Understanding Habitat Quality for Preble’s Meadow Jumping Mouse: How Survival Responds to Vegetation Structure and Composition

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Introduction

Habitat loss and modification are the leading causes of, and challenges to, recovery of rare species (Wilcove et al. 1998; Kerr and Deguise 2004). Thus, understanding habitat suitability and the value certain habitat components have for species’ persistence are important to identifying what habitat modifications are detrimental to species survival (Morris 2003). Habitat descriptions for rare species tend to focus on general vegetative composition, but species-specific needs are more complex (Lindenmayer and Fischer 2006). Tying survival rate...
to habitat components can clarify species’ distribution, viability in different habitats, and conditions for successful habitat improvement (Morrison et al. 1998; Bergman et al. 2014). Researchers have investigated the importance of habitat composition and quality, and their impact on individual survival (Franklin et al. 2000; Breininger et al. 2009), yet for many rare species there is a lack of understanding of the various habitat components and their influence on demographic rates.

The Preble’s meadow jumping mouse *Zapus hudsonius preblei* (PMJM) is a small (< 30 g) rodent (Figure 1A) found in riparian shrublands (Figures 1B and 1C) and wetlands along the Front Range of Colorado and southeastern Wyoming (USFWS 1998). In 1998, PMJM was listed as Threatened under the U.S. Endangered Species Act (ESA 1973, as amended) because of habitat loss and alteration throughout a majority of its range (USFWS 1998). Development along Colorado’s Front Range in the late 1990s and early 2000s was at its highest levels (Baron et al. 2004) when riparian systems, and likely PMJM populations, became more fragmented and isolated (Wohl 2001). Most accounts of PMJM habitat describe it as riparian corridors with dense shrub cover, limited forest canopy, and dense, diverse herbaceous ground cover (Bakeman 1997; Schorr 2003; Trainor et al. 2007). Researchers have investigated the demography of PMJM at select locations (Meaney et al. 2003; Schorr 2012), but there is little understanding of how vegetation components impact parameters, such as survival, abundance, and population change.

The PMJM population along Monument Creek at the U.S. Air Force Academy (Academy) Colorado Springs, Colorado, has undergone the longest-running vegetation and population sampling for PMJM (Schorr et al. 2009). The Academy has 25 km of creeks lined with dense riparian vegetation, which includes cottonwoods *Populus angustifolia* and *Populus deltoides*, various willows *Salix* spp., snowberry *Symphoricarpos occidentalis*, wild rose *Rosa woodsii*, currant *Ribes* spp., and forbs and grasses. The adjacent uplands are mixed grasslands and ponderosa pine *Pinus ponderosa* woodlands with scrub oak *Quercus gambelii*, mountain mahogany *Cercocarpus montanus*, and chokecherry *Prunus virginiana*. Because PMJM are found along many of the stream systems at the Academy, the Academy’s riparian habitats are considered essential for PMJM conservation, but critical habitat is not designated on the installation due to an agreement between the Department of Defense and the U.S. Fish and Wildlife Service (USFWS 2003). We conducted this study along a 7.5-km stretch of Monument Creek at the Academy. Monument Creek is fed by snowmelt and rainfall, with peak flows in midsummer, which average approximately 2.5 m³ s⁻¹ d⁻¹ for the month of June (1985–2004 streamflow data; Kuhn and Arnold 2006). The riparian shrubland habitat along Monument Creek can vary in width from 10 m to more than 100 m because of the natural impacts from beaver dams, periodic flooding, and geology.

**Methods**

**Population and habitat sampling**

We trapped PMJM using four randomly placed permanent transect sets placed along and parallel to
the flow of Monument Creek. Each transect set was two parallel 40-station transects (80 traps total) that were approximately 270 m long, with traps within 20 m of the stream bank. We chose this study area to avoid the trail system to the south and ongoing military training maneuvers to the north. We set one Sherman live trap (7.6 × 8.9 × 22.9 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) at each station, baited it with whole oats, and added polyester batting for insulation. We set traps for five to seven nights in late summer (typically in August, with 2 y extending into early September) from 2000 to 2013. We set traps prior to sunset and checked them the following morning after sunrise. We determined the sex and weight of each PMJM and marked it with a passive integrated transponder (PIT) tag (TX 1406-L sterile tags; Biomark, Inc., Boise, ID). We conducted all work in compliance with institutional guidelines concerning the use of animals in research, including threatened species, as well as all handling requirements under these guidelines (Colorado State University Institutional Animal Care and Use Committee permit 12-3193). We sampled PMJM under authority of the Colorado Division of Wildlife (permit TR976), and the USFWS (permit TE-059369).

For the duration of the study, we collected data on vegetation characteristics at the same six randomly selected trap locations along each transect set (n = 24 per year) in mid-July annually, except in 2008, 2009, and 2011. In each cardinal direction and within a 0.04-ha circular plot (James and Shugart 1970) we recorded canopy cover using a spherical densiometer (n = 24 per transect set per year), shrub density (shrub stems > 1 m tall; n = 24 per transect set per year), and vertical vegetation density. We measured vertical vegetation density using a 0.5- × 3.0-m vertical cover board by estimating the amount of green vegetation obscuring each 0.5- × 0.5-m space (0.0–0.5 m, 0.5–1.0 m, etc.) along the vertical cover board up to 3 m above ground (n = 24 per transect set per year). Shrub density reflected the density of stems above the herbaceous layer (~ 1 m), while vertical vegetation density depicted the height of the shrub cover. Within each circular plot we recorded the number and diameter at breast height (dbh) of canopy trees with dbh > 5 cm (n = 6 per transect set per year), and number of pieces of downed woody debris > 3 cm (n = 6 per transect set per year). Also, at 13 locations (center, and 3, 6, and 9 m along each cardinal direction) within the circular plot we collected measurements of percentage of ground cover of forb, graminoid (grass, sedge, rush; herein called “grass”), rock and soil, moss and lichen, litter (leaves and pine needles), and woody debris (branches and bark) using a 0.1-m² sampling frame (Daubenmire 1959). We allowed estimates of total ground cover to exceed 100% at a plot if some components overlapped. To reduce variability in estimates, the same person (R.A.S.) collected all vegetation measurements over all years of the study.

Models and analysis

We analyzed mark–recapture data using Huggins robust design (Huggins 1989) in Program MARK (Kendall 2001; Data S1, Supplemental Material). The robust design model allows estimation of apparent survival (\(\phi\)), capture probability (\(p\)), recapture probability (\(c\)), probability of returning to the study area given the animal was previously away from the study area (temporary immigration, 1 – \(\gamma\)), and the probability of leaving the study area given an animal is currently in the study area \(\gamma\), temporary emigration). We compared models using Akaike’s information criterion with small sample size bias correction (AIC\(_c\)) and the probability of a model being the most parsimonious model in the model set (AIC\(_c\) weights, \(w_c\); Burnham and Anderson 2002). We modeled \(p\) and \(c\) as trends by year based on models’ previous analysis (Schorr 2012), and model-averaged estimates of parameters over all models to incorporate model selection variability (Burnham and Anderson 2002). We have expressed standard errors (SEs) from model-averaged estimates as “unconditional SE” suggesting that the variance estimates used are not conditioned on the best model, but are weighted by the models having the most support (Burnham and Anderson 2002). We used body mass of PMJM as an individual covariate, and analyzed sex as a group covariate in MARK.

Several droughts occurred during this study, so we used environmental covariates of annual (October to September) rainfall, total precipitation, and snowfall of the previous year and current year (Strategic Climatic Information Center, Air Force Academy Combat Climatology Center, Colorado Springs, CO) to model \(\phi\). Also, we used covariates of total captures of North American deer mice Peromyscus maniculatus, meadow voles Microtus pennsylvanicus, western harvest mice Reithrodonotomys megalotis, and PMJM from the previous and current year, because these species may compete with or have density-dependent impacts on Z. hudsonius (Boonstra and Hoyle 1986; Dueser and Porter 1986).

We used vegetation characteristics from the previous and current year to clarify the role of vegetation structure in PMJM \(\phi\) (Data S2, Supplemental Material). Prior to deciding which vegetation measurements to use as covariates, we assessed correlations among the measurements \((R < 0.50)\). Because of high correlations \((R > 0.60)\) among vertical vegetation measurements, we only used the measurement of vertical vegetation density from 2.5 to 3.0 m. We used mean total of vegetation estimates at each transect set per year as the covariates to estimate \(\phi\). We modeled annual PMJM \(\phi\) using number of canopy trees, total shrub count, total vertical vegetation cover, vertical vegetation density (2.5–3.0 m), total grass ground cover, total forb ground cover, total bare soil ground cover, total woody debris ground cover, total litter ground cover, total moss and lichen ground cover, and total woody debris. For those years when we did not conduct vegetation sampling (2008, 2009, 2011) we used the mean of all years of each
particular vegetation covariate for that missing year. We ran over 130 models of small mammal captures, weather covariates, and vegetation characteristics to model PMJM/.

**Results**

Deer mice were the most frequently captured species, accounting for 56% of captures (4,441), while meadow voles accounted for 26% of captures (2,075). We recorded 1,159 captures (15% of captures) of 499 PMJM over the 14 y (Figure 2). Western harvest mice accounted for 3% of captures (218), while montane shrews *Sorex monticolus*, long-tailed weasels *Mustela frenata*, and silky pocket mice *Perognathus flavus* accounted for less than 2% of captures. We did not include 10 PMJM that died during trapping or handling in the analysis. Sample size for mark–recapture analysis was 489 individuals with an effective sample size (captures and recaptures) of 1,133.

Different components dominated ground cover vegetation over the course of the study. During dramatic drought years of 2000, 2002, and 2006, leaf litter in the form of dead grass dominated the ground cover (Figure 3A). After the first couple of years of the study, when precipitation was below normal (Schorr 2012) forb cover dominated, but it generally was approximately 35% of the ground cover component over the 14 y. Grass cover varied during the study but was generally 30% of the ground cover, becoming more prominent later in the study (Figure 3A). Bare ground (typically sand and small rock) was a major component of the ground cover in 2000, but decreased as other vegetative or litter components increased (Figure 3A). Mean shrub density ranged from 225 to 350 stems per plot (Figure 3B), while percentage of vertical cover (2.5–3.0 m) was usually greater than 20% (Figure 3C). The two metrics did not track each other perfectly, with shrub density being high in some years (2000, 2001), but not consistently reaching the heights seen in 2007 and 2010. Because there were few canopy trees and minimal overstory canopy cover, these data were not valuable predictors and we do not present them in the figures.

The best model ($w_i = 0.64$) used the group covariate of sex, the individual covariate of body mass, environmental covariates of annual precipitation and captures of meadow voles, and vegetation covariates of shrub...
density and grass cover (Table 1). The next best model ($w_s = 0.21$) is similar to the top model, but included the impacts of previous year’s snowfall on $\phi$. The support for the rest of the models was minimal with the next most supported model using covariates of sex, mass, vertical vegetation cover, grass cover, shrub density, precipitation, and vole captures for $\phi$ ($w_s = 0.07$). All other models carried $w_s < 0.05$ (Table 1).

Mean annual PMJM $\phi$ is low, with female mean $\phi$ (0.11 ± 0.005 SE) greater than male mean $\phi$ (0.07 ± 0.004 SE). Estimates of survival varied annually from less than 0.03 from 2003 to 2005 to greater than 0.30 between 2007 and 2008 and 2009 and 2010 (Figure 4). Annual survival increased with body mass (males: logit $\beta = 1.63 \pm 0.45$ SE; females: logit $\beta = 0.93 \pm 0.16$ SE), grass cover (males: logit $\beta = 0.002 \pm 0.001$ SE; females: logit $\beta = 0.005 \pm 0.001$ SE), and shrub density (males: logit $\beta = 0.004 \pm 0.001$ SE; females: logit $\beta = 0.004 \pm 0.001$ SE). Annual survival decreased with current-year precipitation (males: logit $\beta = -0.87 \pm 0.24$ SE; females: logit $\beta = -0.49 \pm 0.12$ SE) and vole captures (males: logit $\beta = -0.022 \pm 0.006$ SE; females: logit $\beta = -0.014 \pm 0.003$ SE).

**Discussion**

The most important driver of PMJM survival rate at the Academy is individual condition (Schorr et al. 2009; Schorr 2012). As with many hibernating mammals, body mass and fat mass are vital for overwinter survival (Murie and Boag 1984; Geiser and Baudinette 1990), and small hibernators may have a greater physiological need for maintaining comparatively larger body mass (French 1988). Although winter survival for hibernators may be less limiting than active-season survival pressures (Schaub and Vaterlaus-Schlegel 2001; Schorr et al. 2009; Lebl et al. 2011), adequate size and fat reserves are important predictors for hibernator survival because they confer overall individual fitness prior to and after hibernation (Humphries et al. 2002). Not surprisingly, the availability of grass cover and shrub cover impacts PMJM survival. Based on habitat descriptions from trapping and telemetry studies, researchers have long suggested that grass cover and shrub cover are vital PMJM habitat components (Bakerman 1997; Clippinger 2002; Schorr 2003; Trainor et al. 2007). This is the first study identifying the influence of these vegetative components on PMJM survival. Grass seeds are valuable feeding resources for jumping mice (Hamilton 1935), and the availability of grass cover may be tied to seasonal dietary needs and refuge from predators (Trainor et al. 2007). These particular riparian vegetation components are important for conserving PMJM, and other riparian-obligate wildlife along the Front Range (Miller et al. 2003). Activities such as excessive grazing (Belsky et al. 1999) and disruptions to natural hydrologic regimes (Poff et al. 1997) that jeopardize the maintenance of this vegetative structure could threaten PMJM survival.

Although the habitat along Monument Creek has been relatively well protected, there are new threats to riparian habitat that impact PMJM survival. In particular, the increased urban development east of the Academy over the past 15–20 y has increased the frequency and severity of flooding events (Lazaro 1990; Wheeler and Evans 2009). Excessive flooding from this increase in hard-surface development has damaged PMJM habitat along the eastern tributaries of the Academy (Kuby et al. 2007; Schorr 2012). This flooding has caused incised creek channels and disconnected floodplains, and has dropped the water table, reducing the viability of the riparian vegetation for PMJM habitat (Possardt and Dodge 1978). Specifically, these impacts make maintenance of both dense herbaceous ground cover and dense shrub cover challenging and expensive (Friedman et al. 1996; Figure 5A–5C). If the frequency and severity

**Table 1.** Akaike’s information criterion for small sample size ($\text{AIC}_c$), $\text{AIC}_c$ difference ($\Delta_i$), model weight ($w_i$), and parameters ($k$) for the most parsimonious models of survival, capture probability, recapture probability, temporary immigration, and temporary emigration of Preble's meadow jumping mouse *Zapus hudsonius preblei* populations along Monument Creek at the U.S. Air Force Academy Colorado Springs, Colorado, from 2000 to 2013. In each model, we modeled capture and recapture probability as a trend each year. We modeled temporary emigration and immigration as constant and equal. MIPE = *Microtus pennsylvanicus*.

| Model name                                                                 | $\text{AIC}_c$ | $\Delta_i$ | $w_i$ | $k$ |
|----------------------------------------------------------------------------|----------------|------------|-------|-----|
| Survival (sex, body mass, grass cover, shrub cover, precipitation, MIPE captures) | 2730.73        | 0.00       | 0.643 | 83  |
| Survival (sex, body mass, grass cover, shrub cover, precipitation, recent snowfall, MIPE captures) | 2732.95        | 2.21       | 0.212 | 85  |
| Survival (sex, body mass, vertical vegetation cover, grass cover, shrub cover, precipitation, MIPE captures) | 2735.29        | 4.55       | 0.066 | 85  |
| Survival (sex, body mass, grass cover, shrub cover, precipitation, past snowfall, MIPE captures) | 2735.37        | 4.64       | 0.063 | 85  |
| Survival (sex, body mass, vertical vegetation cover, grass cover, precipitation, MIPE captures) | 2741.30        | 10.57      | 0.003 | 83  |
of flooding from the surrounding urban development is not controlled it is likely that the erosion and sedimentation, and PMJM habitat loss, will encroach into Monument Creek where a majority of PMJM reside.

The most parsimonious models of PMJM survival included the combination of shrub cover and grass ground cover, suggesting they both need to be present to optimize habitat quality for PMJM. Although grass cover and shrub density are valuable predictors of PMJM survival, it is worth noting that these increases are only within the variability seen at the Academy. We do not believe that increases in grass cover that would preclude the other cover components, such as forbs, would be beneficial for PMJM. Similarly, increases in shrub density that shade out the understory of grass and forbs would likely be detrimental for PMJM (Di Tomaso 1998). In range-wide comparisons, Clippinger (2002) found PMJM-occupied sites had higher plant species diversity, suggesting monocultures of any cover components may not be beneficial for PMJM.

The use of marking techniques that are not permanent can complicate estimates of true survival in small mammals, particularly as this is an assumption of many mark–recapture models, including the robust design (Kendall 2001). For example, studies of deer mice in sage lands of Montana show a high rate (>30%) of PIT tag loss, and a much lower rate (8%) of ear tag loss (Kuenzi et al. 2005), while studies of kangaroo rats Dipodomys spp. of California’s grassy desert plains show lower PIT tag loss (3–9%) compared to ear tag loss (9–15%; Williams et al. 1997). Ear tags were the first marking technique used for PMJM at the Academy, but because of the low retention rate that was based on the number of ripped pinna and few animals with ear tags, and likelihood of induced stress to this threatened subspecies, ear tag use was discontinued in favor or PIT tags. The longest record of PIT tag retention during this study was from an animal captured 4 y after tagging. We assume there is some level of PIT tag loss in PMJM, and there is a concomitant negative impact on survival rate estimates. Further studies will need to clarify this rate of tag loss and its impact on PMJM population parameter estimates.

Findings in this study corroborate the notion that dense grass cover and dense shrub cover are vital components to PMJM habitat. In areas where PMJM habitat has been disrupted, habitat rehabilitation that focuses on restoring the herbaceous understory, the shrub cover, and the hydrology that support them may increase PMJM persistence. Such efforts to mitigate changes to riparian systems have successfully increased vegetation cover and facilitated PMJM recolonization (Bakeman 2005). Additional restoration efforts to connect discontinuous PMJM habitat patches likely will increase the stability of PMJM populations and decrease the timeline for recovery (USFWS 2016).

Supplemental Material

Data S1. Preble’s meadow jumping mouse Zapus hudsonius preblei (PMJM) mark–recapture data from 2000 to 2013 from populations along Monument Creek, U.S. Air Force Academy Colorado Springs, Colorado. Data file (.txt), including description of data used to estimate population parameters for PMJM using a robust design model.

Found at DOI: https://doi.org/10.3996/052018-JFWM-040.S1 (111 KB TXT).

Data S2. Site-specific vegetation covariates from 2000 to 2013 used for modeling Preble’s meadow jumping mouse Zapus hudsonius preblei survival at four sampling
locations along Monument Creek, U.S. Air Force Academy, Colorado Springs, Colorado. Found at DOI: [https://doi.org/10.3996/052018-JFWM-040.S2](https://doi.org/10.3996/052018-JFWM-040.S2) (14 KB XLSX).

**Reference S1.** Bakeman ME. 2005. Monitoring the response of a riparian ecosystem to hydrologic restoration. Report CDOT-DTD-R-2005-10. Colorado Department of Transportation, Denver, Colorado. Found at DOI: [https://doi.org/10.3996/052018-JFWM-040.S3](https://doi.org/10.3996/052018-JFWM-040.S3) (668 KB PDF); also available at: [https://www.codot.gov/programs/research/pdfs/2005/riparian.pdf](https://www.codot.gov/programs/research/pdfs/2005/riparian.pdf).

**Reference S2.** Schorr RA. 2003. Meadow jumping mice (Zapus hudsonius preblei) on the U.S. Air Force Academy, El Paso County, Colorado: populations, movement, and habitat from 2000–2002. Report of Colorado Natural Heritage Program, Colorado State University to U.S. Air Force Academy, Fort Collins, Colorado. Found at DOI: [https://doi.org/10.3996/052018-JFWM-040.S4](https://doi.org/10.3996/052018-JFWM-040.S4) (993 KB PDF); also available at: [http://www.cnhp.colostate.edu/download/documents/2003/AFA_PMJM_2003_report.pdf](http://www.cnhp.colostate.edu/download/documents/2003/AFA_PMJM_2003_report.pdf).

**Acknowledgments**

We are grateful to J.L. Siemers, R.A. Weidmann, J.R. Sovell, and C.M. Hansen for their time, effort, and input on the project. We thank J. Zahratka, D. Middleton, C. Werner, J. Rocchio, R. Gorning, T. Assall, C. Gaughan, A. Kilgore, J. Healy, M. McGee, A. Wagner, J. Ehrenberger, J. Unrein, C. Puntenney, and E. Vavra for their time, effort, and care during field sampling. We thank the Associate Editor, and two Journal Reviewers because their candor improved this manuscript. Funding for this work was provided by the U.S. Fish and Wildlife Service and the U.S. Air Force.

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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