litters lifelong. They have a periparturient estrous and can have litters of approximately four pups every 21 d, although somewhat lower fecundity was typical in the colony. Male and female tolerance and to some extent care of offspring was consistent with observations in the colony, although more research is needed to evaluate whether Amargosa Voles may be monogamous as is characteristic of Prairie Voles (*M. ochrogaster*; DeVries et al. 1995). Although survival in the wild is estimated to be just a few short months (Klinger et al. 2015), Amargosa Voles in captivity live up to 34.5 mo.

In contrast to reports that Amargosa Voles require bulrush for nutrition, other subspecies of California Voles typically consume grasses, sedges, forbs, seeds, and roots (Batzli and Frank 1971) and are often considered pests because they readily consume agricultural crops when available (Clark 1984; Baldwin et al. 2014). In addition to our few observations in the wild of Amargosa Voles consuming plants other than bulrush, colony data helped flesh out our understanding of food preference. Colony voles were initially averse to novel food items, including bulrush, wholly rejecting seeds from non-bulrush plants. Such fastidiousness could potentially hinder their response to shifts in their nutritional landscape, though their eventual acceptance of select root crops suggests they may adapt if palatable resources become available. Furthermore, the inability of captive Amargosa Voles to maintain body mass on bulrush suggests a complex strategy for acquiring sufficient nutrients in an environment where resources are extremely limited. Future research to explore the role of the gut microbiome in vole metabolism, particularly microbial fermentation of plant fibers to extract more energy from low-quality plants (Justice and Smith 1992; Morrison et al. 2009) is needed, and how captive conditions may shift the natural microbiome as has been shown in other species (Nakamura et al. 2011; Nelson et al. 2013; Clayton et al. 2016). Understanding Amargosa Vole nutrition will be critical to successful releases of captive individuals to native habitat.

Captive Amargosa Voles engaged in water-use, digging, and bulrush-scaling behaviors that align with wild vole behaviors observed by remote photography. Their preference for upper stems has been documented in other California Voles (Gill 1977). It is not known whether wild voles also cache their food, but this behavior may be valuable for voles if they can cache bulrush seeds when abundant for seasons when resources are scarce. In addition to feeding and drinking behaviors, the changes in aggression behavior in colony voles were interesting. Differences in aggression between voles housed indoors and outdoors and the more vigorous behavior of voles provided with soil suggest that conclusions drawn solely from animals housed indoors should be interpreted cautiously. Conversely, this difference suggests that our outdoor mesocosms are successfully replicating a more natural environment and are useful as way to prepare candidate individuals for release.

The establishment of captive breeding colonies of endangered species is commonly justified for insurance

against extinction in the wild, as sources for augmentation or reintroduction, or as means of maintaining genetic diversity. Captive breeding has played an integral role in effectively preventing extinction in California Condors (*Gymnogyps californianus*; Snyder and Snyder 1989), Black-footed Ferrets (*Mustela nigripes*; Miller et al. 1994), Mauritius Kestrels (*Falco punctatus*; Jones et al. 1995), and the Arabian Oryx (*Oryx leucoryx*; Spalton et al. 1999) among other species; however, captive breeding colonies are increasingly scrutinized for their overall modest success in serving proposed functions (Beck et al. 1994; Snyder et al. 1996). We propose that a critically important additional service of captive breeding colonies is the facilitation of the valuable study of biological and ecological species characteristics. Wildlife species that are highly secretive, like the fossorial Amargosa Vole, present unique challenges to adequately collecting detailed biological data using field techniques alone. This can be further compounded by the limitations of studying an endangered species where substantial disturbance or manipulation of individuals in the wild is inappropriate. Together, field studies and captive propagation can provide powerful resolution of biological characteristics that are imperative for linking management actions with species biology, protecting field populations from overly invasive sampling, and ultimately increasing the likelihood of successful species recovery.

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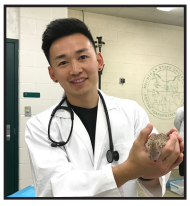

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