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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.

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 × 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