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Using a temporal symmetry model to assess population change and recruitment in the Preble's meadow jumping mouse (*Zapus hudsonius preblei*)

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The Preble's meadow jumping mouse (*Zapus hudsonius preblei* [PMJM]) is a rare rodent of southeastern Wyoming and central Colorado that has been the center of debates regarding subspecies' genetic identity and the application of the Endangered Species Act. I analyzed a 7-year PMJM mark–recapture data set using a temporal symmetry model (Pradel model) to estimate apparent survival (φ), recruitment (*f*), population change (λ), and vital rate influence on λ. Deer mouse (*Peromyscus maniculatus*) captures depressed φ, suggesting that competition for resources may decrease PMJM survival. Vole-mediated habitat changes or voles' affinity for quality riparian habitats may explain why PMJM φ and *f* increased with meadow vole (*Microtus pennsylvanicus*) captures. Based on early-summer and late-summer sampling from 2000 to 2006, λ estimates were 0.87 ± 0.06 *SE* and 0.87 ± 0.11 *SE*, respectively, and *f* had a greater influence on λ than did φ. This PMJM population is losing connectivity to eastern, northern, and southern tributaries from habitat degradation and storm-water and municipal runoff erosion. The loss of the adjoining habitat and the PMJMs that were supported by this habitat prevents new recruitment via immigration. Because of the importance of recruitment to PMJM population stability, tributaries and the riparian habitat along these tributaries are vital to PMJM conservation. Scale-appropriate habitat sampling, assessments of reproductive success, and detailed demographic studies to estimate vital demographic parameters will help identify how particular habitat components impact fecundity and immigration.

Key words: apparent survival, lambda, population change, Pradel model, Preble's meadow jumping mouse, recruitment, *Zapus hudsonius preblei*

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Conservation and recovery plans, delisting protocols, and management strategies for threatened and endangered species typically recommend empirical estimates of population change over time (United States Fish and Wildlife Service 2010a, 2010b). Such estimates provide information for assessing the status of populations, modifying management practices, and updating conservation status and priority (Gerber et al. 2007; Sibly and Hone 2002). For many rare species, initial assessments of listing status are based on changes in distribution or occurrence rather than quantitative assessments of population change (Millsap et al. 1998; Ryon 1996); thus, there is uncertainty as to whether reductions in distribution or occurrence accurately reflect population decline (Cade et al. 1997; Martin et al. 2007). When population change has been investigated, the most common method has been the use of population projection matrices to estimate population growth rate (λ—Caswell 2001). An alternate tool for assessing population change is via direct estimation and modeling of λ using live-capture data (Dreitz et al. 2002; Franklin et al. 2004). The use of live-capture data with mark–recapture models can address sampling variation directly, allow incorporation of individual covariates, and provide temporal estimates of λ (Franklin 2001; Nichols and Hines 2002). Most importantly, these models allow the decomposition of estimated variance into sampling and process variation, thus depicting true population trend (White et al. 2002). The Pradel model is a temporal symmetry model that uses a forward-time model for survival and a reverse-time model for recruitment that, by extension, can estimate λ directly (Pradel 1996;

Williams et al. 2001). Estimates of λ from the Pradel model are comparable to estimates from other techniques (Sandercock and Beissinger 2002), but the Pradel model incorporates changes from immigration (Franklin et al. 2004), allows vital rate comparisons using the model parameters (Nichols et al. 2000), and is robust to animal tag loss (Rotella and Hines 2005), all without the laborious requirement of estimating abundance (Sandercock 2006).

Understanding which vital rate has the greatest influence on λ can be the most valuable information for determining management needs (Heppell et al. 2000a). Analogous to elasticity in matrix-based models, the proportional contribution parameter (γ) for temporal symmetry models can be used to understand the relative contribution of recruitment (f) and apparent survival (φ) to λ (Nichols and Hines 2002). The proportional contribution parameter is time-interval specific and, thus, allows better understanding of temporal dynamics of vital rate influence on λ (Nichols and Hines 2002). Yet γ is restricted to retrospective analysis of vital rate contribution and is not used for projecting contribution into the future (Nichols et al. 2000). The use of temporal symmetry models to study population growth in mammals is increasing (Currey et al. 2010; Lima et al. 2003; Ozgul et al. 2006), but there are fewer applications to rare mammal species (but see Lachish et al. 2007; Lampila et al. 2009).

The Preble's meadow jumping mouse (*Zapus hudsonius preblei* [PMJM]) is a threatened subspecies that occupies riparian shrublands and wetlands adjacent to river corridors along the Front Range of Colorado and southeastern Wyoming (United States Fish and Wildlife Service 1998). Like other jumping mice (Frey and Malaney 2009; Vignieri 2005), PMJMs spend much of their time within the dense cover of wetland and riparian systems, but can disperse >4 km along these linear systems (Schorr 2003). Conservation interest in PMJMs began because of the inability to capture PMJMs at historic populations and because of the rate of habitat loss within PMJM range (Ryon 1996; United States Fish and Wildlife Service 1998). Since being listed as "threatened" under the United States Endangered Species Act, PMJM has become one of the most controversial subspecies in Endangered Species Act history. During the late 1990s, when development along Colorado's Front Range was at its highest levels (Baron et al. 2004), conservation of PMJM habitat was projected to halt Colorado's economy (Woodbury 1998). Then, in 2003, debates on the validity of PMJM taxonomy drove arguments for delisting the subspecies (Ramey et al. 2005). Although genetic identity has been clarified (Brosi and Biber 2008; King et al. 2006; Vignieri et al. 2006), it is unclear whether PMJM population trends warrant continued conservation. Most arguments for PMJM conservation have focused on the mouse's habitat specialization, the limited availability of such habitat, and the declining condition of these habitats with increased urbanization (Miller et al. 2003; United States Fish and Wildlife Service 1998). What are lacking are estimates of PMJM population change that would clarify the health of populations and identify populations at risk.

One of the larger PMJM populations is found along Monument Creek and its tributaries at the United States Air Force Academy (hereafter, Academy), Colorado Springs, Colorado (Schorr 2003). This population represents the southernmost extent of PMJM and it is geographically isolated from populations to the north by Palmer Divide and the town of Monument, Colorado. The Academy's PMJM population is of particular conservation importance because of its large size, taxonomic uniqueness, and the expanse and quality of PMJM habitat on the Academy (Grunau et al. 1999; King et al. 2006; Schorr 2003). Being an obligate hibernator, PMJM experiences higher survival rates in winter than in summer, and overwinter survival is enhanced by long, stable winters (Schorr et al. 2009). The Academy PMJM population is at the southern extent of the subspecies' range and is subjected to shorter winters and longer summers than northern populations. Thus, changes in climatic conditions may impact persistence of southern PMJM populations disproportionately (Beever et al. 2010).

I conducted a mark–recapture study to assess PMJM apparent survival, recruitment, and population change along Monument Creek at the Academy. The intent of this project was to assess the growth rate of the southernmost PMJM population using λ, incorporate environmental and site-specific covariates to refine λ estimates, and identify the most influential vital rates on λ.

Materials and Methods

Study area.—This study was conducted at the Academy, a 7,285-ha education and military training facility located north of Colorado Springs, Colorado (39°00′N, 104°50′W, elevation = 1,940–2,620 m). With 25 km of creeks lined with dense riparian vegetation, the Academy is home to one of the largest PMJM populations (Grunau et al. 1999; Schorr 2003). Animals were sampled from within the broad floodplains of cottonwoods (*Populus angustifolia* and *P. deltoides*), various willows (*Salix* spp.), snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa woodsii*), currant (*Ribes* spp.), and forbs and grasses. The adjacent uplands were mixed grasslands and Ponderosa pine (*Pinus ponderosa*) woodlands with scrub oak (*Quercus gambelii*) and choke cherry (*Prunus virginiana*).

Sampling.—Technicians and I trapped PMJMs using 4 transect sets randomly placed along a 7.5-km segment of Monument Creek. Each transect set was 2 parallel 40-station transects that were 270-m long. I selected this segment of Monument Creek because it was free from pedestrian and bicycle trails to the south and military training maneuvers to the north. At each station, we baited 1 Sherman live trap (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) with whole oats, and we added a ball of polyester batting for insulation. We positioned transects parallel to the flow of the creek and less than 20 m from the creek. We set traps for 5–7 nights in early summer (late May to mid-June) and in late summer (mid-August to mid-September) from 2000 to 2006. 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 each with a passive integrated transponder tag (TX 1406-L sterile tags; Biomark, Inc., Boise, Idaho).

All fieldwork followed guidelines of the American Society of Mammalogists for the use of wild mammals (Sikes et al. 2011) and was done in compliance with institutional, national, and international guidelines concerning the use of animals in research, including threatened species, as well as all handling requirements under these guidelines (Colorado State University International Animal Care and Use Committee permits 97-183A and 01-122A). I collected PMJMs under authority of the Colorado Division of Wildlife (permit TR976), and the United States Fish and Wildlife Service (permit PRT-704930).

Models and analysis.—I analyzed mark–recapture data using the Pradel robust design model (Pradel 1996) in program MARK (Franklin 2001; White and Burnham 1999). This model allows estimation of λ as a sum of φ and f (birth and immigration—Franklin 2001). Apparent survival is the probability that an animal that has not emigrated from the population is alive at $i + 1$, given it was alive at i (Williams et al. 2001). The Pradel model estimates the realized λ, where λ can be estimated at each time step, instead of as a dominant eigenvalue over a projected matrix model (Nichols and Hines 2002). This model uses a time-forward model to estimate φ, where survival is conditioned on releases at earlier time periods and the fates are evaluated at later time steps. However, for estimating f, the capture history is reversed and an animal's prior history is conditioned on the later capture, allowing direct modeling of recruitment process (Pollock et al. 1974; Pradel 1996). In addition to φ and f, population size, capture probability (p), and recapture (c) probabilities are modeled. The assumptions of the Pradel model are as follow. First, the study area does not change in size or boundary and all animals have some probability of being recaptured throughout the study. Second, there is no permanent behavioral response to trapping. Third, there is little heterogeneity in captures because this can cause bias in time-specific (between time steps) estimations of λ (Franklin 2001; Nichols and Hines 2002). However, heterogeneity produces little bias in single estimates of long-term λ (Nichols and Hines 2002; but see Pradel et al. 2010). The Pradel model is an extension of the general Cormack–Jolly–Seber model that has the following assumptions. First, every marked animal present in the population at the sampling period has the same probability of being sampled. Second, every marked animal in the population following the sampling period has the same probability of survival until the next sampling period. Third, marks are not lost, overlooked, or misidentified. Fourth, sampling periods are very short and recaptured animals are released immediately. Fifth, emigration is permanent. Sixth, the fate of each animal is independent of the fate of other animals (Williams et al. 2001).

I estimated λ separately for early-summer sampling and late-summer sampling to determine whether timing of sampling would produce comparable population trends. Early-summer sampling consistently produced more male captures than female captures because females emerge from hibernation later than males (Schorr et al. 2009). I modeled capture and recapture probability as constant by year, constant over all years, temporal by year (unique by day within a year), an independent trend each year, a consistent trend across years, and as a function of the number of trapping nights each year. Because small mammal capture success can be altered by interspecific interactions (Cummins and Slade 2007), I used the numbers of captures of meadow voles (*Microtus pennsylvanicus*), North American deer mice (*Peromyscus maniculatus*; hereafter, deer mice), and PMJMs as capture and recapture covariates. Previous attempts to model PMJM capture and recapture probabilities using daily environmental covariates of nightly precipitation, moon phase, or temperature did not improve models (Schorr et al. 2009), thus they were not used in this study.

A drought occurred during this study, so I used environmental covariates of annual (October–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, Colorado) to model f and φ. Also, I used covariates of total captures of deer mice, meadow voles, western harvest mice (*Reithrodontomys megalotis*), and PMJMs from the previous and current year to model f and φ, because these species may compete with *Z. hudsonius* (Boonstra and Hoyle 1986; Dueser and Porter 1986). Because rodent population sizes undergo periodic fluctuations (Lindstrom et al. 2001), I modeled f and φ using 2-year, 3-year, and 4-year cycles. Lastly, I modeled f and φ as 7-year trends to identify consistent declines or increases. For determining the relative contribution of φ and f on λ, I calculated γ. If γ is greater than 0.5, φ influences λ more than does f.

I 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 (AIC_c weights—Burnham and Anderson 2002). As a general modeling approach I developed possible models of p and c, then used the most-parsimonious models of p and c (AIC_c weight $> 1\%$) to model f and φ. Estimates of parameters were model-averaged over the best models to incorporate model selection variability (Burnham and Anderson 2002). Standard errors from model-averaged estimates are expressed 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). Variances of the geometric means of early-summer λ and late-summer λ were estimated from the variances of the random-effects (variance components) models that were run for each data set. This variance was selected because it better represented the process variance of λ (Link and Nichols 1994). Unless otherwise noted, the time unit for parameter estimates is per year.

Results

Deer mice were captured most frequently, accounting for 60% of captures (4,744), whereas meadow voles accounted for 20% of captures (1,589). There were 1,309 captures (16% of

TABLE 1.—Akaike's information criterion for small sample size (AIC_c), AIC_c difference (Δ_i), AIC_c model weight (w_i), and parameters (K) for the most-parsimonious models of apparent survival (φ), recruitment (f), capture probability (p), and recapture probability (c) of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) population along Monument Creek at the United States Air Force Academy, El Paso County, Colorado, from 2000 to 2006. MIPE = *Microtus pennsylvanicus*; PEMA = *Peromyscus maniculatus*.

Model name	AIC_c	Δ_i	w_i	K
Early-summer mark–recapture analysis[a]				
φ (year), f (cycle over 2 years)	1,719.66	0.00	0.319	90
φ (year), f (constant over all years)	1,720.02	0.36	0.268	89
φ (year), f (MIPE captures in current year)	1,722.17	2.51	0.091	90
φ (year), f (linear trend over 7 years)	1,722.55	2.89	0.075	90
φ (year), f (PEMA captures in current year)	1,722.57	2.91	0.074	90
φ (year), f (MIPE captures in previous year)	1,722.64	2.98	0.072	90
Late-summer mark–recapture analysis[b]				
φ (PEMA captures in current year), f (MIPE captures in previous year)	1,390.18	0.00	0.292	39
φ (PEMA captures in current year), f (cycle over 3 years)	1,390.70	0.53	0.224	39
φ (PEMA captures in current year), f (MIPE captures in current year)	1,392.70	2.52	0.083	39
φ (MIPE captures in previous year), f (MIPE captures in previous year)	1,392.88	2.71	0.075	39
φ (PEMA captures in current year), f (snowfall in previous year)	1,393.44	3.27	0.057	39
φ (MIPE captures in current year), f (cycle over 3 years)	1,393.58	3.40	0.053	39

[a] p and c were time-dependent parameters.

[b] p and c were modeled as independent trends each year.

captures) of 245 PMJMs. Western harvest mice accounted for 3% of captures (218), whereas montane shrews (*Sorex monticolus*), long-tailed weasels (*Mustela frenata*), and silky pocket mice (*Perognathus flavus*) accounted for <2% of captures. Eight marked PMJMs that died during trapping or handling were not included in the analysis.

For the early-summer analysis, the 2 best models (total AIC_c weight = 0.89) of p and c used time-dependent parameterization. The best model was fully time dependent, whereas the 2nd-best model used time-dependent p and c that were equal. For the late-summer analysis, the best model (total AIC_c weight = 0.99) treated p and c as independent trends each year. Except for late summer 2004 the trend in p was increasing, whereas c was decreasing each year except 2003. This suggests that during most late-summer sampling efforts PMJM initial capture probability increased during the trapping session, but recapture probability decreased over the trapping period. In both the early summer and late summer, c was higher than p, suggesting a trap-happy behavioral response by PMJMs.

For the early-summer analyses of φ and f, there was considerable model uncertainty, with 6 models having AIC_c weight > 0.05 (ΔAIC_c < 3; Table 1). The most-parsimonious model (AIC_c weight = 0.32) had φ varying annually, and f as a 2-year cycle. The 2nd-best model (AIC_c weight = 0.27) matched the best model except f was constant over the 7 years. The 3rd-best model (AIC_c weight = 0.09) used f as a function of meadow vole captures during the current year.

There was similar model uncertainty for the late-summer analysis, with 6 models having AIC_c > 0.05 (ΔAIC_c < 3.5; Table 1). The most-parsimonious model used deer mouse captures of the current year for φ and meadow vole captures from the previous year for f (AIC_c weight = 0.29). The 2nd-best model used deer mouse captures to model φ and a 3-year cycle to model f (AIC_c weight = 0.22), whereas the 3rd-best model used deer mouse captures to model φ and modeled f using meadow vole captures from the current year (AIC_c weight = 0.08; Table 1).

In the early-summer analysis, φ varied annually and f showed a 2-year cycle that was strong (logit-scale $\beta = -0.62 \pm 0.37$ *SE*; normal-scale $\beta = -0.38$). Recruitment alternated between approximately 0.60 (± 0.13 unconditional *SE*) and 0.76 (± 0.19 unconditional *SE*; Fig. 1). Apparent survival showed dramatic annual variability with φ of 2004–2005 being extremely low (0.001 ± 0.01 unconditional *SE*) and φ of 2000–2001 being high (0.41 ± 0.13 unconditional *SE*; Fig. 1). Using the most-parsimonious model, the geometric mean of φ was 0.10 ± 0.07 *SE* and the geometric mean of f was 0.67 ± 0.10 *SE*.

In the late-summer analysis, the most-parsimonious models used covariates of deer mouse captures for φ, but the effect was slight (logit-scale $\beta = -0.007 \pm 0.002$ *SE*; normal-scale $\beta =$

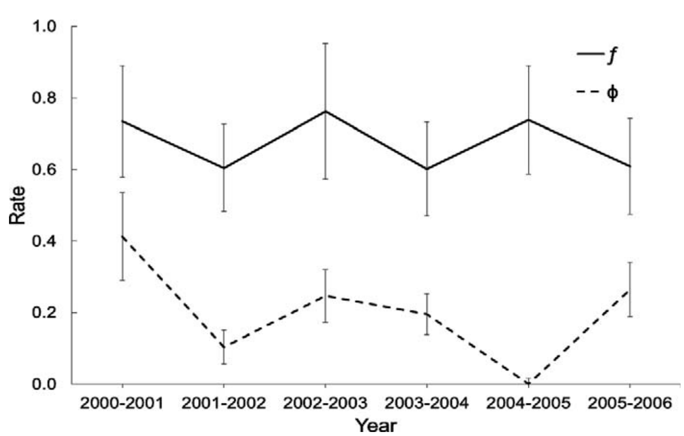

FIG. 1.—Early-summer, model-averaged apparent survival (φ; ± unconditional *SE*) and recruitment (f; ± unconditional *SE*) rates of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) population along Monument Creek, United States Air Force Academy, Colorado Springs, Colorado, 2000–2006.

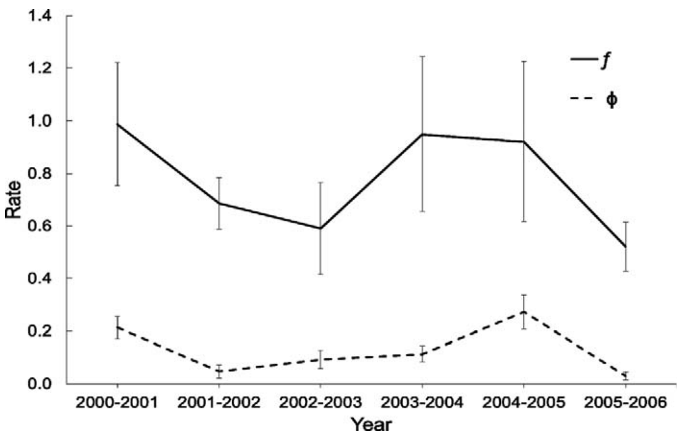

Fig. 2.—Late-summer, model-averaged apparent survival (φ; ± unconditional *SE*) and recruitment (*f*; ± unconditional *SE*) rates of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) population along Monument Creek, United States Air Force Academy, Colorado Springs, Colorado, 2000–2006.

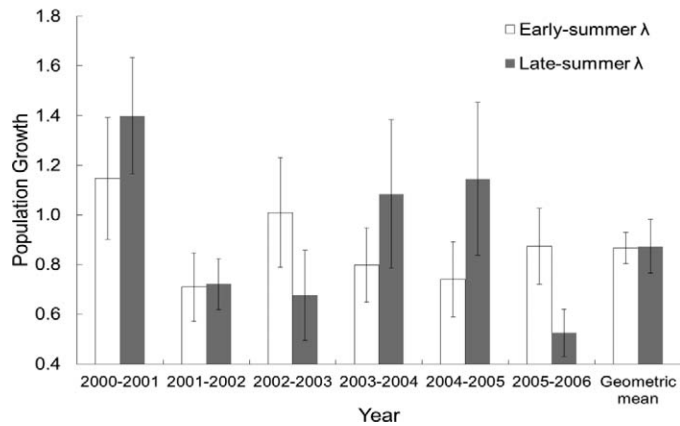

Fig. 3.—Model-averaged (± unconditional *SE*) yearly population increase (λ) of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) population along Monument Creek, United States Air Force Academy, Colorado Springs, Colorado, 2000–2006. Standard error for geometric mean λ is based on process variance *SE* from variance components analysis in program MARK (see "Materials and Methods").

–0.14). For *f*, the slope (logit scale) of the effect from vole captures is 0.003 ± 0.001 *SE* (normal-scale $\beta = 0.37$). In the 2nd-most-parsimonious model, *f* was modeled as a 3-year cycle, and the slope (logit scale) of this effect was –0.40 ± 0.15 *SE* (normal-scale $\beta = -0.34$). Based on the most-parsimonious model, the geometric mean of yearly φ was 0.10 ± 0.05 *SE*, and φ was consistently low (range = 0.03–0.27; Fig. 2). Recruitment showed considerable temporal variation (range = 0.52–0.99; Fig. 2). The geometric mean of yearly *f* was 0.75 ± 0.13 *SE*.

The geometric mean of λ based on early-summer trapping was 0.87 ± 0.06 *SE* (95% confidence interval [95% *CI*]: 0.74, 1.00), whereas the geometric mean of λ based on late-summer trapping was 0.87 ± 0.11 *SE* (95% *CI*: 0.65, 1.09; Fig. 3). Standard error was based on variance components analysis in program MARK (White et al. 2001). From 2000 to 2006, the geometric mean for PMJM γ was 0.11 (± 0.05; range = 0.002–0.360), suggesting that 11% of the individuals in the current year are individuals that survived from the previous year.

Discussion

Estimates of PMJM λ suggest that populations along Monument Creek were declining from 2000 to 2006. Covariates of precipitation were not valuable predictors of φ and *f*, despite annual precipitation averaging 7.8 cm less than normal, and 2002 being the 6th driest year on record. Because grassland seed germination is influenced by current and previous rainfall patterns (Osterheld et al. 2001), I expected changes depicted by these covariates to be reflected in PMJM φ and *f*. As habitat resources are challenged by drought, rodent survival and fecundity can be depressed (Bergallo and Magnusson 1999), and the drought at the Academy was expected to reduce the production of and the ability to detect PMJM's primary food resource, grass and forb seeds (Vander Wall 1998). The drought in 2002 was expected to decrease PMJM survival and fecundity noticeably for that year or the year after; however, the precipitation trough may not have been dramatic enough to cause concomitant responses in PMJM population parameters. Even in desert ecosystems, rodent population dynamics do not always trace precipitation patterns (Brown and Ernest 2002). The riparian habitat in which PMJM are found may provide a forage refuge during drought years. Decreased grass seed production during drought may be mitigated by the soil moisture that can be found near streams and beaver (*Castor canadensis*) dams, and the broad diversity of seeds available in riparian seed banks (Goodson et al. 2001).

Interestingly, estimates of PMJM φ were not impacted by climatic events, but were impacted by captures of sympatric rodents. Competition was expected to decrease PMJM annual φ, which held true for deer mouse captures, but PMJM φ increased with vole captures. Deer mice are the most abundant rodent in riparian areas of the Academy and throughout PMJM range (Meaney et al. 2003; Ryon 1996), and they have the greatest dietary overlap with jumping mice (Maser et al. 1978; Williams 1955), which may influence PMJM survival by reducing the abundance of food items that PMJMs prefer (Bricker et al. 2010). Competition between meadow jumping mice and deer mice has been documented in other areas (Dueser and Porter 1986). When found in greater relative abundance, meadow jumping mice can exclude deer mice (Nichols and Conley 1981), but during no trapping period were deer mouse captures fewer than PMJM captures. Captures of PMJM were typically 34% (± 0.07% *SE*) of deer mouse captures, with several years when PMJM captures were less than 10% of deer mouse captures.

Meadow vole captures were expected to depress PMJM φ because of competition (Adler et al. 1984; Boonstra and Hoyle 1986) and antagonistic behavior (Quimby 1951) between the species. Meadow voles are primarily herbivores, but do demonstrate selective granivory (Howe and Brown 2000).

The slight increase in PMJM φ with vole captures may be a reflection of habitat conditions being simultaneously favorable for both PMJMs and meadow voles. As herbaceous dietary resources increase for the meadow voles, it is likely that the additional seed production from such resources would favor PMJM survival. In bluegrass (*Poa* spp.) meadows of southern Michigan, Blair (1948) found peak meadow jumping mouse abundance following a year with peak meadow vole abundance. Voles can preclude some hardwoods through selective granivory (Ostfeld et al. 1997), delaying succession to drier, mature cottonwood galleries and prolonging the seral stage of dense riparian shrublands that PMJMs prefer (Anderson and Cooper 2000). Also, meadow voles increase forb diversity by selectively foraging on the seeds of some dominant forbs (Howe and Brown 2000), and PMJMs may prefer the variety of food resources created by voles. The increase in PMJM φ may not be influenced by habitat alterations, but rather by changes in predator diet selection when voles are abundant. As vole abundance increases, predators may select voles more frequently (Norrdahl and Korpimäki 2000), thus increasing PMJM φ.

In addition to increasing PMJM φ, meadow voles impacted PMJM *f*. In the early-summer data set, the effect of meadow vole captures was mildly negative (logit $\beta = -0.002 \pm 0.003$ *SE*), and in late summer the effect was mildly positive (logit $\beta = 0.003 \pm 0.001$ *SE*). Only in late summer does the 95% *CI* for *f* not include 0. Meadow vole captures at the Academy show cyclical patterns (396 in 2000, 59 in 2002, and 454 in 2004) similar to patterns observed throughout the species' range (Getz et al. 2007). If the habitat changes caused by meadow voles are advantageous for PMJM, then *f* may be responding to increased breeding success and increased immigration because of these habitat alterations. Small mammal reproduction and recruitment increases with increasing resource availability (Galindo-Leal and Krebs 1998), and PMJMs are known to alter movement patterns to acquire food and cover resources (Trainor et al. 2007). Patterns in small mammal *f* have not received the same attention other small mammal demography parameters have been given (Krebs 1996), but manipulations of sympatric rodent abundance may clarify the impact meadow voles have on PMJM *f*.

In the most-parsimonious models, PMJM *f* was modeled in a 2-year or 3-year cyclic pattern. Other species, including the northern spotted owl (*Strix occidentalis caurina*), demonstrate multiple-year cycles in *f*. Spotted owl populations show alternating years of high and low *f* (Franklin et al. 2004) and Glenn et al. (2010) speculate that spotted owl *f* follows climatic cycles that impact the availability of fungi for rodent prey (Luoma et al. 2003; Pyare and Longland 2001). Many small mammals, including jumping mice, feed on fungal matter (Orrock et al. 2003; Ovaska and Herman 1986; Williams and Finney 1964), and the abundance of fungi is influenced by soil moisture and climatic conditions (Staddon et al. 2003). PMJM *f* may be responding to cyclical soil moisture conditions that influence fungi availability (Johnson et al. 1992) and herbaceous plant productivity (Castelli et al. 2000; Kluse and Allen Diaz 2005), but are not tied to precipitation (Stromberg et al. 1996). For example, periodic raising and lowering of the water table could be a process that influences fungal abundance. Beaver dams along Monument Creek raise the water table, but rarely last more than several years (R. A. Schorr, pers. obs.). If beaver activity creates advantageous moisture conditions for fungi and PMJM *f*, then beavers may play a valuable role in PMJM population health.

The annual PMJM φ estimates presented here are comparable to true survival estimates from PMJM populations in northern Colorado ($\bar{X} = 8.8\% \pm 6.0\%$ *SE*—Meaney et al. 2003) and from other meadow jumping mouse populations (Nichols and Conley 1982). Because φ incorporates both mortality and emigration, I expected φ estimates to be lower than previous estimates of true PMJM survival on the Academy (0.16–0.18—Schorr et al. 2009). The discrepancy between estimated true survival and apparent survival suggests that some PMJMs are dispersing from the study areas between years. Given the linear nature of PMJM habitat and the vagility of PMJM, it is not surprising that nearly half of φ may be explained by emigration. Several PMJMs were captured away from their original capture location, equating to dispersal distances up to 4.3 km (Schorr 2003). These movements were not seen within a trapping session (5–7 days), but were seen between trapping sessions (2–2.5 months). Emigration from sampling areas raises concerns about bias in some λ estimates. For matrix-based estimates of λ, small sampling areas have shown to underestimate true λ (Steen and Haydon 2000). Without adequately incorporating the loss of individuals to emigration, matrix-based λ estimates must address the portion of population, such as juveniles, likely to emigrate permanently. Because the Pradel model incorporates emigration and survival, it is less impacted by the study area size and the implications for negatively biased λ (Boyce et al. 2005; Franklin et al. 2006).

The γ analysis suggests that *f* may drive changes in λ, because 89% of the individuals in the next year are immigrants or young from the previous year. Compared to other mammals, meadow jumping mice are more *r*-selected, having low survival rates (Meaney et al. 2003; Schorr et al. 2009) and being capable of having 2 litters of 8 young per litter per year (Quimby 1951). Typical for many *r*-selected species, population increase would be fueled by increased recruitment rather than increased survival (Heppell et al. 2000b). For the Monument Creek PMJM population to reach $\lambda = 1.0$, it would take approximately a 15% increase in estimated geometric mean λ, which could be accommodated by a 17% increase in *f* or a 135% increase in φ. If *f* remains the vital rate of greatest influence, then bolstering fecundity and immigration should be the primary targets for managing PMJM population increase. However, it is unclear whether fecundity or immigration influences *f* more. Regardless, the greatest gains in *f* likely will be driven by habitat quality, especially for the energetic requirements of reproduction (Bronson 1985). If, as with other threatened species (Root 1998), habitat quality drives the vital rates of PMJM, then changes in habitat quality along

Monument Creek may have precipitated the PMJM population decline from 2000 to 2006.

Historically, the Academy PMJM population was well insulated from the suspected causes of PMJM decline, such as habitat loss from development, flood control, agricultural conversion, grazing, and water development. However, the undeveloped lands along the eastern boundary have undergone rapid urban development (Kuby et al. 2007). With this development, impermeable surface area has increased and, consequently, so has the amount of water runoff that reaches the Academy. These flows have increased erosion and deposition of sandy soils, eliminating the herbaceous and shrub cover along the Academy's eastern tributaries (R. A. Schorr, pers. obs.; B. Mihlbachler, United States Fish and Wildlife Service, pers. comm.). This loss of habitat would eliminate movement corridors for immigrants to the Monument Creek population, reducing f during this time. This is the most obvious landscape change within PMJM habitat of Monument Creek, but other changes may play a role in PMJM λ. For example, the decline of beaver (Wohl 2001) may have reduced the opportunities for expanding the floodplain vegetation (Naiman et al. 1988), constraining PMJM movement corridors. Similarly, PMJM use of tributaries may be limited by mesopredators that have expanded because of the proximate urban development (Miller and Hobbs 2000; Randa and Yunger 2006).

If recruitment via immigration is vital for PMJM population stability, then connectivity of populations is essential for allowing immigrant access. The Monument Creek PMJM population is isolated from other populations within the range because of geography and habitat alterations. To the west, the steepness of the Rampart Range limits the expanse of riparian zones and PMJMs have not been captured above 2,255 m at the Academy (Schorr 2001). As early as 1912, PMJMs (mistakenly referenced as *Z. h. campestris*) were documented along Monument Creek south of the Academy in Colorado Springs (Warren 1942), but in 2004 the United States Fish and Wildlife Service established a "block clearance" for this stretch of Monument Creek, precluding the need for future trapping effort because there was "little likelihood of [PMJM] presence" (United States Fish and Wildlife Service 2004). Individual PMJMs have been captured east of the Academy (12 locations since 2000, but no captures since 2004; United States Fish and Wildlife Service PMJM distribution database, 11 January 2010), yet the aforementioned erosion issues likely limit immigration to the Academy population. The most likely source of new individuals is from the north where Monument Creek extends for >10 km. Unfortunately, the Monument Creek population is unlikely to exchange individuals with the nearest population to the north. Palmer Divide and the city of Monument limit, if not preclude, communication between the Monument Creek population and populations in the South Platte River watershed. Given the limited avenues for immigration, the stability of the Academy PMJM population is questionable unless fecundity compensates for population losses.

This study suggests that connectivity of populations may be vital to persistence of PMJM populations. The Monument Creek PMJM population has little opportunity of incorporating immigrants because of the degradation of surrounding habitat and its isolation from other populations. Whether the population trends at the Academy were similar to trends elsewhere is unknown. A collaborative meta-analysis approach to PMJM population status would be ideal (Boyce et al. 2005; Franklin et al. 2004); however, population monitoring data are unavailable from other areas. In the absence of reliable monitoring data from northern populations, the temptation to use these data as surrogates for other populations will be large. This study provides insights for PMJM population ecology, but is specific to a 7-year interval from habitat at the southern limits of the PMJM range and on a military installation (the Academy) that is actively managed to preclude human use. Regardless, river systems that include multiple tributaries, provide dispersal corridors, and are insulated from habitat loss are likely the most successful landscapes for PMJM conservation.

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