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BODY MASS AND WINTER SEVERITY AS PREDICTORS OF OVERWINTER SURVIVAL IN PREBLE'S MEADOW JUMPING MOUSE

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Meadow jumping mice (*Zapus hudsonius*) reduce their metabolism substantially during hibernation and use stored fat reserves for overwinter energy needs. Preble's meadow jumping mouse (*Z. h. preblei*; PMJM) occurs along the Front Range of Colorado, north into southeastern Wyoming, and is listed as a threatened species under the Endangered Species Act because of the conversion and degradation of riparian habitats. To better understand how increasing fat and body mass before hibernation impact overwinter survival, we conducted a mark–recapture study of PMJM at the United States Air Force Academy, El Paso County, Colorado. We used environmental covariates and individual covariates, such as body mass and fat mass, to improve survival estimates. Overwinter survival of female PMJM was higher during long, cold winters, whereas overwinter survival of males was lower during winters with much snowfall. For both sexes, heavier individuals had higher overwinter survival. A combination of large body mass and colder winters may allow PMJM to conserve valuable fat resources. Because periodic arousal from hibernation is the most energetically expensive activity over winter, increasing body size (reducing surface area-to-volume ratio) should increase energy conservation and probability of survival.

Key words: body mass, hibernation, Huggins robust design, Preble's meadow jumping mouse, riparian habitat, survival, timing of trapping, winter severity, *Zapus hudsonius preblei*

During harsh environmental conditions and low food availability some mammals escape the physiological stress of maintaining their body temperature by migrating, hibernating, or a combination of both strategies (Geiser and Ruf 1995). For species that hibernate, it is assumed that the costs of relying on fat reserves for metabolic energy may be realized in lower overwinter survival rates (Blumstein and Arnold 1998; Karels et al. 2000; Speakman and Rowland 1999). Yet overwinter survival is influenced by a combination of physiological factors, such as fat accumulation, and environmental conditions. Understanding what factors affect overwinter survival may explain the importance of prehibernation condition and provide insight into predicting seasonal survival of hibernators.

Meadow jumping mice (*Zapus hudsonius*) hibernate for a majority of the year, entering hibernation early in fall and emerging the following spring (Whitaker 1972). During this time, body temperature and metabolism drop, and individuals use energy from their fat reserves, which may total 60% of the animal's body mass before hibernation (Cranford 1978, 1983a; Waters and Stockley 1965). One subspecies of meadow jumping mouse, Preble's meadow jumping mouse (*Z. h. preblei*; hereafter PMJM), is restricted to central Colorado and southeastern Wyoming (Cryan 2004), and because of habitat conversion and degradation is listed as a threatened subspecies under the Endangered Species Act (United States Fish and Wildlife Service 1998). Little research has been conducted on the basic population ecology of PMJM, especially regarding the potential effects of hibernation on overwinter survival. The only available estimates of PMJM survival suggest that overwinter survival is higher than that over summer (Meaney et al. 2003). However, basing range-wide conservation strategies on data from a single study at 1 locale can be problematic (Thompson 2004).

One of the largest PMJM populations occurs in riparian habitats along Monument Creek and its tributaries in El Paso County, Colorado (Schorr 2001). This population is important to PMJM conservation because of its large population size, the quality and ecological function of the riparian habitat in which

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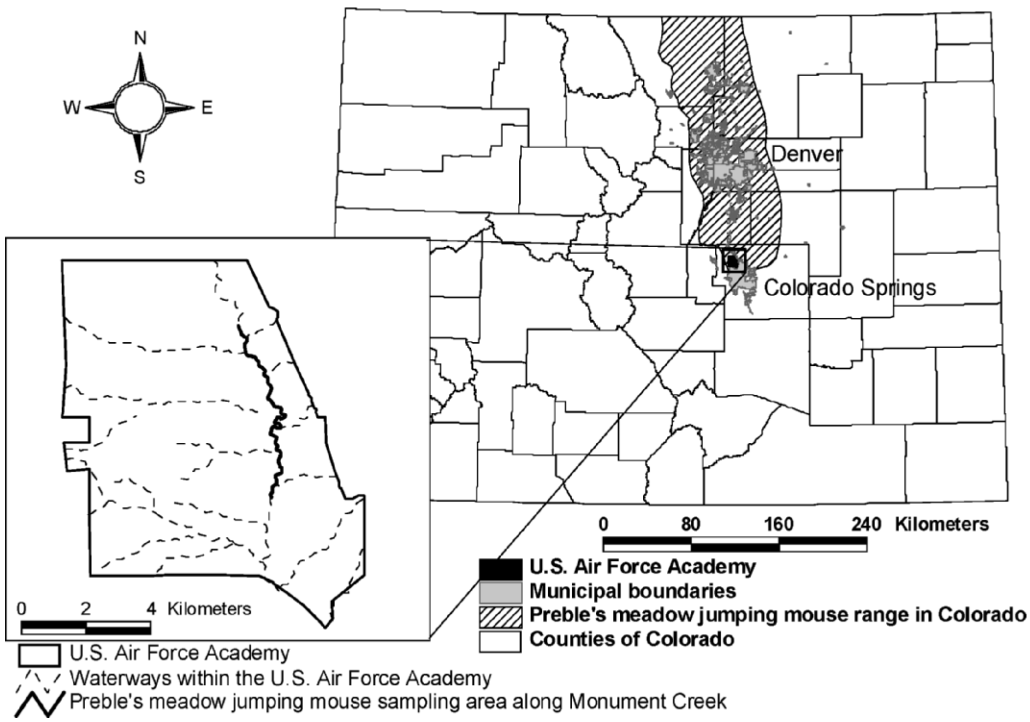

Fig. 1.—Geographic range of Preble's meadow jumping mouse (*Zapus hudsonius preblei*; PMJM) in Colorado, and location of sampling area along Monument Creek at the United States Air Force Academy (inset) in El Paso County.

it exists, the extent of the riparian communities inhabited by PMJM (approximately 25 km—Grunau et al. 1999), and the taxonomic uniqueness of this southernmost population (King et al. 2006). Determining seasonal survival rates and the environmental factors that affect them is vital for the development of effective conservation plans, for incorporation into population viability analyses, and for appropriate management of threats to PMJM populations (Grunau et al. 1999; United States Fish and Wildlife Service 2003).

We conducted mark–recapture studies along Monument Creek to understand the influence of environmental factors and individual physiological covariates on overwinter survival and to estimate seasonal survival for PMJM, a small mammalian hibernator. We predicted that larger individuals and those with larger fat reserves would have higher overwinter survival (Humphries et al. 2003). Additionally, because winter can be a time of particular hardship for hibernators (Blumstein and Arnold 1998; Karels et al. 2000; Whitaker 1963), we focused on estimating seasonal (overwinter and oversummer) survival rates for PMJM. Weather covariates such as snowfall, winter severity, and winter variability were expected to decrease overwinter survival of PMJM, whereas annual and seasonal precipitation were incorporated as covariates into models of oversummer survival because of their potential effects on food availability.

Materials and Methods

Livetrapping.—Small mammals were sampled along Monument Creek at the United States Air Force Academy (Academy), a 7,285-ha (18,000-acre) United States Department of the Air Force education and training facility located at the northern edge of Colorado Springs, Colorado (Fig. 1; 39°00′N, 104°50′W, elevation 1,940–2,620 m above sea level). The riparian corridor of Monument Creek is densely vegetated with various willows (*Salix*), snowberry (*Symphoricarpos occidentalis*), wild rose (*Rosa woodsii*), currant (*Ribes*), forbs, and grasses. Mature cottonwood (*Populus angustifolia* and *P. deltoides*) galleries are found along the creek. The uplands immediately adjacent to the riparian areas are Ponderosa pine (*Pinus ponderosa*) woodlands with scrub oak (*Quercus gambelii*), choke cherry (*Prunus virginiana*), sagebrush (*Artemisia*), and grasses.

Preble's meadow jumping mice were trapped along a 7.5-km segment of Monument Creek free from military maneuvers, which occur to the north, and recreational activity, which occurs to the south. Four randomly placed sets of 2 parallel 270-m-long transects were set for 5–7 nights in early summer (late May to mid-June) and in late summer (mid-August to mid-September) from 2000 to 2005. Timing of prehibernation trapping was determined based on predicted timing of hibernation (Wunder and Harrington 1996), telemetry studies of PMJM, and trapping experience at the Academy (Schorr 2001). Length of transects was based on logistic constraints and expected movement patterns of PMJM, because the mean (± *SD*) farthest distance traveled for radiotelemetered PMJM along Monument Creek was 232 ± 113 m (Schorr 2001). Transects were positioned parallel to the flow of the creek and were 1–20 m from the edge of the creek. One Sherman live trap (7.6 × 8.9 × 22.9 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) was placed at each of 40 stations along each transect and baited with whole oats; polyester batting was provided for insulation. Traps were spaced 7 m apart and were set before sunset and checked between 0600 and 1000 h Mountain Standard Time the following morning.

For each PMJM captured, sex and body mass were recorded, and individuals were permanently marked with unique passive integrated transponder tags (TX 1406-L sterile tags; Biomark, Inc., Boise, Idaho). Individuals captured in early summer were considered adults and juvenile PMJM (typically <17 g) were encountered only during the late-summer trapping period. Juveniles were not included in survival analyses unless they were recaptured as adults during subsequent trapping periods. Species identity was recorded for all other captures. From 2003 to 2005, the 1st PMJM individuals encountered (<30 per season) from 3 transects were brought to a temporary laboratory where they were anesthetized, bled (approximately 200 μl via postorbital sinus) for another study of hibernation physiology, and their relative lean mass was measured using total body electrical conductivity (EM-SCAN model SA-3000 with 3044 measuring chamber; EM-SCAN, Springfield, Illinois). Fat mass was assessed using total body electrical conductivity calibration curves of PMJM from Jefferson County, Colorado (Wunder and Harrington 1996) using EM-SCAN model SA-3000 with a 3044 measuring chamber. The multiple regression model for PMJM fat content was: fat mass (g) $= 14.79 + (0.59 \times$ body mass$) - (0.93 \times$ total body electrical conductivity index). Once animals recovered from anesthesia they were returned to their original capture location (approximately 1–3 h later). Trapping and physiological measurements were conducted in accordance with guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Animal Care and Use Committee of Colorado State University (permit 01-122A-07).

Environmental covariates.—Measurements of daily high and low ambient temperature, rainfall, and total precipitation (snowfall and rainfall) were collected at the Academy (Air Force Combat Climatology Center, Strategic Climatic Information Center). Average phase of the moon was calculated for each trap-night based on a nightly scale from 0 (new moon) to 1 (full moon).

Statistical analysis.—Mark–recapture data were analyzed using the Huggins robust design model (Huggins 1989; Kendall et al. 1997) in program MARK (Kendall 2001; White et al. 2001). Models were compared 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). Estimates of survival (S), capture probability (p), recapture probability (c), temporary immigration ($1 - \gamma''$), and temporary emigration (γ') were estimated by model-averaging over the set of most-parsimonious models (Burnham et al. 1995). Variances of seasonal and annual survival estimates were estimated using the delta method (Seber 1982; Williams et al. 2001). Mark–recapture data were analyzed separately for males and females to reduce the number of parameters to be estimated.

Survival probability was modeled using individual covariates of fat mass and total mass. Also, oversummer survival of PMJM was modeled as a function of the relative abundance (total captures) of possible competitors (*Microtus pennsylvanicus* and *Peromyscus maniculatus*—Boonstra and Hoyle 1986; Dueser and Porter 1986). To determine the effects of drawing blood and measuring body fat with the total body electrical conductivity, these sampling procedures were incorporated into models of survival and compared to other models.

Because hibernators must balance their overwinter energy needs with the expected length of hibernation (Humphries et al. 2003), winter severity, winter variability, and total snowfall (from October 1 to May 31) were used to model overwinter survival. Winter severity was calculated as the proportion of days between October 1 and May 1 with average nightly temperature below 0°C. Winter variability was measured as the variance of mean low ambient temperature for days between October 1 and May 1.

Meadow jumping mice are primarily granivorous (Whitaker 1972), and because precipitation influences vegetation growth and seed production, we used total precipitation (October 1–September 30) and total summer precipitation (May 1–September 30) to predict oversummer survival. Lastly, survival was modeled as a function of season (summer versus winter), constant among trapping sessions, and time-dependent among trapping sessions.

Capture and recapture probabilities were modeled using trapping effort (number of nights trapped), precipitation during trapping (daily and summed over trapping session), high and low temperatures during trapping, and lunar phase during trapping (daily and averaged over trapping period). Additionally, we tested for a behavioral response to trapping. Because we believed years with greater abundance of competitors may affect the probability of capture and recapture of PMJM, relative abundance of these species was used to model capture and recapture probabilities. Immigration and emigration probabilities were modeled as time-dependent, constant over all time periods, or constant and equal to one another.

As a general modeling approach, we developed possible models of p and c, then used the most-parsimonious models of p and c (AIC_c weight > 0.01) to model S, γ'', and γ' (Burnham and Anderson 2002). The most-parsimonious models of S, γ'', and γ' were then modeled using all models of p and c that carried any AIC_c weight.

Results

Three hundred eighty-five PMJM were captured 1,207 times (18% of all captures) in 16,080 trap-nights. Both *P. maniculatus* (56% of captures; 3,641 captures) and *M. pennsylvanicus* (22% of captures; 1,459 captures) were captured more frequently than PMJM. The western harvest mouse (*Reithrodontomys megalotis*) accounted for 2% of captures (160). Shrews (*Sorex*), long-tailed weasels (*Mustela frenata*), and pocket mice (*Perognathus*) accounted for 0.8%, 0.1%, and 0.05% of captures, respectively. On average, 63% of

TABLE 1.—Environmental covariates used to model oversummer and overwinter survival of Preble's meadow jumping mice (*Zapus hudsonius preblei*) at the United States Air Force Academy, El Paso County, Colorado, 2000–2005.

Year	Time period	Total precipitation (water equivalent in cm)[a]	Total snowfall (cm)	Winter severity[b]	Winter variability[c]
2000	October−September	34.4			
	October−May		100.1	0.665	179.4
2001	October−September	34.7			
	October−May		144.3	0.651	183.8
2002	October−September	19.4			
	October−May		74.4	0.621	127.7
2003	October−September	35.1			
	October−May		90.9	0.592	151.4
2004	October−September	37.5			
	October−May		66.8	0.665	99.0
2005	October−September	27.5			

[a] Mean annual precipitation at the United States Air Force Academy is 40.4 cm (1967–2004, Air Force Combat Climate Center, April 2004).
[b] Proportion of days between 1 October and 1 May with minimum temperature below 0°C.
[c] Variance of mean low temperature between 1 October and 1 May.

traps were empty, suggesting that trap competition was not a significant problem.

In each year of the study annual summer precipitation was below average (Table 1), with the 6th driest year on record in 2002 (21 cm below average). Annual snowfall was more than 6 cm below average in each year of the study except winter 1999–2000 and winter 2000–2001. Winter severity ranged from 59% (2003–2004) to 67% (2000–2001, 2004–2005) of winter days with nightly temperatures below 0°C (Table 1).

Early-summer body mass (18.5 g ± 0.13 *SE*, $n = 282$) was lower than late-summer body mass (21.6 ± 0.19 g, $n = 173$; $t = 205$, $d.f. = 172$, $P < 0.001$; Table 2). Fat mass in late summer (5.3 ± 0.15 g, $n = 61$) was significantly greater ($t = 3.51$, $d.f. = 40$, $P < 0.001$) than in early summer (4.6 ± 0.15 g, $n = 57$). Capture probability varied depending on trapping period (range: 0.025–0.448), and recapture probability was greater than capture probability for all sessions (mean difference = 0.21 ± 0.03 *SE*).

All of the best models for male PMJM (accounting for >0.95 total AIC_c weight) modeled capture probability as constant for each trapping period, and recapture probability with a trend for each trapping period. The best approximating model for survival of males modeled oversummer survival of adults as a function of total summer captures of *P. maniculatus*, and overwinter survival of adults as a function of total snowfall and individual mass (AIC_c weight = 0.35; Table 3). The next best approximating model for survival of males modeled oversummer survival of adults as a function of total summer captures of *P. maniculatus*, and overwinter survival as a function of the timing of trapping (AIC_c weight = 0.16). This a posteriori model evaluated the effect of timing of trapping on estimates of overwinter survival. Because the timing of early-summer trapping did not always coincide with the end of hibernation and late-summer trapping did not coincide with the beginning of hibernation, estimates of overwinter survival may have been reduced or inflated by the inclusion of portions of the summer months (June and August). The next-best approximating model for survival of males was identical to the best model except overwinter survival was modeled using body mass (AIC_c weight = 0.10).

Based on the most-parsimonious model for survival of males (Table 3), the slope of effect on the logit scale (β) for the effects

TABLE 2.—Mean body mass (± *SE, n*) and fat mass (± *SE, n*) of male and female Preble's meadow jumping mice (*Zapus hudsonius preblei*) from Monument Creek, United States Air Force Academy, El Paso County, Colorado, from 2000 to 2005. Dashes (—) designate when data were not collected.

	2000		2001		2002		2003		2004		2005	
	Early summer	Late summer	Early summer	Late summer	Early summer	Late summer	Early summer	Late summer	Early summer	Late summer	Early summer	Late summer
Body mass (g)												
Male	18.5 (1.6, 40)	23.0 (2.8, 21)	18.6 (2.8, 27)	20.2 (2.3, 26)	17.6 (1.5, 24)	20.7 (1.7, 24)	19.0 (2.1, 48)	22.0 (1.8, 14)	18.7 (2.5, 34)	19.6 (1.2, 8)	19.0 (2.4, 35)	20.8 (0.3, 3)
Female	18.2 (2.0, 29)	22.0 (3.0, 17)	18.1 (2.5, 10)	21.0 (2.6, 15)	17.0 (2.0, 14)	21.5 (2.0, 15)	19.0 (2.8, 13)	23.9 (2.2, 14)	20.5 (NA, 1)	21.7 (2.6, 7)	17.5 (4.8, 3)	23.6 (2.4, 8)
Fat mass (g)												
Male	—	—	—	—	—	—	4.2 (1.1, 26)	5.5 (0.9, 9)	5.4 (0.9, 26)	5.6 (0.3, 4)	—	6.3 (0.6, 3)
Female	—	—	—	—	—	—	2.5 (0.5, 4)	5.3 (0.8, 8)	NA	5.9 (1.9, 3)	—	6.8 (0.7, 6)

Table 3.—Most-parsimonious models of survival (S), immigration (γ''), emigration (γ'), capture probability (p), and recapture probability (c) of the Preble's meadow jumping mouse (*Zapus hudsonius preblei*) population at the United States Air Force Academy, El Paso County, Colorado, from 2000 to 2005. For all models, immigration and emigration were modeled constant and equal. *Peromyscus maniculatus* (PEMA) and *Microtus pennsylvanicus* (MIPE) captures were used to model some parameters.

Model name[a]	AIC_c	ΔAIC_c	AIC_c weight	No. parameters
Male Preble's meadow jumping mice[b]				
S[summer(PEMA captures), winter(body mass + snowfall)]	2,768.23	0.00	0.352	41
S[summer(PEMA captures), winter(proportion of summer)]	2,769.80	1.57	0.160	40
S[summer(PEMA captures), winter(body mass)]	2,770.68	2.46	0.103	40
S[summer(constant), winter(body mass + snowfall)]	2,770.71	2.48	0.102	41
S[summer(summer rainfall), winter(snowfall)]	2,771.17	2.94	0.081	40
S[summer(MIPE captures), winter(body mass)]	2,771.20	2.97	0.080	40
S[summer(summer rainfall), winter(body mass)]	2,771.26	3.03	0.077	40
Female Preble's meadow jumping mice				
S[summer(constant), winter(body mass + severity)][c]	1,180.93	0.00	0.192	19
S[summer(constant), winter(severity)][c]	1,181.56	0.63	0.140	18
S[summer(constant), winter(severity)][d]	1,181.73	0.80	0.129	19
S[summer(constant), winter(body mass + severity)][d]	1,181.84	0.91	0.121	20
S[summer(annual precipitation), winter(severity)][d]	1,182.93	2.00	0.070	19
S[summer(annual precipitation), winter(body mass)][d]	1,182.98	2.05	0.069	19

[a] Capture probability (p) and recapture probability (c) were modeled as described in footnotes b, c, and d.
[b] p was constant by trapping session; c was modeled as a trend each trapping session.
[c] p was modeled using number of nights of trapping; c was constant by trapping session.
[d] p was modeled using number of nights of trapping and total PEMA captures; c was modeled as constant by trapping session.

of captures of *P. maniculatus* on oversummer survival of PMJM was -0.0019 ± 0.0012 *SE*. The β for total snowfall effects on overwinter survival of adult males was -0.029 ± 0.013 and the β for body mass effects on overwinter survival of adult males was 0.088 ± 0.040. Mean oversummer survival of adult males was 0.42 ± 0.06 *SE* ($n = 6$), and mean overwinter survival was 0.45 ± 0.01 ($n = 5$). Mean annual survival of adult males was 0.18 ± 0.06 ($n = 5$). Temporary movement probabilities (γ', γ'') were low and had poor precision (0.009 ± 0.063 unconditional *SE*).

For female PMJM, the most-parsimonious models modeled capture probability as a function of the number of nights of trapping, and recapture probability as a trend by trapping session. The best approximating model for survival of adult females modeled oversummer survival as constant, and overwinter survival using winter severity and individual body mass (AIC_c weight = 0.19; Table 3). The next-best model was identical to the top model, but did not incorporate body mass in estimates of overwinter survival (AIC_c weight = 0.14). An identical model used total captures of *P. maniculatus* as a covariate of capture (AIC_c weight = 0.13), as did a similar model that incorporated body mass back into overwinter survival (AIC_c weight = 0.12).

Using the most-parsimonious model for female PMJM, β for oversummer survival of adults (modeled as constant) was 18.3 ± 8.6 *SE*, and the β for effects of winter severity on overwinter survival was 24.6 ± 10.6, whereas the β for individual body mass was 0.18 ± 0.12. Mean oversummer survival of adult females was 0.46 ± 0.08 ($n = 6$), and mean overwinter survival was 0.33 ± 0.03 ($n = 5$). Mean annual survival of adult females was 0.16 ± 0.06 ($n = 5$).

Mean annual survival of adults was low (<0.20) and comparable for males and females, but with greater precision for estimates of male survival rate (Fig. 2). For both sexes, models that included the effects of total body electrical conductivity sampling on PMJM survival explained virtually no variation in the data.

Discussion

Overwinter survival of both male and female PMJM were best predicted by models that incorporated individual body mass and measures of winter severity or total snowfall. For adult females, heavier individuals and winters with more daily low temperatures below freezing provide the best conditions for surviving the hibernation period. For males, the best model suggested that heavy individuals have a better chance of surviving overwinter, but that winters with much snowfall may reduce overwinter survival.

Because hibernators sustain long periods at low body temperature, reduced heart rate, and very low metabolic rates (Carey et al. 2003), they must accumulate and conserve sufficient fat reserves or food items to sustain them over winter (Lyman et al. 1982). Hibernators that store fat instead of caching food, such as PMJM, deplete most of those fat resources through energetically expensive arousals (Kenagy 1989; Thomas et al. 1990), and warm ambient temperatures can increase the frequency of arousal bouts (French 1982; Geiser and Kenagy 1988). Not surprisingly, arousal patterns of jumping mice are influenced by photoperiod and soil temperature (Cranford 1978; French and Forand 2000; Muchlinksi 1980). At the Academy, hibernacula of PMJM have northern aspects and are located at the base of shrubs (Schorr 2001) where exposure is minimized and fluctuations of soil temperature likely are reduced. The energetic savings provided by thermally stable hibernacula may explain the

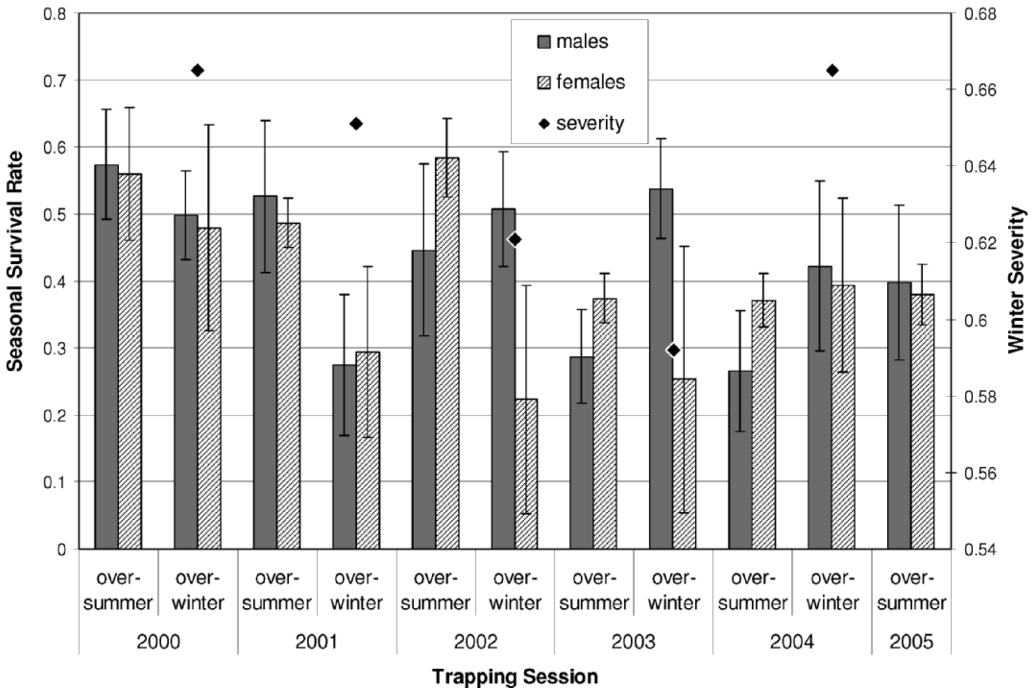

FIG. 2.—Mean survival (± *SE*) of Preble's meadow jumping mice (*Zapus hudsonius preblei*; PMJM) along Monument Creek, United States Air Force Academy, Colorado, and winter severity (proportion of winter days when overnight low temperature was less than 0°C) between 2000 and 2005.

importance of long, cold winters to overwinter survival of female PMJM. Cranford (1983b) found that survival of adult western jumping mice (*Z. princeps*) was not reduced by long winters, and some individuals emerged with available fat reserves. Weather conditions during winter may act as a proxy for thermal stability of hibernacula, where the energetic costs of hibernation are realized (Arnold et al. 1991; Buck and Barnes 1999). For other hibernators, overwinter survival is more consistent than oversummer survival (Schaub and Vaterlaus-Schlegel 2001; Sendor and Simon 2003), which may reflect the thermal stability of hibernacula (Humphries et al. 2002).

The importance of hibernacula microclimate may help explain the affinity of PMJM for densely vegetated riparian corridors. PMJM may select riparian areas for the low variability in soil temperatures that dense vegetation provides (Balisky and Burton 1995; Buck and Barnes 1999). Under prolonged winter and drought, female Townsend's ground squirrel (*Spermophilus townsendii*) experienced decreased persistence and later emergence times, but these effects were mitigated by denser shrub habitats (Van Horne et al. 1997). Understanding the role of habitat in mitigating environmental stochasticity will be valuable for managing habitat for expected environmental changes (Geiser and Broome 1993; Stenseth et al. 2002).

Although overwinter survival of female PMJM was improved by long, cold winters, overwinter survival of male PMJM was unaffected by winter severity. Total snowfall was the best predictor of overwinter survival of males, but the odds ratio of the influence was 1 ($\beta = -0.03$), suggesting that snowfall may be of little biological importance. Male jumping mice are more sensitive to increases in soil temperature and emerge from hibernation earlier than females (French and Forand 2000). Males that emerge early may be exposed to late-winter or early-spring snowfall and may have limited access to food resources (Farand et al. 2002; Van Vuren and Armitage 1991).

The importance of large body size to overwinter survival of hibernators has been demonstrated for other hibernators (Michener and Locklear 1990; Murie and Boag 1984) and may be explained by the tendency to accumulate fat before hibernation (Huang and Morton 1976). Because body size is inversely related to rewarming rate (Geiser and Baudinette 1990), larger individuals may have reduced frequency of arousal bouts and be less affected by energy loss from rewarming. An alternate explanation is that larger individuals can store more fat and have energy for longer euthermic arousal bouts (French 1988). Longer arousal bouts late in hibernation may allow individuals to test environmental conditions and emerge at an optimal time. Also, because larger individuals typically have more fat reserves, they may be less dependent upon food availability (French 1988). Male hibernators become euthermic for longer periods of time than females (Young 1990) and adequate fat stores would be essential for overwinter survival. Although prehibernation fat mass was not a predictor of overwinter survival of PMJM, measurements from more individuals over more than 2 hibernation periods (2002–2003 and 2003–2004) may be necessary to detect an effect. Compared to fat mass, body mass was easy to measure in the field and was collected for all 5 overwinter survival periods.

Because 1 highly supported model of overwinter survival of males included timing of sampling, care should be taken to match the timing of field sampling with the phenology of hibernation. In our study, survival of adults differed between seasons, but some estimates of overwinter survival likely incorporated oversummer effects. For example, because warm fall weather may not have triggered hibernation until October, trapping conducted in early September would add 1 month of oversummer survival effects to estimates of overwinter survival. We tested this by developing an a posteriori model that included the proportion of June (posthibernation) and August (prehibernation) in each estimate of overwinter survival of adult males. As expected, models of overwinter survival that included more summer months (large proportion of June and August) had lower overwinter survival (β on normal scale = 0.33, *SE* = 0.07). We caution that researchers seeking to estimate seasonal differences in survival rates of hibernators should attempt to account for potential variability in emergence and immergence dates in their field sampling. Unfortunately, because it is usually difficult to predict these dates with any accuracy, the timing of trapping necessarily reflects a trade-off between sampling key events in hibernation phenology and capturing sufficient numbers of individuals aboveground.

Annual survival of PMJM was lower than expected, but our survival estimates may be negatively biased because of permanent emigration from the sampling sites. Although radiotelemetry studies indicate that kernel home ranges of PMJM are typically <1 ha (Schorr 2001), in our study, we identified 1 PMJM moving >4 km between captures. Such movements, if permanent, would decrease estimates of survival. Alternatively, lower survival rates may reflect high predation pressure (Schorr 2001; Whitaker 1972). Habitat quality may help mitigate mortality because densely vegetated riparian habitats reduce exposure to avian predators (Trainor et al. 2007). Moreover, these habitats help to create thermally stable microclimates for hibernation, and therefore may reduce overwinter mortality caused by exhaustion of fat reserves.

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