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Implications of scale-independent habitat specialization on persistence of a rare small mammal

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ABSTRACT

We assessed the habitat use patterns of the Amargosa vole *Microtus californicus scirpensis*, an endangered rodent endemic to wetland vegetation along a 3.5 km stretch of the Amargosa River in the Mojave Desert, USA. Our goals were to: (1) quantify the vole's abundance, occupancy rates and habitat selection patterns along gradients of vegetation cover and spatial scale; (2) identify the processes that likely had the greatest influence on its habitat selection patterns. We trapped voles monthly in six 1 ha grids from January to May 2012 and measured habitat structure at subgrid (225 m^2) and trap (1 m^2) scales in winter and spring seasons. Regardless of scale, analyses of density, occupancy and vegetation structure consistently indicated that voles occurred in patches of bulrush (*Schoenoplectus americanus*; Cyperaceae) where cover >50%. The majority of evidence indicates the vole's habitat selectivity is likely driven by bulrush providing protection from intense predation. However, a combination of selective habitat use and limited movement resulted in a high proportion of apparently suitable bulrush patches being unoccupied. This suggests the Amargosa vole's habitat selection behavior confers individual benefits but may not allow the overall population to persist in a changing environment.

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1. Introduction

Habitat selection occurs as a result of the additive or multiplicative effects of biological interactions (Rosenzweig, 1991; Morris, 1996, 2003), resource availability (Wasko and Sasa, 2012), and physiological constraints (Huey, 1991). Depending on local, landscape, and regional conditions though, these patterns can vary both temporally and spatially (Kotler, 1989; Morris, 1990; Sundell et al., 2012). Indeed, there has been an increasing awareness that habitat selection patterns are highly scale-dependent (Morris, 1987a; Bowers and Matter, 1997; Orrock et al., 2000). For example, a species may only occur in one or two habitat types at a local scale and would appear to be a specialist, but at larger scales it may occupy many more types and appear to be a generalist. This is because the variety of suitable habitat types often increases with scale, and processes that influence selection behavior can vary in intensity or even direction at different scales (Stapp, 1997; Kelt et al., 1999).

Understanding how habitat selection patterns vary with scale is particularly important in regard to rare species. Rarity is an emergent pattern along axes of distribution, abundance, and the range of habitat types that a species occupies (Rabinowitz, 1981; Rabinowitz et al., 1986). A species is most vulnerable to extirpation when it has a restricted distribution, low abundance, and narrow habitat breadth. These patterns are not static though; habitat selection patterns may vary in different parts of a species range, abundance fluctuates, and a species range can contract or expand. Nor are the three

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attributes necessarily independent of one another. There is theoretical and empirical evidence for density-dependent habitat selection (Holt, 1987; Morris, 1987b; Morris and MacEachern, 2010), and directional trends in abundance can alter species distributions (Gaston, 2009; Sexton et al., 2009). For rare species, scale would be expected to become progressively more important as the relative proportion of individuals that are affected by changes in distribution, abundance, or habitat increases. For instance, being a habitat generalist is often an important factor in maintaining populations of species with restricted distributions (Devictor et al., 2010). This is because a large-scale disturbance would likely be required to affect all of the habitat types the species used. In contrast, if a species was a habitat specialist with a restricted distribution, then a small-scale disturbance could affect a greater proportion of individuals in the population.

Some species that are widely distributed and abundant throughout most parts of their range can have isolated subpopulations that are rare. An example is the California vole *Microtus californicus* (Cricetidae; Arvicolinae), a small mammal with 17 recognized subspecies (Hall, 1981). California voles occur from northern Baja California, Mexico to southern Oregon, USA, in a variety of habitat types with dense herbaceous layers. Most subpopulations occur in mesic ecosystems in the central and western part of California, but several disjunct subpopulations are found in very arid ecosystems east of the Sierra Nevada and Transverse ranges (Conroy and Neuwald, 2008). The most isolated of these is the Amargosa vole (*Microtus californicus scirpensis*; Bailey, 1900) in the central Mojave Desert. The range of the Amargosa vole (vole from hereon) was never extensive, being entirely restricted to the Amargosa River watershed (Neuwald, 2010). The Amargosa River is one of four rivers in the Mojave Desert and runs approximately 235 km from Nevada into the southern Death Valley region of California. The main source of water for the river is seeps and springs, which historically formed wetland and riparian communities that occurred throughout the watershed (Izbicki, 2007). Over the last 100 years though, groundwater pumping and land clearing has resulted in significant loss or alteration of these communities.

A consequence of the altered hydrology in the Amargosa watershed is that the distribution of the vole became even more restricted. It was extirpated from the northern part of its range circa 1920 and was once thought to be entirely extinct (Bleich, 1979). The vole was listed as endangered by the U.S. Fish & Wildlife Service in 1984, primarily because of destruction and alteration of its habitat. Currently it occurs only within a stretch of approximately 3.2 km $\times$ 1.5 km in the lower reach of the Amargosa River. Genetic studies indicate the vole has low levels of variation compared to other subspecies of *M. californicus*, and also suggest there is substantial subdivision and little dispersal among subpopulations (Neuwald, 2010). An extensive trapping effort by the California Department of Fish & Wildlife (CDFW) in 2010 and 2011 established that the vole has a disjunct distribution within its current range (T. Branston, CDFW, pers. comm.), while more limited historic trapping efforts indicated it was confined to isolated and often small fragments of wetland vegetation usually dominated by bulrush (*Schoenoplectus americanus* [Pers.] Volkart ex Schinz & R. Keller; Cyperaceae) (Rado and Rowlands, 1984; McClenaghan and Montgomery, 1998).

Although it is apparent that voles require wetland vegetation and that bulrush is important to them, some data indicated they used other types of wetland vegetation, especially areas with significant cover of salt grass (*Distichlis spicata* [L.] Greene; Poaceae) (Gould and Bleich, 1977; Rado and Rowlands, 1984; McClenaghan and Montgomery, 1998). Salt grass occurs throughout the lower Amargosa River watershed, often in dense stands nearly 0.5 m in height. These stands are usually adjacent to bulrush and could potentially be used by voles at moderate to low levels throughout the year or during periods when density was high. Most trapping efforts though had targeted stands of bulrush, which biased evaluation of the vole's habitat breadth and selection patterns. More broadly, California voles occur in many types of habitats with well-developed herbaceous layers, including annual-dominated grasslands, oak savannas and woodlands, ruderal fields, and wetlands (Cockburn and Lidicker Jr., 1983, Getz, 1985; Geissel et al., 1988). Thus, beyond just theoretical advantages for having broader habitat breadth (Futuyma and Moreno, 1988; Howe et al., 1991; Clavel et al., 2011), the empirical data also suggested that the Amargosa vole used vegetation types other than bulrush.

The purpose of our study was to evaluate the habitat use patterns of the vole relative to the availability of wetland vegetation types. Because the influence of habitat structure on animal abundance and habitat use can vary temporally and spatially (Garshelis, 2000; McLoughlin et al., 2010), we designed the study to quantify use and selection across three scales: grid (1 ha), subgrid (225 m^2), and trap (1 m^2). We expected to find that proportional use of bulrush would become less common and that of salt grass more common as scale and vole abundance increased. Our objectives were to: (1) estimate population density in grids that varied in relative cover of bulrush and salt grass; (2) estimate occupancy of grids and subgrids that varied in relative cover of bulrush and salt grass; and, (3) quantify habitat structure at the three scales and then analyze the selection patterns of the voles relative to the habitat variables.

2. Materials and methods

2.1. Study area

The study was conducted in the lower Amargosa River valley near the town of Tecopa Hot Springs in southeastern Inyo County, California. Vegetation along the river has been highly fragmented and it now occurs as patches interspersed with extensive bare areas and salt pans (a natural depression with a surface salt layer deposited by evaporation). Common plant species besides bulrush and salt grass include alkali heath (*Frankenia salina* (Molina) I.M. Johnst; Frankeniaceae), Cooper's rush (*Juncus cooperi* Engelm.; Juncaceae), yerba mansa (*Anemopsis californica* (Nutt.) Hook. & Arn.;Saururaceae), and slender arrow-grass (*Triglochin concinna* Burtt Davy; Juncaginaceae). Bulrush and salt grass-dominated vegetation are the two most

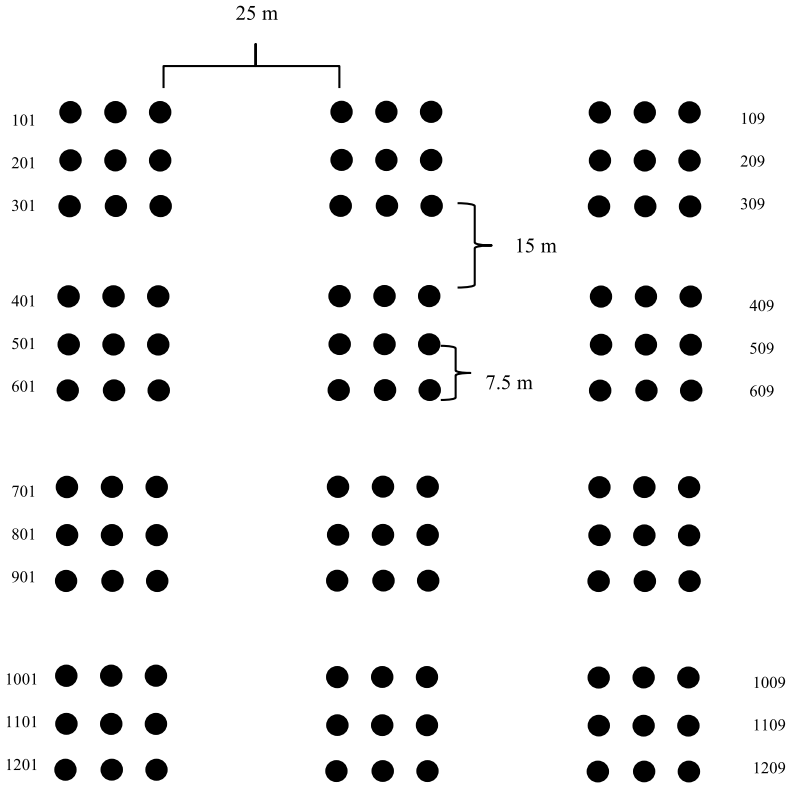

Fig. 1. Grid design used to trap Amargosa voles (*Microtus californicus scirpensis*) in the lower Amargosa River Valley, Inyo County, California, January–May 2012. Numbers are the beginning and ending trap numbers for each trap row ($N = 12$ rows).

common community types, but relatively small areas dominated by one or a combination of the other species occur as well.

The climate in the lower Amargosa River valley is extremely harsh, particularly during summer months. Mean daytime temperatures in the winter typically range from 15 °C to 23 °C and in the summers from 37 °C to 43 °C. Mean annual precipitation (1972–2011) is 12 cm, with approximately 70% occurring from November through March.

2.2. Trapping

We conducted trapping at each of six 1 ha grids in five periods between January and June 2012. The grids were located randomly along a 1.5 km stretch of the river starting at the northern limit of the vole's range, with distances between adjacent grids ranging from 75 m to 150 m. Each grid was 105 m × 95 m in dimension, with twelve 15 m × 15 m subgrids nested within each grid. Each subgrid consisted of nine trap stations in a 3 × 3 arrangement with traps spaced 7.5 m apart ($N = 108$ traps per grid; Fig. 1).

The five trapping periods were separated by 4-week intervals. Trapping was done for five consecutive days in each grid during the last two weeks of each month (Pollock, 1982), hence we refer to each period by the name of the month from hereon. Traps were baited with a mixture of 4-way livestock feed, alfalfa pellets, peanut butter, and oatmeal. Depending on temperature, the traps were checked 2–4 times per day between 0600 h and 2100 h. All captured animals were given a uniquely numbered ear tag and identified to species, sex, and age class (adult, subadult, or juvenile), weighed, then released at the point of capture.

2.3. Habitat measurements

Ocular estimates of the percent cover of each plant species, bare ground, organic litter (dead plant material), and salt pan in a 1 m^2 quadrat (1 m × 1 m) centered on each trap station were made in February–March (winter) and May–June (spring). These seasons coincided with periods of dormancy (winter) and active growth and greening (spring) of vegetation along the Amargosa River.

Measurements of plant species composition and habitat structure were made in the winter and again in the spring in eight randomly located quadrats (1 m × 1 m) at each subgrid. Four quadrats were inside and four outside the perimeter of the subgrid. Quadrats outside the subgrid were within 1 m of its perimeter. Measurements included ocular estimates of

Table 1
Variables used in analyses of gradients in habitat structure and vegetation composition at six grids (1 ha) and 72 subgrids (225 m^2, 12 subgrids per grid) where trapping for Amargosa voles (*Microtus californicus scirpensis*) was conducted from January to June 2012. Differences in vegetation composition and habitat structure among grids and subgrids were analyzed with Redundancy Analysis (RDA). Occupancy of grids and subgrids was analyzed with dynamic hierarchical models. Gradients in habitat structure for the analyses of occupancy were derived with Principal Components Analysis (PCA). Variables with blank cells were considered for inclusion in the analyses but not used because they had variance inflation factors (VIF's) that were >5 or pairwise correlations with other variables >0.70. ***Included*** = a variable included in the PCA and initial RDA models because pairwise correlations with other variables were <0.70 and VIF's were <5. ***Final*** = variables in the RDA's retained after forward stepping multiple regression indicated they had a significant influence on the ordination. Bulrush = *Schoenoplectus americanus* and salt grass = *Distichlis spicata*.

Variable	Definition	RDA Grids	RDA Subgrids	PCA Grids	PCA Subgrids	Occupancy
Schamecov	Cover of bulrush (%)					
Disspicov	Cover of salt grass (%)					
SchDis	$\log_e$ bulrush/salt grass cover					***Included***
Bare	Cover of bare ground (%)	***Final***	***Final***	***Included***		
Salt	Cover of salt pan (%)					
Water	Cover of standing water (%)	***Final***	***Included***			
Vegcover	Total plant cover (%)	***Final***	***Final***	***Included***		
VegcovCV	Coefficient of variation in Vegcover		**Included**			
Veghtavg	Mean height of vegetation (cm)	***Final***	***Final***	***Included***		
VeghtCV	Coefficient of variation in Veghtavg		***Final***			
Veghtmax	Maximum height of vegetation (cm)					
Litter	Cover of dead plant material (%)	***Final***	***Included***			
LittCV	Coefficient of variation in Litter		***Included***			
Litdepth	Mean litter depth (cm)					
LitdepCV	Coefficient of variation in Litdepth					
Litdepmax	Maximum litter depth (cm)					
PCA 1	First principal component axis					***Included***
PCA 2	Second principal component axis					***Included***

the percent cover of each plant species, bare ground, organic litter, and salt pan, as well as maximum height of each plant species, organic litter depth, and depth of standing water.

The plant species are listed in Appendix 1.

2.4. Data analysis

2.4.1. Vole abundance

The robust-design model with heterogeneity in individual capture probability was used to derive seasonal estimates of abundance (N) of voles in each grid (Pollock et al., 1990; Huggins, 1991). Because our primary interest was to evaluate seasonal differences in abundance among grids and not conduct a formal demographic analysis, we constructed a simple robust design model with constant parameters for survival, movement, and capture. A more comprehensive demographic analysis is being conducted in another study (Klinger et al., in preparation). Seasons were defined as winter (January–mid March) and spring (late March–June). Program MARK was used to derive the estimates of N.

2.4.2. Vole abundance and habitat structure

We used Redundancy Analysis (RDA) (Legendre and Legendre, 2012) to analyze habitat structure and plant species composition at grid and subgrid scales. RDA combines linear regression with Principal Components Analysis (PCA) to jointly model species abundances and environmental gradients in a collection of sampling units. The Hellinger transformation was applied to the mean cover of each plant species at both scales (Legendre and Gallagher, 2001). We developed a parsimonious model for the subgrid scale by only including habitat variables in a starting model where pairwise correlations <0.70 and variance inflation factors (VIF's) <5 (Table 1). We then applied a forward stepping procedure to eliminate variables that did not make significant contributions to the ordination (Blanchet et al., 2008). After the parsimonious model was developed we used permutation tests to evaluate the significance of the overall ordination, the significance of each RDA axis, and each habitat structure variable. Grids were considered a random factor in the permutation tests. We also included variables where pairwise correlations <0.70 and VIF's <5 in the model at the grid scale, but we did not use either the forward stepping procedure or permutation tests because the small number of grids could have made results of these tests spurious.

We used generalized linear mixed models (GLMM's) with a log link and Poisson error structure to analyze the relationship between the number of individual voles captured in the subgrids and four habitat structure variables: percent cover and height ($\log_{10}+1$ transformed) and the coefficient of variation (CV) for the percent cover and height of bulrush. Grid was modeled as a random factor. We developed an initial set of 14 models to evaluate whether a random slope and intercept or random intercept-only structure was most appropriate for the starting model (Zuur et al., 2009). We used the bias-corrected Akaike's Information Criterion (AICc) to rank the models and standardized AICc weights (wAICc) to compare and select the starting one. After selection of a starting model with the most appropriate random effects structure, we developed a 95% confidence set of models (Burnham and Anderson, 2002) from 29 candidate models that included the individual and additive

effects of the habitat structure variables, as well the interactive or additive effect of season (winter or spring; Appendix 2A). We compared the 29 models with AICc and selected the ones that accounted for 95% of the cumulative wAICc. If wAICc for the model with the most support was <0.80 we used model averaging within the 95% confidence set to estimate the parameters. The cumulative wAICc's were used to rank the relative importance of each habitat structure variable (Zuur et al., 2009).

We also used GLMM's with a log link and Poisson error structure to analyze the relationship between the number of individual voles captured at a trap station and the percent cover of *S. americana* and percent cover of litter. Similar to the analysis of the subgrids, we developed an initial set of models ($N = 4$) to evaluate whether a random slope and intercept or random intercept-only structure was the most appropriate starting one. We modeled subgrids nested within grids as random factors. After selection of the best starting model we developed 10 candidate models that included the individual and additive fixed effects of bulrush and percent cover of litter as well the interactive or additive effect of season (Appendix 2B). We compared the models with AICc and selected those that accounted for 95% of the cumulative wAICc.

RDA's were conducted with the 'vegan' package, GLMM's with the 'lmer' package, and derivation of the 95% confidence sets of models with the 'AICcmodavg package' in R (R Development Core Team 2013).

2.4.3. Occupancy of grids and subgrids

We used dynamic hierarchical models (Royle and Dorazio, 2010) to analyze the relationship between habitat structure and occupancy of the grids and subgrids. Dynamic hierarchical models allowed us to estimate the proportion of area among and within grids that was occupied by voles each month, as well as rates of colonization and extirpation. We constructed two sets of models; a set of seven initial "null" models (no habitat variables) and a set of "habitat" models (habitat variables included as covariates). We used AICc to compare the null models and wAICc to determine the most supported one. We then used the null model with the most support (constant or time-varying rates of occupancy, colonization, extirpation, and detection probability) to compare with models where occupancy was constrained by the habitat variables.

We used PCA to derive gradients of habitat structure for the models within the habitat set. We took this approach because it reduced the number of variables in the models while capturing the habitat complexity within and across the grids. Mean values of each habitat variable (Table 1) were calculated at the subgrid (across quadrats within subgrids) and grid (across quadrats and subgrids) scales. We only included variables in the PCA with pairwise correlations <0.70. PCA axes with eigenvalues >1 were retained for inclusion in the habitat model set. We also derived the $\log_e$ ratio in cover between bulrush and salt grass as a habitat variable (Table 1). Ratios can be potentially misleading measures because, for example, sampling units with very low and very high total cover of bulrush and salt grass could have very similar ratios. However, the total cover of bulrush and salt grass at both subgrid and grid scales tended to be high; 97% of the subgrids had total bulrush/salt grass cover values $>25\%$ and 85% had values $>50\%$ (range 5.2%–110.2%), while all of the grids had values $>58\%$ (range 58.5%–81.3%). Correlation coefficients (r) between bulrush and salt grass cover were 0.724 and 0.840 at the subgrid and grid scales, respectively. The correlations of the $\log_e$ ratio with bulrush and salt grass at the subgrid scale were 0.90 and 0.85, respectively, and >0.95 for both species at the grid scale. Correlation of the $\log_e$ ratio with total vegetation cover was 0.498. Thus, we felt that the ratio provided an intuitive and sensitive measure of the gradient from bulrush to salt grass that was not redundant with total vegetation cover.

The habitat model set for the subgrids included the additive and individual effects of the PCA axes and the bulrush/salt grass ratio, but to reduce the chance of overfitting the models at the grid scale we only included the individual effects of the PCA axes and bulrush/salt grass ratio. We derived a 95% confidence set of models and compared them with AICc. Model selection, parameter estimation and ranking of variable importance followed the procedures described above for the GLMM's. The analyses were conducted with the 'unmarked' and 'AICcmodavg' packages in R.

3. Results

We captured a total of 166 voles across the five months. The mean number of captures per individual per month was 2.46 ($\pm$0.32 SD) with an overall capture probability of 0.37 ($\pm$0.02 SE). The estimated mean number of voles per ha was 4.3 ($\pm$0.3 SE) in the winter and 5.1 ($\pm$0.3 SE) in the spring.

3.1. Grid scale

3.1.1. Habitat structure and abundance

Five habitat structure variables had pairwise correlations <0.70 and were used in the RDA of the grids (Table 1). The first axis was a gradient from grids with tall, dense stands of bulrush to those with lower, less dense vegetation comprised predominantly of salt grass (Fig. 2). The second axis separated five grids that had a relatively high proportion of alkali heath and a dense litter understory from a single grid that had a relatively high proportion of rush and bare ground (Fig. 2 and Table 2). The first axis explained 39% of the unconstrained variation and 71% of the constrained variation among the grids, while the second axis explained an additional 11% of the unconstrained and 20% of the constrained variation (Table 2). Overall, the habitat structure variables accounted for 55% of the variation in species composition in the ordination. Seasonal

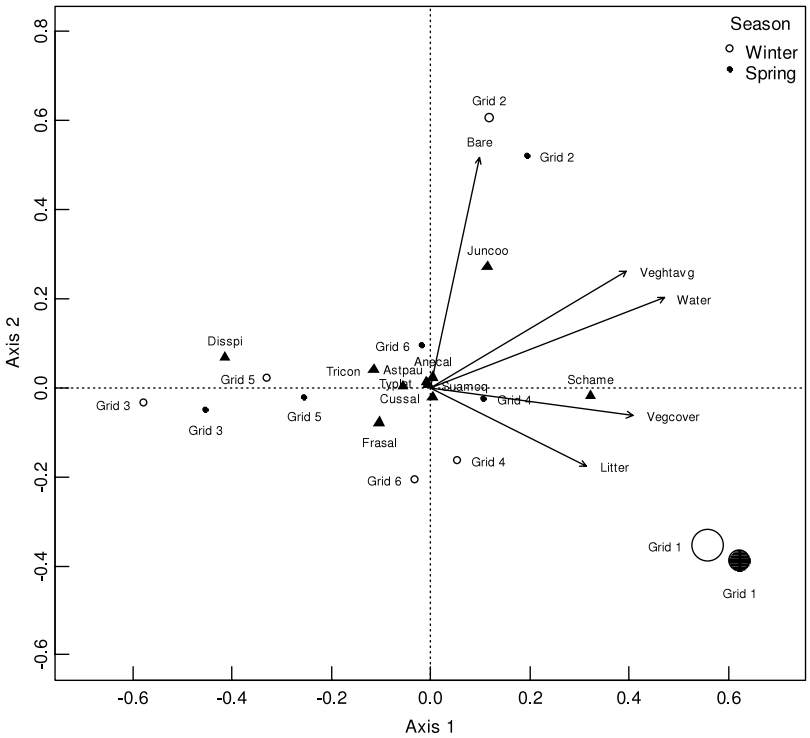

Fig. 2. Triplot of a Redundancy Analysis (RDA) of the percent cover of plant species relative to five habitat structure variables measured during two seasons (Winter = January–March, Spring = April–May) in six grids where Amargosa voles (*Microtus californicus scirpensis*) were trapped in the lower Amargosa River Valley, Inyo County, California, 2012. Abbreviations of the variable are: Bare = cover of bare ground (%), Litter = cover of dead plants (%), Vegcover = total cover of all live plants (%), Veghtavg = mean height of vegetation, and Water = cover of open water (%). The two dominant plant species in the grids were bulrush (Schame; *Schoenoplectus americanus*) and salt grass (Disspi; *Distichlis spicata*); acronyms of the other plant species are given in Appendix 1. Symbols are proportional to the number of voles trapped in the grids within each season.

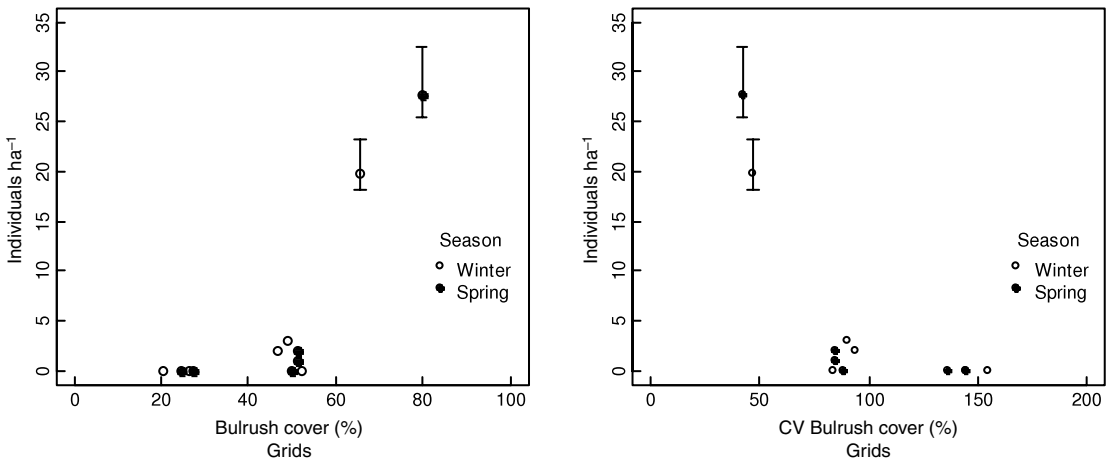

Fig. 3. Density (±95% CI's) of Amargosa voles (*Microtus californicus scirpensis*) along gradients of percent cover and the coefficient of variation (CV) of cover of bulrush (Schame; *Schoenoplectus americanus*) in the lower Amargosa River Valley, Inyo County, California. Trapping was conducted monthly from January through May 2012 in each of six grids. Density estimates are mean values within winter (January–March) and spring (April–May) seasons.

variation in vegetation species composition and habitat structure was relatively low in five of the grids (Grids 1–5; Fig. 2). There was low seasonal variation in habitat structure in Grid 6 but an increase in relative abundance of arrowgrass and Cooper's rush from winter to spring (Fig. 2).

Grid 1 had the greatest mean cover (72.7%) and the lowest coefficient of variation (34.2%) of cover of bulrush among the grids. Abundance of voles was 4x–30x greater in Grid 1 than in the other five grids (Fig. 3). Abundance of voles in Grid 1 was 35% greater in spring than winter, but there was little seasonal variation in relative abundance among the grids (Figs. 2 and 3). Voles were not captured in the two grids with the lowest cover of bulrush.

Table 2
Results of a Redundancy Analysis (RDA) of composition and structure of vegetation in six grids (1 ha) and 72 subgrids (225 m^2, 12 subgrids per grid) where trapping for Amargosa voles (*Microtus californicus scirpensis*) was conducted from January to June 2012.

Variation	Axis 1	Axis 2
(a) ***Grid scale***		
Eigenvalue	0.0235	0.0065
Unconstrained		
Explained	0.387	0.107
Cumulative	0.387	0.494
Constrained		
Explained	0.709	0.197
Cumulative	0.709	0.906
Variable correlation		
Bare (%)	0.179	0.936
Water (%)	0.853	0.366
Vegetation cover (%)	0.739	−0.114
Vegetation height	0.714	0.474
Litter (%)	0.569	−0.321
(b) ***Subgrid scale***		
Eigenvalue	0.1410	0.0142
Unconstrained		
Explained	0.529	0.053
Cumulative	0.530	0.582
Constrained		
Explained	0.898	0.090
Cumulative	0.898	0.988
Variable correlation		
Bare (%)	0.149	0.680
Vegetation cover (%)	−0.599	−0.436
Vegetation height	−0.971	0.016
CV Vegetation height	−0.044	−0.627

3.1.2. Habitat structure and occupancy

Percent vegetation cover, mean vegetation height, and percent cover of bare ground had pairwise correlations <0.70 and were used in the PCA of habitat structure. The first two PCA axes had eigenvalues >1 and accounted for 94% of the variation among the grids. The first axis explained 61% of the variation and represented a vegetation cover and height gradient while the second axis represented a gradient from bare ground to continuous vegetation cover.

The null model with constant rates of occupancy, colonization, extirpation, and detection accounted for 52% of the wAICc and had at least 4x more support than the other models (ΔAICc $= 2.78$), so it was selected to compare with the habitat models. The habitat model with the bulrush/salt grass ratio had overwhelming support compared to the models with the PCA axes and the best supported null model (wAICc $= 0.951$). The estimated mean proportion of area occupied from January through May was 0.501 (±0.146 SE). Rates of colonization (0.091 ± 0.087 SE) and extirpation (0.077 ± 0.074 SE) were similar. The probability that a wetland area was occupied was very low unless the ratio of bulrush and salt grass cover >1 ($\log_e$ ratio $= 0$; Fig. 4a) and bulrush cover >50%. Voles occurred in all five trapping periods in Grid 1, which had 8.5x more bulrush than salt grass, and Grid 2, where bulrush cover (48.8%) was nearly twice that of salt grass (Fig. 4a). Voles only occurred in three trapping periods in Grid 4 (January–March) and Grid 6 (March–May), each of which had similar levels of bulrush cover and bulrush/salt grass ratios as Grid 2 (Fig. 4a).

3.2. Subgrid scale

3.2.1. Habitat structure and captures

Eight habitat structure variables had pairwise correlations <0.70 and were used in the RDA at the subgrid scale (Table 1). The forward stepping procedure indicated that the proportion of area covered by water, variability in vegetation cover, cover of litter, and variability in cover of litter did not have significant importance in the ordination ($P \geq 0.124$), therefore they were removed from the final model.

The overall ordination, first two axes, and the four habitat variables in the most parsimonious RDA model were significant ($P \leq 0.001$). The total variation accounted for in the ordination was 54%. Unconstrained variation accounted for 38% and variation associated with grids (random factor) accounted for 8%. The first axis was a gradient from subgrids with tall, dense vegetation comprised of bulrush to those with lower vegetation comprised of salt grass (Fig. 5). The second axis was a

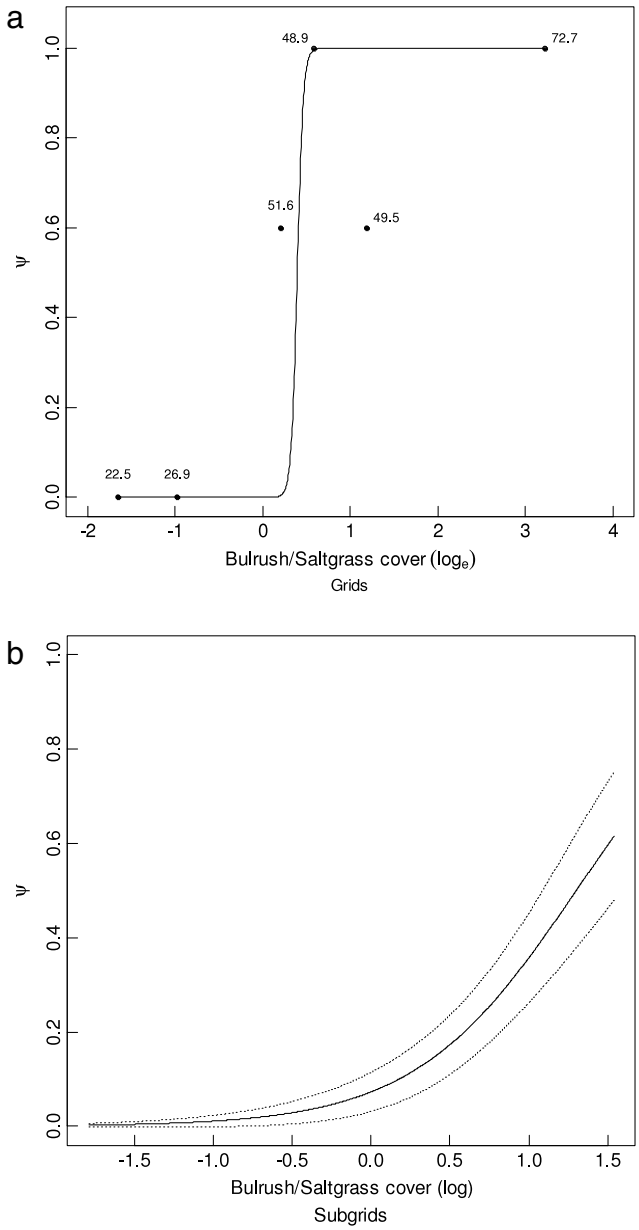

Fig. 4. Relationship between proportion of area occupied (ψ) and the $\log_e$ ratio of bulrush (*Schoenoplectus americanus*) and salt grass (*Distichlis spicata*) cover in (a) grids (1 ha) and (b) subgrids (225 m^2) where trapping for Amargosa voles (*Microtus californicus scirpensis*) was conducted from January to June 2012. The numbers above the points in (a) is the mean cover value (%) of bulrush in that grid.

gradient from subgrids with a high proportion of bare ground to those with high variability in height of the vegetation canopy (Fig. 5 and Table 2). The first axis accounted for 53% of the unconstrained variation and 90% of the constrained variation, while the second axis accounted for 5% of the unconstrained and 9% of the constrained variation (Table 2). In general, a high proportion of voles were captured in subgrids with moderate to high vegetation cover dominated by bulrush (Fig. 5). Nine voles were captured during the winter at one subgrid with patchy, low cover of bulrush (mean = 12.1%, CV = 93.7%), however no voles were captured in that subgrid during the spring.

The GLMM with random slope (cover of bulrush) and intercept terms had wAICc = 0.68 and 4x more support than any of the other candidate starting models, so it was used as the structure in the subsequent GLMM's for the subgrids. Nine models comprised the 95% confidence set of the subgrid GLMM's (Appendix 3a). The model-averaged parameter estimates for bulrush height and CV bulrush height overlapped zero in all nine models and the percent cover and CV in cover of bulrush had 2.5x to almost 4x the variable importance as height and variation in height of bulrush (Appendix 3a). We concluded that bulrush height and CV bulrush height provided little meaningful information so we did not derive model-averaged estimates

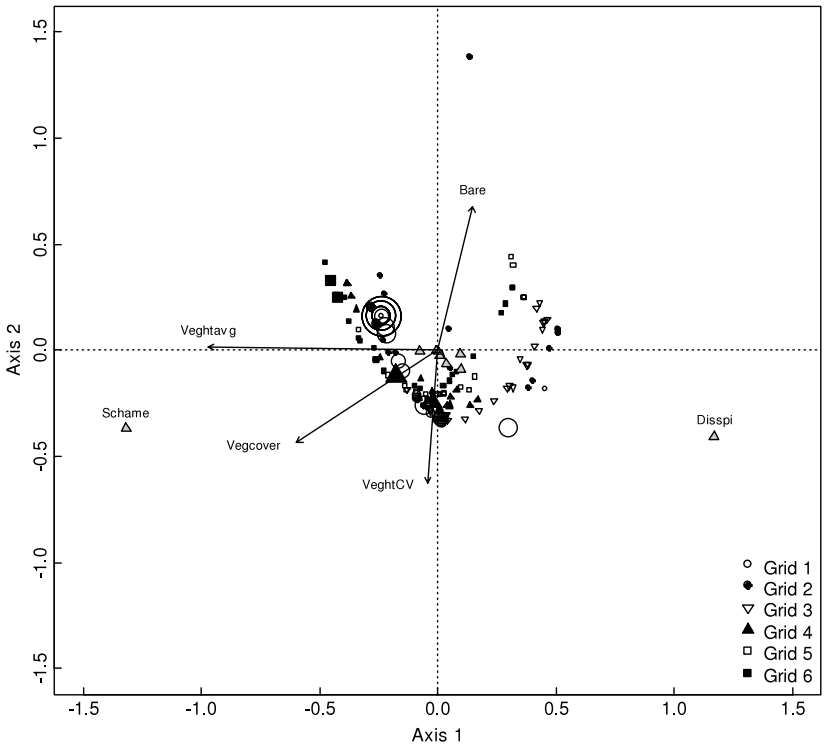

Fig. 5. Triplot of a Redundancy Analysis (RDA) of the percent cover of plant species relative to four habitat structure variables measured in 72 subgrids ($N = 12$ subgrids in each of six grids) where Amargosa voles (*Microtus californicus scirpensis*) were trapped in the lower Amargosa River Valley, Inyo County, California, 2012. Variable abbreviations are: Bare = cover of bare ground (%), VeghtCV = coefficient of variation in mean vegetation height, Vegcover = total plant cover (%), and Veghtavg = mean height of vegetation. The two dominant plant species in the grids were bulrush (Schame; Schoenoplectus americanus) and salt grass (Disspi; *Distichlis spicata*); acronyms of the other plant species (gray-shaded triangles) are not shown but are given in Appendix 1. Symbols are proportional to the number of voles trapped in the subgrids within each season.

Table 3
Parameter estimates from generalized linear mixed effects models of the relationship between the number of captures of Amargosa voles (*Microtus californicus scirpensis*) and habitat structure variables at subgrid (225 m^2) and trap (1 m^2) scales from January through May 2012 in the lower Amargosa River Valley, Inyo County, California. The habitat structure variables are the percent cover of bulrush (*Schoenoplectus americanus*), the coefficient of variation (CV) in bulrush cover, and the percent cover of litter.

Variable	Estimate	SE	Z	P
Subgridscale				
Intercept	−1.1688	1.1917	−0.981	0.32668
Bulrush cover (%)	4.6203	1.5744	2.935	0.00334
Bulrushcover^2 (%)	−2.8945	1.2114	−2.389	0.01688
CV Bulrush cover (%)	−1.9267	0.4673	−4.123	0.00004
Trapscale				
Intercept	−12.9614	2.1849	−5.932	0.00001
Bulrush cover (%)	10.2101	2.2345	4.569	0.00001
Litter cover (%)	2.0855	0.7979	2.614	0.00001

for them. The final model for the number of captures per subgrid included a second-order relationship with bulrush cover and a linear relationship with variation in bulrush cover (Table 3). Estimates of the number of captures increased to an asymptote at approximately 70% cover of bulrush and decreased monotonically as the CV in bulrush cover increased (Fig. 6a and Fig. 6b, respectively).

3.2.2. Habitat structure and occupancy

Vegetation cover, mean vegetation height, CV of mean vegetation height, and cover of bare ground had pairwise correlations <0.67 and were used in the PCA. The first two PCA axes had eigenvalues >1 and accounted for 79.8% of the variation among the subgrids. The first axis (variation explained = 52.6%) was a gradient from subgrids with tall dense

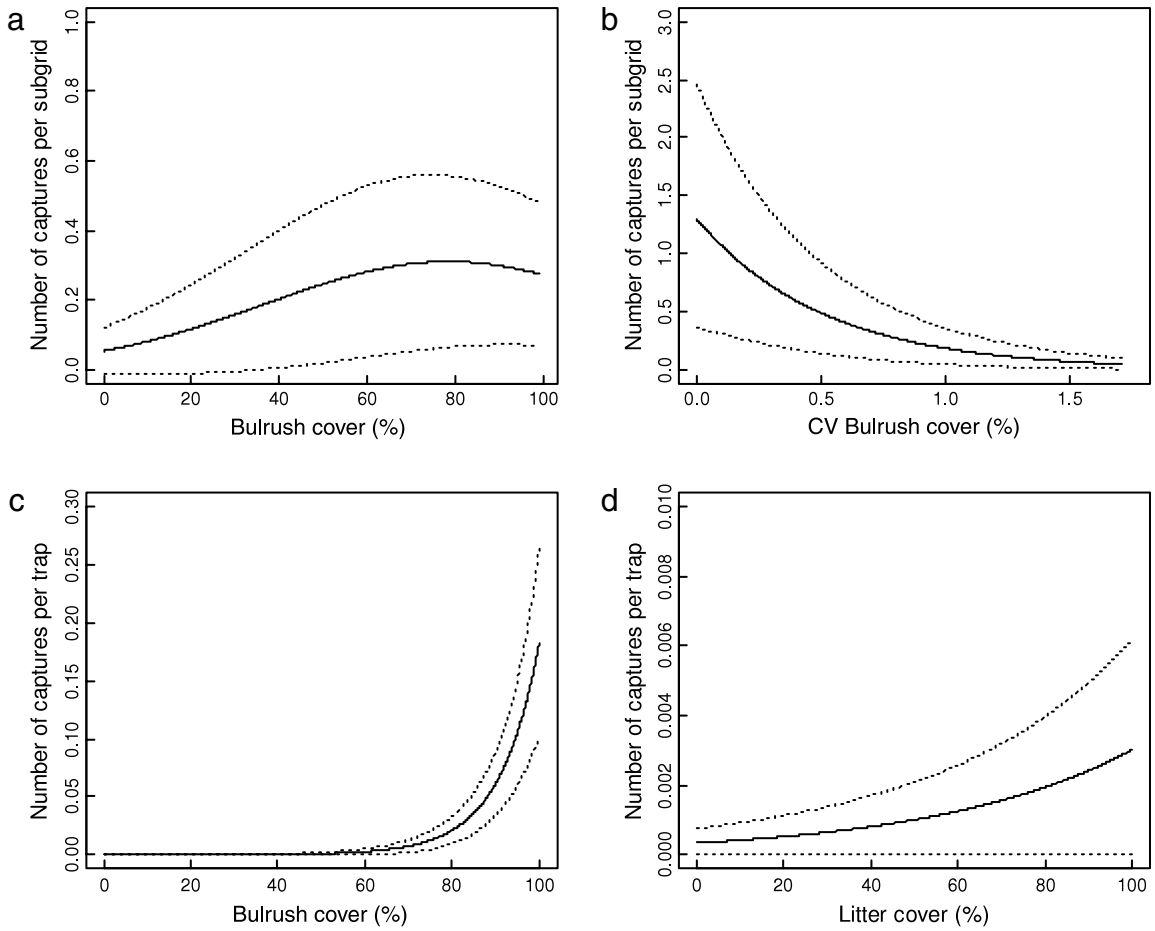

Fig. 6. Model derived estimates ±95% CI's (generalized linear mixed effects models) of the number of Amargosa voles (*Microtus californicus scirpensis*) trapped along gradients of three habitat structure variables in the lower Amargosa River Valley, Inyo County, California, January–May 2012. Panels a and b are for the subgrid scale (225 m^2) and panels c and d are for the trap scale (1 m^2). The habitat structure variables are cover of bulrush (*Schoenoplectus americanus*), the coefficient of variation (CV) in bulrush cover, and cover of dead plant material (Litter).

vegetation to those with variable vegetation height and less cover. The second axis was a gradient from subgrids with a high proportion of vegetation cover to those with a high proportion of bare ground.

The two most supported null models cumulatively accounted for 71% of the wAICc and each included time-varying rates of local colonization and detection probability. The model with the lowest AICc value had time varying rates of local extirpation and more than 2x the support of the other models (Appendix 4), therefore we selected it as the null model to compare with the habitat models.

Three habitat models comprised the 95% confidence set (Appendix 4). The ΔAICc for these models <1.5 (Appendix 4), but the 95% CI's of the model-averaged parameter estimates for the PCA axes included zero and the bulrush/salt grass ratio had 3.5x–5x the variable importance as the PCA axes (Appendix 4). We concluded that the two PCA axes did not provide meaningful predictive information so we did not include them in model-averaged estimates of the proportion of area occupied by voles within the subgrids.

The estimated mean proportion of area occupied within the subgrids ranged from a high of 0.256 (±0.053 SE) in March to a low of 0.140 (±0.035 SE) in April (Fig. 7a). There was little chance of voles using an area within a grid until the bulrush/salt grass ratio was approximately equal ($\log_e$ ratio $= 0$; Fig. 4b), and the probability increased rapidly once the ratio $>1.6:1$ ($\log_e$ ratio $= 0.5$; Fig. 4b). Approximately half of the subgrids where voles occurred in March were unoccupied in April (Fig. 7b); rates of colonization and extirpation were low but similar in the other months.

3.3. Trap scale

The GLMM with random slope (cover of bulrush) and intercept terms had wAICc $= 0.79$ and 5x more support than any of the other candidate starting models, so it was used as the structure in the subsequent GLMM's for the traps. The 95%

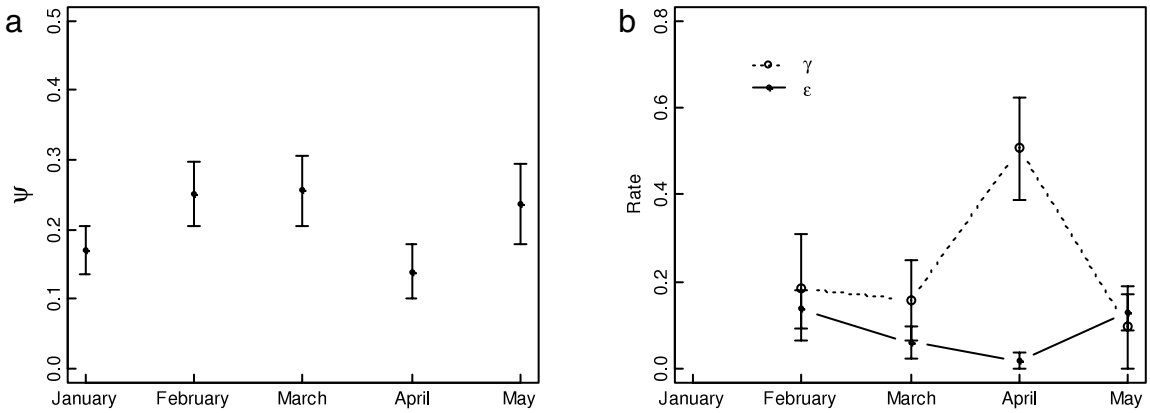

Fig. 7. Mean ±95% CI's of monthly proportion of area occupied (ψ), colonization rates (ε), and extirpation rates (γ) of Amargosa voles (*Microtus californicus scirpensis*) within six grids where they were trapped in the lower Amargosa River Valley, Inyo County, California, in 2012.

confidence set of trap GLMM's was comprised of two models (Appendix 3b). The variable importance for bulrush cover was overwhelmingly greater than litter cover, but the ΔAICc between the two models was only 0.55 (Appendix 3b) and the model-averaged 95% confidence intervals for litter cover were greater than zero so we derived model-averaged parameter estimates for both variables (Table 3b). The estimate for the number of captures remained near zero until bulrush cover was approximately 70%, then increased rapidly when bulrush cover >80% (Fig. 6c). The 95% confidence intervals for the estimate of the number of captures and the percent cover of litter were wide, but the estimate increased monotonically with increasing litter cover (Fig. 6d).

3.4. Movements

Based on a generalized linear model (Poisson error structure and log link), there was no evidence of a relationship between frequency of capture of voles that were captured on multiple occasions and the number of subgrids that they occurred in ($z = 1.106$; $P = 0.269$). Of the 131 voles that were captured on multiple occasions, 87 (66.4%) occurred in only one subgrid and 40 (30.5%) occurred in only two. The distribution of the maximum distance moved by the voles had a strong right skew (Fig. 8). The maximum recorded distance moved was 109 m, but the mean recorded distance moved was only 24.5 m (±2.2 SE) and 75% of the individuals moved <34 m. We did not record any voles moving among the grids.

4. Discussion

Regardless of scale, Amargosa voles were highly dependent on cover of bulrush. Abundance at the grid scale, the proportion of area occupied among and within grids, and use at subgrid and trap scales all had strong positive relationships with bulrush cover. Litter cover had importance at the trap scale (1 m^2), but the magnitude of its effect was low relative to total cover of bulrush. However, at grid (1 ha) and subgrid scales (225 m^2) it was not just the total cover of bulrush that influenced habitat use, but also continuity of the bulrush canopy. This was especially so at the subgrid scale, where the capture rate of individuals was related more to continuity than just total cover of bulrush. Moreover, these patterns were consistent irrespective of density or season.

There are several potential explanations why Amargosa voles show such a high degree of habitat specialization, including favorable microclimatic conditions, differing food resources, reduction in competition, lack of access to alternative habitats, and predator avoidance. Voles in general lack physiological and anatomical adaptations that would allow them to tolerate high temperatures (Carleton, 1985; Rose and Birney, 1985), and the Amargosa vole occurs in one of the driest and hottest environments in North America. This explains why the vole occurs only in wetland habitats, but it is not a satisfactory explanation for why it seldom occurs in salt grass vegetation. Temperatures at the ground surface are modified considerably from shading by both bulrush and salt grass. In August 2012 we arranged thermometers at 36 stations in patches of bulrush and salt grass. We recorded daytime (1400–1600 h) mean temperatures of 41 °C (±4° SD) at 2 m above ground level in dense patches of bulrush and 44 °C (±2° SD) at 2 m above ground level in dense patches of salt grass (R. Klinger, unpubl. data). However, at ground level, temperatures were 30 °C (±2° SD) in bulrush and 32 °C (±3° SD) in salt grass. Moreover, voles adjusted their activity to shifts in temperature; captures were common during the morning and afternoon hours January through March but were infrequent during those hours in April and May. Given the similarity in temperatures between bulrush and salt grass patches and seasonal shifts in their activity times, differing microclimatic conditions is an unlikely reason for the vole's habitat specialization.

Food availability can have a strong effect on population dynamics and habitat selection of voles (Ford and Pitelka, 1984; Turchin and Batzli, 2001; Morris and MacEachern, 2010). While we did not measure food resources, the wetland

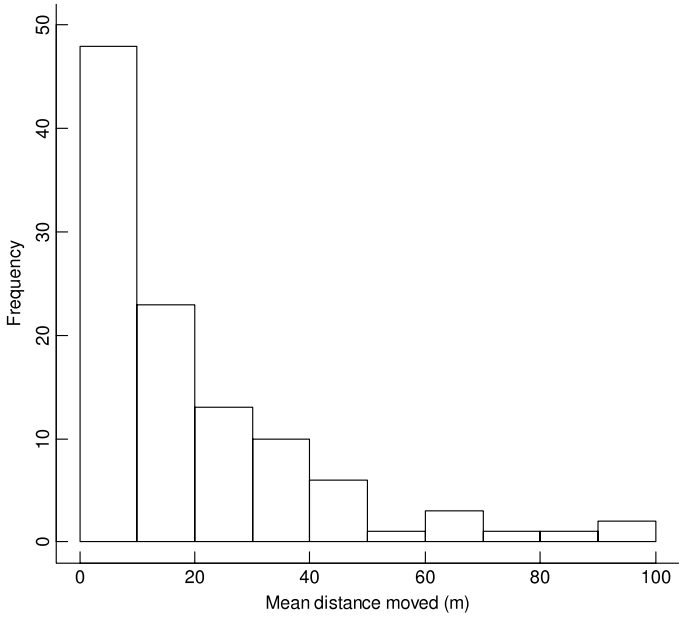

Fig. 8. Frequency distribution of the mean distance moved by 131 Amargosa voles (*Microtus californicus scirpensis*) captured at least twice in six grids where they were trapped in the lower Amargosa River Valley, Inyo County, California, January–May 2012.

areas inhabited by the vole are the most productive communities in the lower Amargosa River valley. Voles are generalist herbivores that feed on leaves, shoots, roots, and seeds of many plant species (Batzli and Pitelka, 1971; Gill, 1977; Batzli, 1985). Bulrush and salt grass are relatively dry during the winter, but leaves and moist roots are still abundant. Preliminary cafeteria feeding trials of captive Amargosa voles indicate they feed on the culms and rhizomes of bulrush but not salt grass (J. Foley, U.C. Davis, pers. comm.). Green shoots and seeds of other plant species become available in the spring and are abundant through the mid-summer. Animals captured in both seasons were generally in good body condition and showed little evidence of nutritional stress, and their abundance was greatest in the late spring (Klinger et al. *in prep*). This implies that there could be a link between food availability and the population dynamics of the vole. But, while we think it would be premature to rule out a link between availability of food resources and the Amargosa vole's habitat specificity, evidence for it being an important factor is not strong.

It is unlikely that competition from other rodents is influencing the vole's habitat selection patterns. Out of 16,200 trap nights, only two other species were captured in the study; house mice (*Mus musculus*) and western harvest mice (*Reithrodontomys megalotis*). Only two house mice were captured during the study, and while western harvest mice were captured in all of the grids their abundance was low and they tended to occur in grids and subgrids without voles. This is consistent with studies of sympatric voles and western harvest mice in grasslands in the Coast Ranges of California, which have repeatedly reported voles being the dominant competitor and displacing western harvest mice (Blaustein, 1980; Heske et al., 1984; Heske and Repp, 1986).

Salt grass forms extensive stands that are intermixed with stands of bulrush throughout the lower Amargosa River valley, so voles have ready access to both types. California voles use grassland communities intermixed with wetlands in other parts of their range (Getz, 1985), but there is little evidence of Amargosa voles persisting in other wetland vegetation types, including patches of Cooper's rush, alkali heath, common reed (*Phragmites australis* Cav.), or cattail (*Typha latifolia* L.). McClenaghan and Montgomery (1998) reported trapping voles in a patch of marsh dominated by Cooper's rush, but this was only 1 of 51 sites where they searched for them. Our findings and those of other studies (Bleich, 1979; McClenaghan and Montgomery, 1998, CDFW pers. comm) consistently indicate that, while Amargosa voles occasionally occur in other vegetation types, their persistence in these types is ephemeral. Thus, lack of access to other habitat types does not appear to be a plausible explanation of their selection behavior.

We suggest that structural differences between bulrush and salt grass dominated vegetation provides the most likely explanation of the strong selection the Amargosa vole has for bulrush. Predation can be an extremely important influence on vole populations (Turchin and Hanski, 1997; Korpimaki et al., 2002; Sundell, 2006), and their habitat use patterns can vary according to predation intensity (Sundell et al., 2012). Although we did not formally collect data on predation, much of the evidence strongly suggests that habitat selection by the Amargosa vole is predator-mediated. We observed three incidents of predation on Amargosa voles by great blue herons (*Ardea herodias*; Ardeidae), American bittern (*Botaurus lentiginosus*; Ardeidae), and coyotes (*Canis latrans*; Canidae), and at least nine other potential mammalian and avian predators occur along the lower Amargosa River. We hypothesize that the combination of fragmented vegetation, number of predator species, and few alternative prey species has resulted in predation intensity on the Amargosa vole that is so high they have been forced

to restrict their habitat use to patches of bulrush. Voles occurred in patches of mixed bulrush/salt grass, but persistence in these areas was low. Moreover, within subgrids with low or moderate levels of bulrush cover, voles were captured at trap stations where cover of bulrush was high. Salt grass patches are often dense, uniform and thick, but the canopy is usually 1.5–2.0 m lower than bulrush and has a much sparser, shallower cover of litter. We strongly suspect if predation intensity were lower the vole would use other vegetation types, particularly salt grass patches. But in the lower Amargosa River valley bulrush patches are likely the only type of vegetation structurally complex enough to provide them with adequate cover from predation.

Although it is apparent that the vole is closely tied to bulrush, their patchy distribution is not entirely explained by their habitat selection behavior. Genetic evidence suggests that there is limited dispersal among segments of the voles population (Neuwald, 2010), which is consistent with our data on the proportion of area used by the voles and the distances they moved. The proportion of area they used within the 1 ha sites was low, and the RDA's clearly showed that many patches of what appeared to be suitable habitat were not occupied by voles. Voles were capable of moving relatively long distances but this occurred infrequently; site fidelity was generally strong, most individuals moved only short distances, and the movements were usually within patches of bulrush. This suggests that dispersal limitation is interacting with availability of bulrush cover to structure the distribution of the vole along the lower Amargosa River.

The scale independent habitat selection behavior of the vole has important implications for long-term persistence of their population. An animal's habitat selection behavior is a response to the interactive effects of abiotic conditions, biotic interactions, and resource availability that, ultimately, should maximize its fitness (Morris et al., 2001). In all likelihood the vole's highly selective habitat use behavior maximizes fitness because individuals that use dense stands of bulrush are more likely to survive and reproduce than those that occur in stands with sparser cover. While this may benefit individuals though, it creates a potentially precarious situation for the population. Our study indicates a combination of disjunct and often small bulrush stands, predation, and limited dispersal by voles results in many unoccupied patches, small populations within most of the patches that are occupied, and greatly reduced chances of rescue effects (Gotelli, 1991). It is unlikely the distribution of bulrush in the Amargosa River Valley was ever extensive and yet the vole has persisted there for millennia. But as the loss of bulrush stands in the Amargosa River Valley over the last century show, the voles are highly vulnerable to further loss or degradation of the habitat type that it is able to maintain populations in.

Because bulrush appears to be the highest quality habitat available to the vole and there is evidence they have always preferred it to other types, it does not meet the definitions of being an ecological (Robertson and Hutto, 2006) or evolutionary trap (Schlaepfer et al., 2002). However, the limited distribution of bulrush has resulted in the vole functionally being "trapped". They are confined to wetland areas in the Amargosa watershed because temperature and moisture regimes impose severe physiological constraints on them. Several types of wetland vegetation occur in the watershed and are available to the vole, but, if our hypothesis is correct, predation acts as the main proximate factor that drives their habitat selection and confines them to bulrush dominated vegetation. Finally, their limited movements prevent them from occupying a higher proportion of suitable bulrush habitat. If this scenario is true, the Amargosa vole could be a species whose habitat selection behavior confers considerable individual benefits but may not allow them to persist in a changing environment. More broadly, they are likely representative of many species that tend to be habitat specialists in having high exposure and low adaptive capacity to changes in the environment (Foden et al., 2013).

The short duration of the study imposes some limitations on the inferences we can make. One is it is possible that what we are interpreting as habitat selection is more an artifact of undetected demographic processes. Specifically, voles could be using salt grass but are being predated on before being observed in salt grass. We think this is highly unlikely though. Our trapping only spanned six months but we had a reasonably high number of large grids that spanned a gradient in habitat conditions. Moreover, the trapping grids were designed specifically to detect voles in multiple vegetation types. And, as mentioned above, we consistently trapped voles in bulrush regardless of scale. Out of 16,200 trap nights, if voles had been moving into salt grass we almost certainly would have captured more in that vegetation type. Furthermore, even though they tended to be biased towards bulrush vegetation, previous studies also found infrequent use of vegetation other than bulrush. Finally, habitat selection has likely evolved to maximize an organism's fitness, and survival is a fundamental component of fitness. Therefore, habitat selection and demographic processes are not independent and vital rates will generally reflect where organisms occur in their environment (Morris, 2003).

A more serious limitation was our ability to evaluate the role that density-dependent habitat selection could play in the patterns we observed. Spatial and temporal densities of the Amargosa vole varied >7x, which suggests that their selection for bulrush was density-independent. Voles in general though are well-recognized to reach densities well above those we observed in this study (Taitt and Krebs, 1985). It is possible then that if the Amargosa vole reached such densities they would occur more frequently in vegetation types other than bulrush. However, the duration of periods when voles reach very high abundance tend to be short and we strongly suspect that the densities we observed during our study were likely representative of those the Amargosa vole typically achieves. In addition, movement into sub-optimal salt grass vegetation during periods of very high abundance would likely be better interpreted as evidence of source–sink dynamics (Pulliam, 1988) than density-dependent habitat selection (Morris, 2003). Nevertheless, periods of very high abundance when Amargosa voles might disperse into other vegetation types could decouple the interaction among predation, limited dispersal, and habitat fragmentation that we hypothesize is the underlying dynamic in their habitat selection behavior. It is during these times when inter-patch dispersal might be high enough to maintain gene flow among sub-populations.

5. Conservation implications

The greatest threat to the Amargosa vole is further loss or deterioration in quality of bulrush stands. *Schoenoplectus americanus* occurs across much of North America in a broad range of climatic conditions, but stands are susceptible to drying, especially in arid regions (Shupe et al., 1986). In the lower Amargosa watershed there are several real and potential threats to stands of bulrush, including water diversions for road maintenance, renewable energy development, and climate shifts. Local and regional threats (water diversions and renewable energy projects) could potentially be mitigated, but climate shifts in the Mojave ecoregion (Redmond et al., 2009) are a very serious long-term problem. The Bureau of Land Management is in the process of developing management plans for the lower Amargosa River, and a vulnerability assessment of the bulrush stands and potential marsh restoration would be crucial components of the plans. Not only could they increase the likelihood of persistence of the vole, but they would likely benefit many other species as well.

It is apparent that its highly restricted range, limited and fragmented habitat, low abundance, and dependence on bulrush make the Amargosa vole one of the most endangered mammals in North America. Long term habitat management will be essential if they are to persist, but there are more immediate actions that could be taken as well. Population viability analyses (PVA) would provide models and insights for designing translocation and reintroduction programs, and exclosures could be used in a field experiment to test our hypothesis of the interaction among predation, dispersal, and habitat use. The exclosures could also be used as protected source areas for translocations and reintroductions, and animals from a captive breeding program could be used as stock in those programs.

Despite being highly threatened, it is important to note that the Amargosa vole has persisted for millennia. There has been substantial climatic variability during this time and likely dynamics in the vole's habitat. In terms of vulnerability, it may be that the vole has high exposure and low adaptive capacity. But there is substantial indirect evidence indicating it may not be as sensitive to extinction as might be initially presumed. This provides optimism that an integrated program consisting of captive breeding, translocation, and habitat management could be successful in helping the Amargosa vole persist well into the future.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.gecco.2014.10.003.

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