USING SURVIVAL OF RODENTS TO ASSESS QUALITY OF PRAIRIE HABITATS

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ABSTRACT—Estimates of abundance commonly are used for assessing quality of wildlife habitat. However, disparities between abundance and fitness parameters make the utility of abundance for predicting quality of habitat questionable. We used survival of rodents and rates of capture to assess quality of habitat in greasewood scrub and sandhill prairie habitats at the United States Army Pueblo Chemical Depot, Pueblo, Colorado. Only the Ord's kangaroo rat (*Dipodomys ordii*) and the North American deermouse (*Peromyscus maniculatus*) were captured and recaptured enough to warrant statistical analysis. Apparent survival was modeled using temporal and seasonal patterns, vegetation cover, type of habitat, abundance of sympatric rodents, and abundance of grasshoppers. The most parsimonious models for survival of Ord's kangaroo rat incorporated abundance of bare ground at trapping sites, while the most parsimonious models for survival of North American deermice included amount of shrub cover at trapping sites. Although rates of capture for Ord's kangaroo rats and deermice were different between habitats, rates of survival did not differ between habitats. Suggestions that particular xeric-shrub habitats provide better quality of habitat for deermice and kangaroo rats should be framed using the relationship between rates of survival and abundance, instead of relying on abundance or rates of capture.

RESUMEN—Las estimaciones de abundancia por lo general sirven para evaluar la calidad ambiental silvestre. Sin embargo, las discrepancias entre los parámetros de abundancia y de adecuación causan que se cuestione la utilidad del de abundancia para predecir la calidad ambiental. Utilizamos las tazas de supervivencia y la captura de roedores para evaluar la calidad ambiental en áreas de la planta *Sarcobatus vermiculatus* y en las praderas arenosas en el United States Army Pueblo Chemical Depot, Pueblo, Colorado. Sólo se capturó y se recapturó a la rata canguro (*Dipodomys ordii*) y al ratón ciervo (*Peromyscus maniculatus*) lo suficiente para justificar el análisis estadístico. Se modeló la supervivencia aparente en los patrones temporales y estacionales, la cubierta de vegetación, el tipo de hábitat, la abundancia de roedores simpátricos y la abundancia de saltamontes. Los modelos más parsimoniosos para la supervivencia del *D. ordii* incluyeron la abundancia de suelo abierto en los sitios de trampa, mientras los modelos más parsimoniosos para la supervivencia del *P. maniculatus* incluyeron la cantidad de cubierta de arbustos en los sitios de trampa. Aunque las tazas de captura para el *D. ordii* y el *P. maniculatus* se diferenciaron entre hábitats, las tazas de supervivencia aparentes no se diferenciaron entre hábitats. La sugerencia de que ciertos hábitats de arbusto xérico proveen un hábitat de mejor calidad para el *P. maniculatus* y el *D. ordii* debe ser formulada en base a la relación entre las tazas de supervivencia y abundancia, en lugar de sólo depender de la abundancia o de las tazas de de captura.

Historically, density of individuals was a common tool for predicting quality of habitats (Rosenzweig, 1981; Fagen, 1988). Such assessments were based on the belief that individuals reside in areas where resources are plentiful and where survival or fitness of individuals is greatest. Thus, density of individuals could be a surrogate for quality of habitat; however, the relationship

between population density and quality of habitat has not been well established (Battin, 2004). Van Horne (1983) explained three scenarios in which density of animals may not be indicative of quality of habitat for that species. Critical habitat for a species may be temporally specific and estimates of density may not have been conducted at the appropriate time to elucidate true habitat needs. Also, densities of animals may be indicative of small-scale variability in predators, availability of food, or other factors, and may not reflect current conditions at the location. Temporary abundance of resources may accommodate higher densities, but only for short periods of time (Martin, 1992; Wheatley et al., 2002). Finally, behavioral interactions among individuals may preclude subdominant individuals from using high-quality habitats, and these individuals may accumulate in less-optimal habitats. Individuals in these areas may show greater density, but have lower rates of survival, reflecting source-sink dynamics (Pulliam, 1988). Thus, assessments of quality of habitat must compare density, survival, and reproduction of individuals at multiple locations (Van Horne, 1983).

Some assessments of habitat quality for rodents have discovered that the simple use of abundance is misleading. In altered landscapes, such as timber-harvested, boreal forests, patterns of abundances of individuals have not been similar to patterns of survival. Incongruous patterns may illustrate source-sink dynamics (Tallmon et al., 2003) or suggest the importance of intermediate disturbance of habitat (Hadley and Wilson, 2004). Temporal patterns of abundance of resources may alter measures of fitness disproportionately to abundance. For example, when abundance of spruce cones decreased, survival of red squirrels (*Tamiasciurus hudsonicus*) dropped precipitously despite abundances matching those of the surrounding types of forest (Wheatley et al., 2002).

The relationship between survival and abundance of rodents may be impacted by the rodents themselves. Rodents may alter abiotic and biotic components of native communities, and these changes may influence interspecific and intraspecific relationships, differentially impacting survival and abundance of rodents and other species. Prairie and desert rodents modify structure and composition of vegetation by selectively eating vegetative parts and seeds, dispersing and hoarding seeds, and disturbing

soil, allowing seedling establishment (Brown and Heske, 1990; Heske et al., 1993; Kerley et al., 1997; Whitford and Kay, 1999; Brock and Kelt, 2004). Kangaroo rats (*Dipodomys*) compete with sympatric congeners and other species of rodents (Brown and Munger, 1985; Bowers and Brown, 1992), but also provide food resources and shelter for other small mammals (Brown and Heske, 1990; Chew and Whitford, 1992; Guo, 1996; Price et al., 2000).

Some prairie rodents alter structure of small mammal communities by exerting competitive and predatory pressures. Via interspecific interference, heteromyid rodents can exclude other rodents and create habitats suitable for conspecifics (Bowers and Brown, 1992). Similarly, predation pressure from northern grasshopper mice (*Onychomys leucogaster*) modifies abundance and behavior of mammalian prey in shortgrass prairies (Stapp, 1997), and competitive interference from prairie voles (*Microtus ochrogaster*) can exclude Northern American deermice (*Peromyscus maniculatus*; Abramsky et al., 1979). An understanding of interspecific impacts on survival of rodents may allow interpretations of quality of habitat to be framed within the context of presence or abundance of sympatric rodents.

To understand how rates of capture, a commonly used surrogate for abundance, and patterns of rate of survival differ among populations of rodents in xeric-prairie shrublands, we conducted a mark-recapture study of small mammals in south-central Colorado. We examined whether rodents of greasewood-scrub and sandhill-prairie systems have different rates of survival and capture, and how probability of survival and capture are impacted by weather, abundance of other species of rodents, abundance of grasshoppers (Order Orthoptera), and composition and structure of vegetation.

METHODS—*Study Area*—Small mammals were sampled from the Pueblo Chemical Depot, a 9,300-ha United States Department of the Army ammunition and materials storage facility east of Pueblo, Pueblo Co., Colorado. Pueblo Chemical Depot is comprised of northern sandhill prairie, greasewood (*Sarcobatus vermiculatus*) scrub, shortgrass prairie, riparian woodlands, and wetlands. The three dominant vegetation types, shortgrass prairie, northern sandhill prairie, and greasewood scrub, occupy 4,600, 1,600, and 1,000 ha, respectively.

Mammal Trapping—From January 2000 to July 2003, trapping was conducted along 18, 285-m-long, 20-

station transects where traps were set for 3–4 nights in winter, spring, summer, and autumn (January, April, July, and October, respectively). Trapping was not conducted in October 2002. Transects were oriented southeast to northwest to avoid conflicts with efforts to sample vegetation. All transects were trapped for 3–4 consecutive nights, but not all transects were trapped on the same nights during a trapping visit.

Ten transects were randomly placed in greasewood-scrub and eight were randomly placed in northern-sandhill-prairie habitats. Shortgrass-prairie habitats were not trapped because preliminary trapping surveys in 1998 and 1999 yielded low trap success. Two Sherman live traps (7.6 by 8.9 by 22.9 cm or 7.6 by 8.3 by 30.5 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) were placed at each station and baited with whole oats. In each trap, a ball of polyester batting was provided for insulation. Traps were set prior to dark and checked the following morning after first light. During trapping sessions in winter, traps were checked during the night to prevent mortality, and those traps that were successful were closed for the rest of the night.

We recorded species and sex of each animal, and permanently marked animals with passive integrated transponder (PIT) tags (TX 1406-L sterile tags; Biomark, Inc., Boise, Idaho). Because of the difficulty in distinguishing species of woodrats (*Neotoma*), pocket mice (*Perognathus*), and harvest mice (*Reithrodontomys megalotis* and *R. montanus*), individuals in these genera were identified only to genus. Animals were released immediately after examination and tagging at the location of capture, except for Ord's kangaroo rats (*Dipodomys ordii*), northern grasshopper mice, and *P. maniculatus* captured along five transects also used in a separate study. Trapping was conducted in accordance with guidelines of the American Society of Mammalogists (Animal Care and Use Committee, 1998) and was approved by the Animal Care and Use Committee of Colorado State University (Permit 98-257A-01).

Habitat and Sampling of Grasshoppers—Vegetation sampling was conducted on four 50-m-long transects that radiated in the four cardinal directions from the midpoint of each trapping transect. Shrub-canopy cover was estimated using a line-intercept method along each transect (Bonham, 1989). Herbaceous ground cover was estimated using eight microplots (55 by 30 cm, with 50 points spaced 5 cm apart), that were located every 5 m along each transect.

Populations of grasshoppers were sampled using two 100-m transects placed perpendicular to each other. Transects were oriented in the cardinal directions and intersected each other about 30 m southwest of the middle of the small-mammal-trapping transect. Each transect consisted of 20 0.1-m² circular hoops with one hoop placed every 5 m (Onsager and Henry, 1977). Total hoop-area/plot was 4 m². Densities of grasshoppers were estimated by counting grasshoppers found within hoops twice per active season (August and September).

Environmental Covariates—Measurements of high and low ambient temperature, rainfall, and total precipitation were collected from Pueblo Memorial Airport National Climatic Data Center weather station, which is located 11 km W Pueblo Chemical Depot (elevation

1,420 m–National Oceanic and Atmospheric Administration, National Climatic Data Center). Average moonphase was calculated for each trapping visit (typically 5–6 days) based on a scale of 0–1 with 0 being a new moon and 1 being a full moon.

Statistical Analysis—Mark-recapture data were analyzed using the Cormack-Jolly-Seber model (Lebreton et al., 1992) in Program MARK (White and Burnham, 1999). Models were compared using Akaike's Information Criterion with small-sample-size bias correction (AIC$_c$; Burnham and Anderson, 2002). Estimates of apparent survival (φ) and probability of capture (p) were averaged over the set of models (Burnham et al., 1995). Capture data for each species were analyzed separately. Rates of capture (captures/100 trapnights) were arcsine-square-root transformed and analyzed using PROC TTEST in SAS, version 9.1 (SAS Institute Inc., 2003).

Prior to analysis, we developed a candidate list of models to be analyzed (Table 1). Abundance of kangaroo rats decreases with increase in shrub cover (Reichman and Price, 1993) and we believed *D. ordii* may experience comparatively lower rates of survival in habitats with greater shrub cover. Exclusion of kangaroo rats in desert environs has increased abundance of grasses (Brown and Heske, 1990; Heske et al., 1993) and we hypothesized that areas with greater grass cover may have greater rates of survival for *D. ordii*. Comparatively, attempts to model habitat preferences of *Dipodomys* have shown greater abundances in areas with greater proportion of bare ground (Jones et al., 2003). Thus, we suggested that survival of *D. ordii* would be greater in areas with greater amounts of bare ground. Abundance of *D. ordii* increases when northern grasshopper mice are removed from shortgrass prairie (Stapp, 1997) and we believed that rates of survival of *D. ordii* may be lower in areas with greater abundance of northern grasshopper mice.

Peromyscus maniculatus has an omnivorous diet and we believed rates of survival would be impacted by abundance of grasshoppers, grass cover, and shrub cover. Also, *P. maniculatus* selects areas with greater cover of shrubs and grasses (Stapp, 1997), so estimates of bare ground were used to model survival. In areas where northern grasshopper mice were removed from prairie shrublands, abundances of *P. maniculatus* increased (Stapp, 1997) and we believe that rates of survival of *P. maniculatus* may be impacted by northern grasshopper mice.

Probabilities of capture were modeled using precipitation data during trapping, trapping effort (number of nights of trapping), high and low temperatures during trapping, and average moon phase during trapping. Temporal models of probability of capture and models in which probability of capture was assumed nearly constant were included.

RESULTS—Eight species of small mammals were captured 4,305 times in 30,240 trapnights at Pueblo Chemical Depot (Table 2). *Dipodomys ordii* was the most frequently captured small mammal at Pueblo Chemical Depot, accounting for 49% (2,095) of captures. *Peromyscus manicu-*

TABLE 1—A priori models proposed for modeling apparent survival of small mammals (φ) and probability of capture (p) on Pueblo Chemical Depot, Pueblo Co., Colorado.

Species	Parameter	Constraint	Time periods applied
Dipodomys ordii,	φ	Constant	All
Peromyscus maniculatus		Time	All
		Time and habitat	All
		Season	All
		Habitat	All
		Total percentage of bare ground	Summer
		Total percentage of shrub cover	Summer
		Total percentage of grass cover	Summer
		Total percentage of species of grasses[a] in cover (%)	Summer
		Number of northern grasshopper mice captured	All
		Total body electrical conductivity	All
Peromyscus maniculatus	φ	Constant	All
		Density of grasshoppers	Summer
Dipodomys ordii,	p	Constant	All
Peromyscus maniculatus		Time	All
		Trapping effort[b]	All
		Average high temperature (°C)	All
		Average low temperature (°C)	All
		Total precipitation (cm)	All
		Trapping effort and high temperature	All
		Trapping effort and low temperature	All
		Average phase of moon	All

[a] Estimates of cover for each important species of grass were used.

[b] Trapping effort is measured as number of nights of trapping completed on a transect during a trapping visit.

latus accounted for 32% (1,386) of captures, and harvest mice and northern grasshopper mice each comprised 7% (316 and 318, respectively) of all captures. Pocket mice, woodrats, cotton rats (*Sigmodon hispidus*), and spotted ground squirrels (*Spermophilus spilosoma*) each comprised ≤2% of all captures. Only *D. ordii* and the *P. maniculatus* were captured frequently enough to permit analyses of survival.

Annual precipitation was below average in each year of the study except 2000 (<1 cm above average), with the greatest deviation from normal mean precipitation occurring in 2002. In 2002, annual precipitation was 67% below average making it the second lowest recorded annual rainfall at Pueblo Memorial Airport in 47 years. Seventeen consecutive months of average or below-average monthly precipitation were recorded from September 2001 to January 2003.

Amount of vegetative cover in greasewood scrub and sandhill prairies was relatively low, comprising about 30–50% of ground cover in years with average precipitation. Amount of cover decreased for most species during the drought. Blue grama grass (*Bouteloua gracilis*), alkali sacaton grass (*Sporobolus airoides*), and galleta grass (*Hilaria jamesi*) were present consistently in greasewood-scrub habitats, but their cover decreased dramatically (Table 3). Similarly, blue grama grass, three-awns (*Aristida*), sand dropseed (*Sporobolus cryptandrus*), and needle-and-thread grass (*Stipa comata*) in sandhill prairies decreased in cover during the drought (Table 3).

Shrub cover in greasewood-scrub and sandhill prairies did not respond similarly during the drought. Cover of rabbitbrush (*Chrysothamnus*) and greasewood, the dominant shrubs of greasewood habitats, did not decrease substantially (Table 3). Cover of the dominant shrub on sandhill prairies (*Artemisia filifolia*) did decrease and failed to recover completely with increased precipitation in 2003 (Table 3).

Densities of grasshoppers in greasewood-scrub and sandhill-prairie habitats peaked in 2001,

Table 2—Captures and recaptures of small mammals from Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.

Species	Greasewood scrub (16,800 trap nights)		Northern sandhill prairie (13,440 trap nights)		Total number of individuals (percent recaptured)	Percentage of captures
	Number of individuals/ recaptures	Average rate of capture/100 trap nights	Number of individuals/ recaptures	Average rate of capture/100 trap nights		
Dipodomys ordii	431/769	4.6[a]	554/1,326	9.9[a]	985 (53)	49
Neotoma	60/74	0.4	10/13	<0.1	70 (20)	2
Onychomys leucogaster	40/52	0.3[a]	207/266	2.0[a]	247 (22)	7
Perognathus	24/30	0.2	25/27	0.2	49 (14)	1
Peromyscus maniculatus	730/1,146	8.5[a]	154/240	1.8[a]	884 (36)	32
Reithrodontomys	145/239	1.5[a]	62/77	0.6[a]	207 (34)	7
Sigmodon hispidus	18/20	0.1	1/1	<0.1	19 (10)	<0.01
Spermophilus spilosoma	2/2	<0.1	16/23	0.2	18 (28)	<0.01

[a] Rates of capture were different between types of habitat within species ($P < 0.05$).

Table 3—Average vegetative cover ($\pm SE$) and average abundance of grasshoppers (Orthoptera) ($\pm SE$) on greasewood-scrub and sandhill-prairie habitats at Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.

Component	Greasewood scrub				Sandhill prairie			
	2000	2001	2002	2003	2000	2001	2002	2003
Shrub cover (%)	7.0 (0.3)	7.0 (0.3)	6.0 (0.4)	9.0 (0.6)	14.0 (1.3)	16.0 (1.3)	4.0 (0.5)	8.0 (1.2)
Grass cover (%)								
Aristida	0.4 (0.2)	0.5 (0.3)	0.0	0.1 (0.1)	4.0 (1.6)	4.0 (1.7)	0.0	1.0 (0.5)
Bouteloua gracilis	14.0 (2.0)	17.0 (2.0)	0.3 (0.1)	7.0 (1.4)	9.0 (2.3)	9.0 (2.3)	1.0 (4.0)	5.0 (2.3)
Hilaria jamesii	5.4 (1.0)	7.2 (1.3)	0.2 (0.1)	5.4 (1.4)	—	—	—	—
Sporobolus airoides	14.4 (3.3)	16.4 (3.2)	4.6 (1.2)	13.5 (2.7)	—	—	—	—
Sporobolus cryptandrus	—	—	—	—	5.0 (8.0)	6.0 (1.1)	1.0 (0.2)	3.0 (0.6)
Stipa comata	—	—	—	—	4.0 (1.8)	4.0 (1.9)	0.0	0.0
Total cover of grasses	34.2 (3.6)	41.4 (3.2)	5.1 (1.2)	2.0 (1.6)	24.0 (1.6)	24.0 (1.0)	30.0 (0.9)	25.0 (1.1)
Bare ground	16.0 (1.2)	2.0 (1.3)	15.0 (1.2)	2.0 (1.6)	24.0 (1.6)	24.0 (1.0)	30.0 (0.9)	25.0 (1.1)
Density of grasshoppers (number/m²)	0.62 (0.13)	1.00 (0.13)	0.29 (0.06)	0.08 (0.04)	0.91 (0.13)	0.91 (0.16)	0.39 (0.08)	0.05 (0.03)

following a year of above-average annual precipitation. Densities were lowest in 2003 following the year of lowest annual precipitation. Fifty-eight species of grasshoppers were identified from 35 genera and 2 families. The most abundant species were *Cordillacris occipitalis*, *Eritettix simplex*, *Melanoplus bowditchi*, *Opeia obscura*, *Psoloessa delicatula*, *Psoloessa texana*, and *Trimerotropis pallidipennis*.

Rates of capture for *D. ordii* and *P. maniculatus* differed between habitats. *Dipodomys ordii* was captured more frequently in northern-sandhill-prairie than in greasewood-scrub habitats ($P = 0.020$), while *P. maniculatus* was captured more frequently in greasewood-scrub habitats ($P < 0.001$, Table 2).

The best approximating model for probability of capture of *D. ordii* included trapping effort, average high temperature during the trapping period, and total precipitation. Probabilities of capture were greater for trapping periods that were longer, had lower high temperatures, and received little precipitation ($\beta_{effort} = 0.91$, $\beta_{high\ temp.} = 0.002$, $\beta_{precip.} = -1.23$). This parameterization of probability of capture was used for all survival models because the number of potential models became unwieldy if all capture probability parameterizations were included, and because our primary interest was to model φ of *D. ordii*.

The most parsimonious model of φ of *D. ordii* included parameters of time-specific effects and total amount of bare ground in summer (AICc weight = 80.7%; Table 4). The next most parsimonious models included time-specific effects and habitat-specific effects, but were not strongly supported by the data (Table 4). The model that best explained φ and probability of capture for *P. maniculatus* included parameters of time-specific effects and total shrub cover in summer for φ, and a constant probability of capture (AICc weight = 55.6%; Table 4). The next most-parsimonious model used time-specific parameters for survival and a constant probability of capture (AICc weight = 31.2%). The third best model used time-specific effects and total cover of grasses in summer to explain φ (AICc weight = 7.7%).

There was no seasonal pattern in φ for *D. ordii* (Fig. 1), while *P. maniculatus* experienced greater mortality from spring to summer in all years (Fig. 2). Probability of capturing *D. ordii* was high during most trapping events, but dropped during trapping in autumn 2000 and spring

2001 (Table 5). Probability of capturing *P. maniculatus* was best modeled as a constant value over all seasons and was lower than most probabilities of capture for *D. ordii* (Table 5).

DISCUSSION—*Peromyscus maniculatus* and *D. ordii* showed little variation in φ between greasewood-scrub and northern-prairie-shrubland habitats. Models of φ of *P. maniculatus* showed no support for between-habitat differences, and models of φ of *D. ordii* showed only weak support for variation between habitats. However, vegetation cover rather than habitat type was important in modeling φ of *D. ordii* and *P. maniculatus*.

Vegetative cover impacted rates of φ for the two species of rodents, but in opposite ways. The best predictor of φ for *D. ordii* was amount of bare ground present on transects during summer. During years with little bare ground, φ of *D. ordii* from spring to summer was lowest. The highest rate of φ during spring-to-summer occurred in 2002, a year in which combined total bare ground on sandhill-prairie and greasewood-scrub plots was highest. Similarly, low rates of survival during spring-to-summer were seen in 2003, a year of recovery following several years of drought. Conversely, φ of *P. maniculatus* during spring-to-summer increased as amount of shrub cover increased at Pueblo Chemical Depot. During the peak of drought at Pueblo Chemical Depot (2002) both shrub cover and φ of *P. maniculatus* by season were at their lowest.

Higher rates of φ for *D. ordii* following summers with little bare ground may be a function of their impact on xeric-grassland habitats. In southeastern Arizona, kangaroo rats (*D. ordii*, *D. merriami*, *D. spectabilis*) maintained desert-grassland systems with appreciable bare ground by depredating larger-seeded grasses and disturbing the soil via digging and caching seeds (Brown and Heske, 1990). These modifications to components of vegetative cover may create habitats that support higher rates of survival for kangaroo rats than surrounding environs. Although there are few data associating rates of survival of kangaroo rats to cover, others have noted that the relationship between abundance of kangaroo rats and vegetation cover is complex, and localized patterns of abundance are not merely a function of vegetative cover (Ernest et al., 2000; Brown and Ernest, 2002).

In this study, we attempted to compare quality of habitat occupied by rodents between two

TABLE 4—Most-parsimonious models of apparent survival (φ) and probability of capture (p) for *Dipodomys ordii* and *Peromyscus maniculatus* captured at Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.

Species/model	AICc	ΔAICc	AICc weight	Number of parameters
Dipodomys ordii[a]				
apparent survival (time, cover of bare ground in summer)	2,055.38	0.00	0.807	18
apparent survival (time)	2,059.02	3.64	0.131	18
apparent survival (time + habitat)	2,060.66	5.28	0.058	19
apparent survival (time, cover of blue gramma)	2,066.88	11.50	0.003	18
Peromyscus maniculatus				
apparent survival (time, summer shrub cover) probability of capture (constant)	1,034.25	0.00	0.556	14
probability of capture (constant) apparent survival (time, cover of grass in summer) probability of capture (constant)	1,038.21	3.96	0.077	14
apparent survival (time)	1,035.40	1.15	0.312	14
apparent survival (time, cover of shrubs in summer) probability of capture (trapping effort + high temperature + precipitation)	1,039.85	5.60	0.034	18
apparent survival (time) probability of capture (trapping effort + high temperature + precipitation)	1,042.08	7.83	0.011	18
apparent survival (time, cover of grass in summer) probability of capture (trapping effort + high temperature + precipitation)	1,043.14	8.89	0.007	18

[a] Models of survival of *D. ordii* were modeled using probability of capture (p) modeled as a function of trapping effort, average high temperature over the trapping period, and total precipitation.
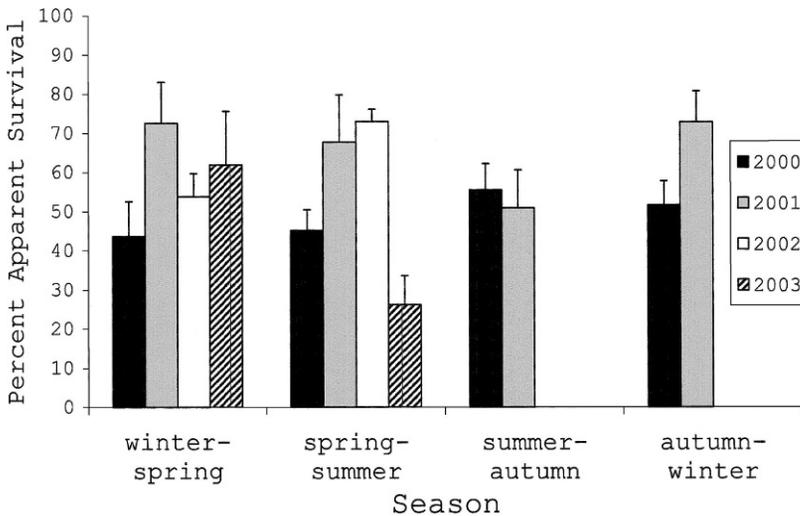
FIG. 1—Apparent survival by season (±1 unconditional *SE*) of *Dipodomys ordii* at Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.
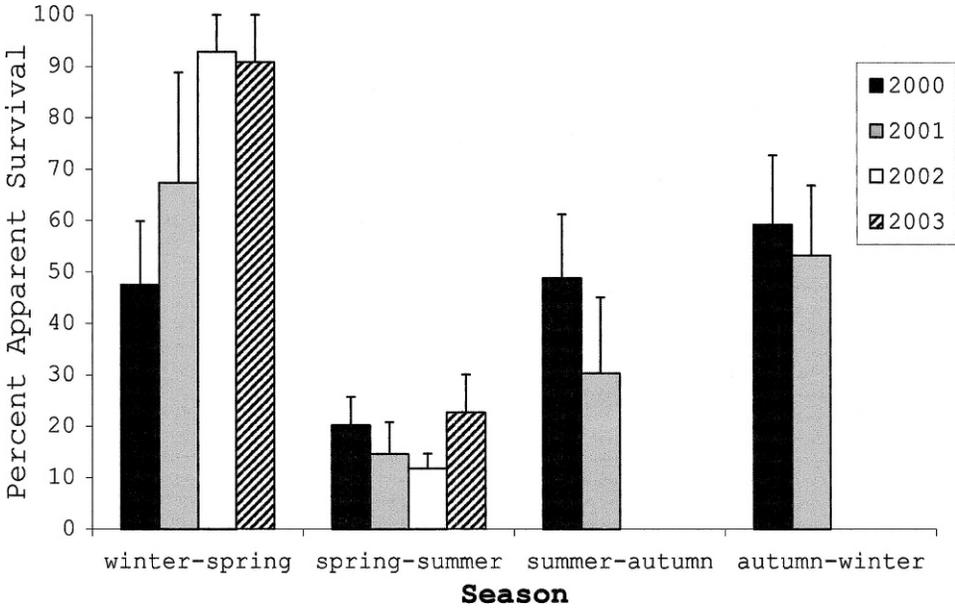
FIG. 2—Apparent survival by season (±1 unconditional *SE*) of *Peromyscus maniculatus* at Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.

TABLE 5—Model-averaged estimates of apparent survival (φ) and probability of capture (p; unconditional *SE*) for *Dipodomys ordii* and *Peromyscus maniculatus* captured at Pueblo Chemical Depot, Pueblo Co., Colorado, 2000–2003.

	Dipodomys ordii		*Peromyscus maniculatus*	
Year/season	Apparent survival	Probability of capture	Apparent survival	Probability of capture
2000				
Winter-spring	43.6 (9.0)	0.78 (0.032)	47.5 (12.4)	0.42 (0.059)[a]
Spring-summer	45.2 (5.2)	0.79 (0.039)	20.2 (5.5)	—
Summer-autumn	55.5 (6.7)	0.78 (0.033)	18.3 (12.4)	—
Autumn-winter	51.6 (6.2)	0.66 (0.069)	59.2 (13.5)	—
2001				
Winter-spring	72.6 (10.4)	0.76 (0.033)	67.3 (21.5)	—
Spring-summer	67.7 (12.1)	0.37 (0.088)	14.6 (6.2)	—
Summer-autumn	50.9 (9.7)	0.78 (0.032)	30.3 (14.8)	—
Autumn-winter	72.8 (7.9)	0.76 (0.038)	53.2 (13.6)	—
2002				
Winter-spring	53.8 (5.9)	0.78 (0.033)	92.8 (10.8)	—
Spring-summer	73.0 (3.1)	0.76 (0.043)	11.8 (2.9)	—
Summer-winter	32.1 (4.2)	0.77 (0.043)	31.1 (8.0)	—
2003				
Winter-spring	61.9 (7.9)	0.78 (0.035)	90.8 (13.7)	—
Spring-summer	26.2 (5.3)	0.79 (0.047)	22.7 (7.4)	—

[a] Because p of *Peromyscus maniculatus* was best modeled using a constant rate of capture over time, estimates range from 0.42 to 0.43 (with *SE* 0.059–0.060).

xeric-prairie habitats using rate of φ. Estimates of survival are being used more frequently to assess quality of habitat (Wheatley et al., 2002; Manning and Edge, 2004) because abundance alone can be misleading as an indicator of the ecological value of habitats. We detected similar intraspecific rates of φ between the two xeric-shrubland communities. However, differences in rate of capture we observed may lead one to suggest that greasewood-scrub habitats are preferred habitats for *P. maniculatus*, and that northern-sandhill prairies are preferred habitats for *D. ordii*. Such interpretations would neglect other population parameters (survival and fecundity) that have a greater impact on quality of habitat. Rates of capture, although sometimes used as surrogates for abundance, are influenced by a host of factors that may not be linked to abundance, such as behavior, movement patterns, and trapping techniques. Thus, comparisons of habitats require additional population parameters, such as survival or fecundity, to make valid inference about selected habitats.

Our study only addressed how well species survive in each habitat and did not estimate fecundity rates, which are critical population parameters when assessing quality of habitats. It is possible that differences in fecundity exist and would allow better assessments of quality of habitats for *D. ordii* or *P. maniculatus*, but we were unable to test this with our data. Additionally, because we estimated only φ, immigration to and emigration from our study sites may have impacted our comparisons. Analysis using population models that allow estimation of movement parameters, such as robust design and multi-strata models (Brownie et al., 1993; Kendall et al., 1997), can allow better comparisons of rates of survival among habitats.

Although there appears to be no difference in rate of φ between xeric-prairie habitats in this study, estimates of φ can be used for comparisons with other habitats and other species of rodents. Estimates of φ of *P. maniculatus* and *D. ordii* were comparable to estimates of survival in several previous studies. At Pueblo Chemical Depot, annual rates of φ for *D. ordii* were 0.05–0.18. Annual rates of survival for other species of kangaroo rats (*D. merriami*, *D. spectabilis*) range from 0.04 to 0.54 (Waser and Jones, 1987; Zeng and Brown, 1987; Andersen, 1994). Skvarla et al. (2004) incorporated dispersal into estimates of survival for banner-tailed kangaroo rats (*D.*

spectabilis) and determined that median annual survival was about 0.40. *Peromyscus maniculatus* has relatively short life spans (Blair, 1948) and the low annual rates of survival seen at Pueblo Chemical Depot (0.02–0.03) closely match the reported annual estimates of survival for *P. maniculatus* in other environments (Anderson, 1994; Tallmon et al., 2003; Hadley and Wilson, 2004,).

At Pueblo Chemical Depot there is much temporal variability in φ of rodents. The strength of a temporal model of φ for the *P. maniculatus* and the *D. ordii* indicates that fluctuations in rates follow time-specific patterns, but we were unable to predict these patterns with most components of vegetative structure, competing rodents/abundance of predators, or abundance of grasshoppers. Similar temporal variability in rates of survival has been seen in banner-tailed kangaroo rats, in which the most parsimonious models of survival used effects of time and sex (Skvarla et al., 2004).

Although *D. ordii* feeds on the grasses available at Pueblo Chemical Depot (Flake, 1973; Garrison and Best, 1990), its φ was not impacted by availability of grass cover or species of grass. Even during 2002, when total grass cover dropped by an order of magnitude, rates of φ for *D. ordii* were unaffected (Table 5). It could be argued that because *D. ordii* are granivores, grass cover may not reflect availability of seed resources. However, there is mounting evidence that diet of kangaroo rats is more varied than once believed and much vegetative material is ingested (Sipos et al., 2002; Tracy and Walsberg, 2002). A model of φ of *D. ordii* using blue grama grass as cover carried virtually no weight (AIC*c* weight. = 0.3%). Yet, the importance of this species of grass to *D. ordii* should be investigated by experimentally manipulating its availability.

Although *P. maniculatus* ate many species of grasses and arthropods at Pueblo Chemical Depot (Williams, 1959; Stancampiano and Caire, 1995), neither estimates of cover of grasses nor indices of abundance of grasshoppers were valuable predictors of φ. Apparent survival of *P. maniculatus* was impacted marginally by total amount of grass cover, but it is unclear what specific resource from grass cover aids in prediction of φ.

Models for probability of capture for *P. maniculatus* were not impacted by trapping effort, abundance of *D. ordii*, abundance of

northern grasshopper mice, weather, or moon-phase covariates. The most-parsimonious models of probability of capture of *P. maniculatus* used a constant rate of capture over time ($\hat{p} = 0.450$, Table 5). Probabilities of capture for *D. ordii* were best modeled using amount of trapping effort, amount of rainfall, and mean high temperature during trapping. Mathematically, the model for *D. ordii* explained probability of capture as a function of how much trapping was conducted and whether heavy rains or low temperatures occurred during nights of trapping. Success of capture increased with trapping effort, and decreased on days with either increased rainfall or low temperatures. Success of capture was greater for those transects that received an additional day of trapping effort, which occasionally occurred when success was low during the initial 3 days of trapping. Lowest success occurred in summer 2001 during a time when nearly 3.8 cm of rain fell. Also, success of capture was lower (0.66) in winter 2001 when average high temperature over the trapping period was 2°C (National Oceanic and Atmospheric Administration, National Climatic Data Center). Consistent with earlier research results (Calisher et al., 2005), we detected that extremely high temperatures did not impact success of capture, as rates remained high (0.79) during summer 2003 when average high temperatures was >37°C.

Although no habitat-specific patterns of φ were observed in this study, estimates of rate of survival may facilitate an understanding of other ecological phenomena associated with prairie rodents, e.g., the dynamics of rodent-borne diseases. Because *P. maniculatus* is a carrier of hantaviruses and plague-infected fleas (Childs et al., 1994; Anderson and Williams, 1997), the rates of φ presented in this study may be useful in modeling disease dynamics in prairie ecosystems. With the discovery of hantavirus pulmonary syndrome in 1993, efforts to understand dynamics of rodent populations have increased (Calisher et al., 2001, 2005), but few estimates of rates of survival for *P. maniculatus* are available. This study provides estimates of φ for *P. maniculatus* in a prairie region where hantaviral infections have been documented (Calisher et al., 2001).

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