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Survival and causes of mortality for pygmy rabbits (*Brachylagus idahoensis*) in Oregon and Nevada

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Factors influencing the survival of pygmy rabbits (*Brachylagus idahoensis*) are poorly understood and have received minimal attention in previous studies. We investigated survival and causes of mortality of pygmy rabbits in southeastern Oregon and northwestern Nevada. We trapped 298 rabbits on 4 sites and fitted each with radiotransmitters. We used known-fate models in program MARK to estimate survival rates of radiomarked pygmy rabbits from September 2005 to August 2006. The best model, based on Akaike's information criterion, indicated that survival rates varied among study sites, sexes, and with monthly interval in a parallel pattern [model S (area * sex + t)]. The estimated annual survival rate on the 4 study sites was notably low and varied from 0.003 ($SE = 0.003$) to 0.173 ($SE = 0.066$). Predation on radiomarked rabbits was high for both adult (88.6%) and juvenile (89.4%) rabbits. When the predator species could be determined, the most common predators of pygmy rabbits were coyotes (*Canis latrans*; 19.6%), avian predators (18.5%), and weasels (*Mustela* spp.; 9.8%). Population monitoring, which attempts to document local trends in pygmy rabbit abundance, should account for both the temporal and spatial variability of survival identified by this study. DOI: 10.1644/09-MAMM-A-068.1.

Key words: big sagebrush (*Artemisia tridentata*), Great Basin, known-fate models, mortality, predation, pygmy rabbit (*Brachylagus idahoensis*), radiotelemetry, survival rates

The pygmy rabbit (*Brachylagus idahoensis*), the smallest member of the leporid family in North America, is endemic to sagebrush-steppe habitats within the Great Basin and adjacent intermountain areas of the western United States (Green and Flinders 1980a; Katzner and Parker 1998). The distribution of this species is disjunct within a geographic range that reaches its westernmost extent in Oregon (Hall 1981). However, the current range is thought to have shrunk substantially from historical distributions (Verts and Carraway 1998). This leporid is considered a sagebrush obligate species (Heady et al. 2001) and is typically associated with dense, clumped stands of big sagebrush (*Artemisia tridentata* spp.—Green and Flinders 1980b; Katzner 1994; Orr 1940; Weiss 1984) where soils usually are deep and friable (Campbell et al. 1982; Green and Flinders 1980b; Himes and Drohan 2007; Janson 1946; Orr 1940; Weiss 1984). Type and availability of suitable habitats are considered critical determinants of size, survival, and stability of populations of these rabbits (Katzner and Parker 1997). Abundances of the pygmy rabbit are believed to be declining throughout most of its range (Dobler and Dixon

1990); as a result, the United States Fish and Wildlife Service has designated the pygmy rabbit as a Federal Species of Concern, and the agency has been petitioned to list this species as threatened or endangered under the Endangered Species Act (United States Fish and Wildlife Service 2003, 2005, 2008a).

Compared to larger leporids, pygmy rabbits are less swift and may effectively elude terrestrial and avian predators when under a tall, dense stand of big sagebrush (Gabler et al. 2001; Weiss 1984). Dense shrub habitats reduce vulnerability to predation for relatively slow-moving mammals whose abilities to evade predation in open areas are limited (Hallett 1982). Carnivores and raptors known to prey on pygmy rabbits include weasels (*Mustela* spp.), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), badgers (*Taxidea taxus*), northern harriers (*Circus cyaneus*), and owls. During winter periods pygmy rabbits use subnivean environments in

dense shrub communities, created by the accumulation of drifting snow, which provide access to a relatively dependable food source and protection from most predators and temperature extremes (Katzner and Parker 1997; Weiss and Verts 1984).

Few studies have investigated annual or monthly survival of pygmy rabbit populations (Sanchez 2007; Westra 2004; Wilde 1978). Wilde (1978) estimated survival rates in southern Idaho from recapture data at 2-week intervals using a standard life table. The lowest estimated 2-week survival rate was 0.69 on 1 March 1976, and annual adult survival was 0.12 for males and females. The annual survival of captive-reared pygmy rabbits released at different time periods in Idaho was 0.32 (95% confidence interval [95% CI] = 0.26–0.38), which did not differ significantly between sexes (Westra 2004). Annual survival of radiomarked pygmy rabbits in the Lemhi Valley in Idaho ranged from 0.07 to 0.45 (Sanchez 2007). Other investigations of annual survival rates of leporids range from 0.10 to 0.40 (Bond et al. 2001; French et al. 1965; Gibb 1990; Hartman and Barry, in press; Meslow and Keith 1968; Rose 1977; Wagner and Stoddart 1972), but these studies used different estimation methods, which makes comparisons difficult. Unlike pygmy rabbits (Green and Flinders 1980a), many leporid species undergo population cycles that influence estimates of annual survival; however, long-term population trends are poorly understood.

Given the concern over the status of this species throughout its range (United States Fish and Wildlife Service 2008a) and loss of big sagebrush communities (Knick et al. 2003; Rowland 2006), a more thorough understanding of survival rates of this sagebrush obligate is essential to understand population fluctuations and identify factors influencing their conservation. We used radiotelemetry methods to investigate survival rates and causes of mortality of pygmy rabbits on 4 study sites. We predicted that survival rates would differ between sexes, with male rabbits having a greater risk of predation due to their increased movements during the breeding season. Second, we predicted that survival rates would vary monthly and be lowest during winter when terrestrial predators may be able to track rabbits more effectively. Our study sites differed in grazing management, topographic position, and elevation, potentially influencing forage availability; therefore, we predicted that survival rates would differ among study sites. We also predicted that survival rates would be influenced by the mass : length ratio at time of capture, which served as an index of physical condition. We expected rabbits with higher mass : length ratios to be in better physical condition and therefore have greater survival rates than rabbits with lower ratios. Herein, we report estimates of monthly and annual survival rates for pygmy rabbits and known causes of mortality.

MATERIALS AND METHODS

Study area.—Four study sites were chosen from Sheldon National Wildlife Refuge in northwestern Nevada and the
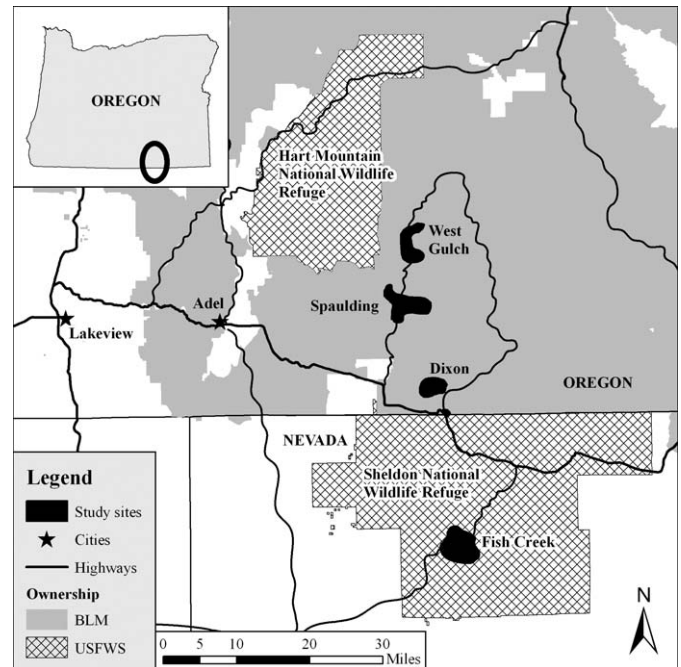
FIG. 1.—Four study sites chosen to investigate survival and causes of mortality for pygmy rabbits in southeastern Oregon and northwestern Nevada from June 2005 to June 2007.

Beatys Butte Allotment in southeastern Oregon (Fig. 1). Sheldon National Wildlife Refuge is administered by the United States Fish and Wildlife Service and encompasses 575,000 ha. The Beatys Butte Allotment is administered by the Bureau of Land Management and consists of 220,301 ha. These areas are characteristic of shrub-steppe communities (West 1983) and consist of flat sagebrush plains interrupted by rolling hills, ridges, and draws. Elevations range from 1,200 to 2,400 m in each area. Annual precipitation and temperature average 28 cm and 21°C, respectively (Gregg 2006).

Study sites were primarily located in bottomlands, which influenced their soil characteristics and vegetative community. Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) and basin big sagebrush (*A. t. tridentata*) were consistently identified as the dominant shrub species on the study sites (Crawford 2008; Table 1). Vegetative characteristics, including shrub density, maximal shrub height, percent shrub canopy cover, and percent understory cover, also did not vary among study sites (Crawford 2008). Soil textures measured at the 4 study sites were consistently sandy loam (Crawford 2008). Domestic livestock were grazed during alternate years on parcels within the Beatys Butte Allotment as part of a 2-year grazing rotation management plan. The Spaulding site, however, was grazed every year because it was used for cattle gathering in the fall (L. Boothe and T. Forbes, Bureau of Land Management, pers. comm.). Domestic livestock grazing was eliminated from the Sheldon Wildlife Refuge in 1994 (Gregg 2006); however, an estimated population of approximately 800 nonnative horses and 90 burros directly and indirectly impact wildlife and their habitats by consuming forage, trampling vegetation, and compacting soils (United States Fish and

TABLE 1.—Years livestock were present and grazed, elevation, topographic position, and dominant and subdominant shrub species on 4 study sites in southeastern Oregon and northwestern Nevada from June 2005 to June 2007.

Study site	Livestock grazing year	Elevation (m)	Topographic position	Dominant shrub species	Subdominant shrub species
Dixon	2006	1,780	Bottomland	Wyoming big sagebrush	Low sagebrush and green rabbitbrush
Spaulding	2005 and 2006	1,600	Bottomland and side slope	Wyoming big sagebrush and basin big sagebrush	Green rabbitbrush
West Gulch	2005	1,650–1,700	Bottomland and terrace	Wyoming big sagebrush and basin big sagebrush	Green rabbitbrush
Fish Creek	None	1,860	Bottomland and side slope	Wyoming big sagebrush and basin big sagebrush	Bitterbrush and green rabbitbrush

Wildlife Service 2008b). Since 1994 prescribed fire has been the primary management tool used to manage refuge habitats. However, <6% of the refuge has been burned by wild or prescribed fires since the early 1980s (Gregg 2006), including ~0.02 km² of the Fish Creek study site. Periodic wild fires have been part of the natural disturbance regime of shrub-steppe communities on Beatys Butte; however, no fires occurred on this allotment during our study.

Capture and handling.—Individual pygmy rabbits were livetrapped on 4 study sites from June to September 2005 to maximize the number of rabbits sampled after juvenile emergence. During June and July trapping was conducted during morning hours (0400–1000 h) to minimize the risk of separating juveniles from nursing females. During August and September, after juveniles were weaned, trapping was conducted overnight (1900–1000 h) to maximize trapping effort. Collapsible traps (Tomahawk Live Trap Co., Tomahawk, Wisconsin) with double doors (#203, 23 × 23 × 60 cm) or single doors (#201, 12 × 12 × 40 cm) were set in areas that exhibited rabbit activity, including burrow entrances and runways. Traps were covered with brown burlap bags or white plastic feed sacks to provide protection from thermal stress and predators and were camouflaged with vegetation. Initially, 120 radiotransmitters were distributed evenly among the 4 study sites to ensure a sufficient sample size. During fall 2005 we observed substantial rabbit mortality due to predation. Consequently, a concentrated effort to opportunistically trap new individuals was made to maintain a minimal number (15–20) of radiomarked rabbits on each study site from November 2005 to April 2007. Capture and handling of pygmy rabbits followed animal care and use guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by Oregon State University (Animal Care and Use Proposal 3744), the Oregon Department of Fish and Wildlife (Scientific Take Permit 008-05), and the Nevada Department of Wildlife (Scientific Collection Permit 84-0437540).

Captured rabbits were transferred from traps into a cloth bag to minimize stress during handling and were marked with a uniquely numbered passive integrated transponder tag. Very-high-frequency radiotransmitters (164 and 165 MHz band, 7.1 g and 10.6 g, model RI-2DM; Holohil Systems Ltd., Carp, Ontario, Canada) were attached to all adult rabbits and juveniles weighing >250 g. Transmitters were attached to each individual on a zip-tie encased in flexible rubber tubing (2.0 g) to minimize abrasion. Each transmitter was equipped with a motion-sensitive switch that doubled the transmitter's pulse rate when inactive for 12 h. Sex and age were recorded for each captured individual. Age classifications (adult or juvenile) were based on weight and relative coat condition of individuals; adult rabbits were generally >325 g and had more buff-colored fur, especially inside the ear. Reproductive condition, when discernable, was noted. Males were classified as sexually active when testes were descended, and females were considered sexually active when lactating (when hair was matted around nipples or milk was observed) or when the vagina was perforate. Weight, body length, right ear, and right hind-foot length were recorded for all individuals captured. We examined monthly differences in mass : length ratios, an index of physical condition (Bailey 1968; Jakob et al. 1996), using an analysis of variance procedure (Ramsey and Schafer 2002) in S-plus software, version 7.0 (Insightful Corporation, Seattle, Washington). Differences were considered significant at $\alpha = 0.05$.

Monitoring.—Locations and fate of radiomarked rabbits were monitored from June 2005 to April 2007. Individuals were located 4 or 5 times per week using a handheld receiver (model R2000 receiver; Advanced Telemetry Systems, Isanti, Minnesota, and model TR-2 receiver; Telonics Inc., Mesa, Arizona) and a directional yagi antenna. Monitoring times of radiomarked rabbits varied to accumulate locations during crepuscular, midday, and occasionally night hours, which provided a more thorough representation of each individual's daily movements and avoided autocorrelation of locations (Otis and White 1999; Swihart and Slade 1985a, 1985b). Radiomarked animals were tracked to within 3 m, and positive visual identifications were made. Locations were recorded using a global positioning system (Garmin International, Inc., Olathe, Kansas).

Dead rabbits were examined to identify causes of mortality when possible. Raptor predation was apparent from bird fecal sprays at the kill site and the presence of feathers. Other predator-caused mortalities were determined from examination of rabbit carcasses or tracks surrounding the location. Weasels tended to inflict distinctive injuries on the animal such as unique bite marks on the neck or decapitation. Coyote

TABLE 2.—A list of a priori hypotheses and models for testing the effects of various factors on survival rates of pygmy rabbits in southeastern Oregon and northwestern Nevada from September 2005 to August 2006.

Hypothesis description	Model
1. Survival rates are different between sexes	S (sex)
2. Survival rates are different among study sites	S (area)
3. Survival rates are different among monthly time intervals	S (t)
4. Survival rates are constant among sites, monthly time intervals, and between sexes	S (.)
5. Survival rates decline linearly from May through April	S (T)
6. Survival rates fluctuate quadratically from May through April	S (TT)
7. Survival rates are different among study sites with an interaction with monthly intervals	S (area * t)
8. Survival rates are different between sexes with an interaction with study site	S (sex * area)
9. Survival rates are different between sexes with an interaction with monthly intervals	S (sex * t)
10. Survival rates are different among study sites in a parallel pattern with monthly intervals	S (area + t)
11. Survival rates are different between sexes in a parallel pattern with monthly intervals	S (sex + t)
12. Survival rates vary between sexes in a parallel pattern with study sites	S (sex + area)
13. Survival rates vary among study sites, monthly time intervals, and between sexes	S (area * sex * t)
14. Survival rates vary among study sites and between sexes in a parallel pattern with monthly intervals	S (area * sex + t)
15. Survival rates vary between sexes in a parallel pattern with study sites and monthly interval	S (area + sex + t)
16. Survival rates vary by morphometric covariate(s)	S (X_i)[a]
17. Survival rates vary by adults and juveniles (covariate)	S (age)

[a] The symbol X_i represents the potential effects of weight (kg), right ear length (cm), right foot length (cm), total body length (m), mass : length ratio (kg/m), or a combination of these, at time of capture.

kills were identified by presence of tracks near the carcass, scat, and regurgitation. Mortality dates were centered within time intervals for individuals that were found dead >24 h since their last location.

Survival analysis.—Survival rates (S) were estimated for radiomarked individuals from 1 September 2005 to 31 August 2006, the 12-month interval that included the most radio-marked rabbits. Estimates of survival and potential influences of sex, study site, time, age class, and physical condition were done with known-fate models in program MARK (White and Burnham 1999). This procedure allowed staggered entry and censoring of individuals that left the study area or could not be found. Survival was estimated on monthly intervals with data entered as either the individual survived the month, died during the month, or was censored from the data set. To minimize the influence that mortalities related to capture stress would have on survival estimates, pygmy rabbits were entered into the data set during the month after they were captured, unless capture occurred during the 1st 7 days of the month. Individuals were censored from the data set if they were missing during the 1st or last 7 days of the month. This eliminated any bias in our survival estimates due to right-censoring, individuals lost to follow-up, when mortality could have been associated with transmitter failure (Murray 2006). Additionally, rabbits that had transmitter failure were censored, unless they were recaptured and fitted with a new transmitter.

Program MARK used maximum-likelihood estimation to optimize model parameters and to fit models to the data (White and Burnham 1999). We used the 2nd-order Akaike information criterion corrected for small sample sizes (AIC_c) and Akaike weights in program MARK for model selection (Burnham and Anderson 2002). We considered the model with the smallest AIC_c value to be the best model to fit the data and any model within 2 AIC_c values as a competing model

(Burnham and Anderson 2002). To identify any competing models we used the difference between the AIC_c value for the best model and the ith model (Δ_i), and the Akaike weights were used to assess the strength of evidence of one model versus another model. Pygmy rabbits are usually found in aggregations because of their association with sagebrush and they maintain weak social associations within populations (Green and Flinders 1980a; Janson 1946; Weiss and Verts 1984). However, individuals were captured at different times and places, so we had no reason to suspect dependence among individuals. No appropriate goodness-of-fit test for known-fate data with individual covariates exists (G. C. White, Colorado State University, pers. comm.); therefore, we assumed that little to no overdispersion existed in the data ($\hat{c} = 1.0$), so we did not use $QAIC_c$ for model selection. Additionally, we used the regression coefficients (β) and their 95% *CI*s as evidence or lack thereof of an effect for various factors or covariates in competing models.

To test for potential effects on survival rates, a list of a priori candidate models was developed based on our hypotheses (Table 2). The most general model hypothesized that survival rates would vary among study sites, sexes, and over monthly time intervals [model S (area * sex * t)]. Additional hypotheses included: survival would be constant throughout the study (.), vary by monthly interval (t), follow linear (T) or quadratic (TT) trends from May through April, vary by sex (sex), or vary by study site (area). To test models that incorporated differences in survival between sexes or among study sites, individuals were assigned to 1 of 8 possible groups. Analyses that included 2 or more groups explored additive (+) and interactive (*) effects between group variables and time effects. Models including individual covariates (X_i) were compared to model S(.) to determine if the covariate models improved the fit to the data. Individual covariates included age (adult or juvenile), weight (kg), ear

length (cm), foot length (cm), total body length (m), and mass : length ratio (kg/m) at time of capture. We used the mass : length ratio as an index of physical condition (Bailey 1968). Because pygmy rabbits have a short life span (Sanchez 2007), correlating survival with individual covariates that were measured at the time of capture was considered appropriate.

RESULTS

Capture.—We radiomarked 121 pygmy rabbits from June–September 2005; 90 were distributed evenly among the Dixon, Spaulding, and West Gulch study sites, and 31 were marked on the Fish Creek site. Trapping effort needed to mark 30 rabbits was relatively consistent on 3 study sites: Fish Creek (15 trap days), Spaulding (16 trap days), and West Gulch (22 trap days). Trapping success on the Dixon site was considerably less, because it took 33 trap days to capture 30 rabbits despite our efforts to vary trapping techniques. In addition, we began to trap opportunistically in early November 2005 to offset the substantial loss of radiomarked animals due to predation. During June 2005–April 2007 we radiomarked 298 rabbits (132 males and 166 females), 62% of which were adults; the distribution follows by study site (adults and juveniles): Dixon (54 and 29), Fish Creek (36 and 38), Spaulding (56 and 24), and West Gulch (39 and 22). Trapping effort was substantially more effective during winter months, November–March, because we were able to locate active burrow use during periods of fresh snow and trap those individuals. We found no evidence of variation in the index of physical condition among months ($F_{11,211} = 1.05$, $P = 0.4080$; Fig. 2), because these data were quite variable and lacked the precision to detect differences. Nevertheless, monthly trends in mass : length ratios were prominent for both males and females (Fig. 2), so we used this index of condition to investigate possible reasons for any monthly variation in survival rates. We did not correct the index of physical condition for pregnant individuals because only 3 of 166 females were suspected of being pregnant, and they were from different study sites.

Survival.—Annual and monthly survival rates were estimated from 1 September 2005 to 31 August 2006 because this time period included the most radiomarked rabbits over any 12-month interval ($n = 241$; 110 males, 131 females). During this year 169 (70%) rabbits died due to predation. We censored 7 (3%) rabbits from the data set because they disappeared from the study area or their transmitters failed during the study. Therefore, the survival estimates were biased minimally due to right censoring when the censoring could have been associated jointly with transmitter failure and mortality (Murray 2006).

The best model for the data [S (area + sex + t)], based on AIC_c, indicated that survival rates varied between sexes in a parallel pattern with study site and monthly time interval (Table 3). This model accounted for 52% of the AIC_c weight of all models considered and was ~1.8 times more likely than
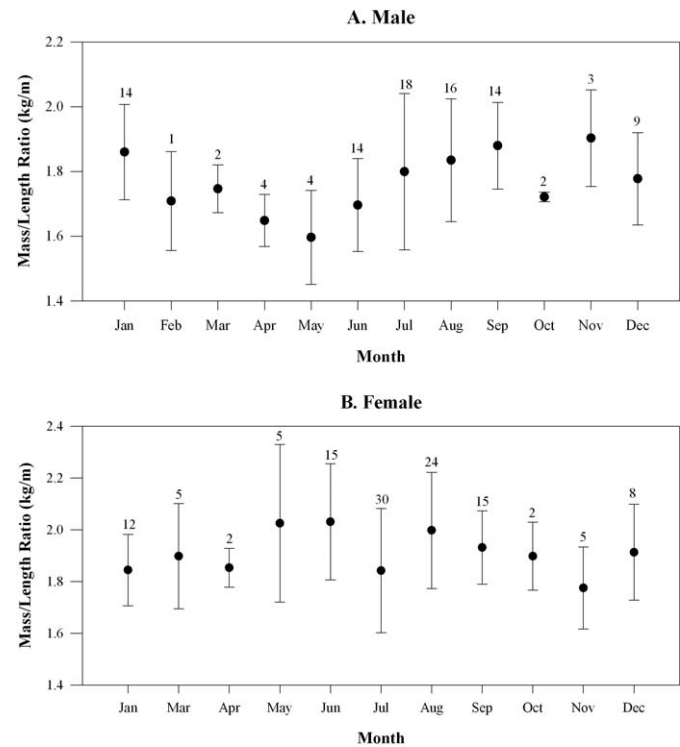
FIG. 2.—Mass : length ratios of adult A) male ($n = 101$) and B) female ($n = 123$) pygmy rabbits at monthly intervals. Error bars represent 95% *CI*s around means. Individuals were sampled on 4 study sites in southeastern Oregon and northwestern Nevada from June 2005 to April 2007. No adult females were captured in February. Numbers of pygmy rabbits sampled each month, not total sample size, are listed above *CI*s.

the 1 competing but very similar model [S (area * sex + t)], which accounted for 28% of the AIC_c weight. The competing model suggested that survival rates varied among study sites, sexes, and with monthly intervals in a parallel pattern and had a ΔAIC_c value of 1.24. We considered model S (area * sex + t) to be the most appropriate model for our data because it had a lower deviance (766.97) and fit the data better. Further, the area * sex interaction in this model does not constrain survival among sites and sexes to be parallel. Rather, it is more biologically appropriate because it allows survival among sites and sexes to vary independently, as appeared to be the case in this study.

Based on this analysis, we found no evidence that survival rates varied solely among monthly time intervals, among study sites, or only between sexes, because models S (t), S (area), and S (sex) had ΔAIC_c values > 8.0 (Table 3). Model S (age) had a ΔAIC_c value of 79.5, indicating no support for differences in survival rates between adults and juveniles. Also, no evidence existed for a linear or quadratic time trend in survival estimates from May through April, because both models S (T) and S (TT) had ΔAIC_c values > 73.0. Finally, no evidence was produced for an effect of individual covariates on survival rates; all models with individual covariates (weight, ear length, foot length, total body length, or mass : length ratio) had ΔAIC_c values > 79.0 and did not

TABLE 3.—Model selection results for estimation of survival rates of pygmy rabbits ($n = 241$) on 4 study sites in southeastern Oregon and northwestern Nevada from September 2005 to August 2006.

Model[a]	AIC$_c$	ΔAIC$_c$	AIC weight	Model likelihood	K[b]	Deviance
{S (area + sex + t)}	804.56	0.00	0.52	1.00	16	771.96
{S (area * sex + t)}	805.80	1.24	0.28	0.54	19	766.97
{S (area + t)}	806.76	2.20	0.17	0.33	15	776.23
{S (sex + t)}	811.31	6.75	0.02	0.03	13	784.91
{S (area * t)}	811.72	7.16	0.01	0.03	48	710.36
{S (t)}	814.56	10.00	0.00	0.01	12	790.22
{S (sex * t)}	826.68	22.12	0.00	0.00	24	777.35
{S (area * sex * t)}	864.72	60.17	0.00	0.00	96	650.31
{S (area + sex)}	877.41	72.85	0.00	0.00	5	867.34
{S (TT)}	878.25	73.69	0.00	0.00	3	872.22
{S (area)}	878.83	74.27	0.00	0.00	4	870.79
{S (sex * area)}	879.82	75.26	0.00	0.00	8	863.66
{S (sex)}	880.63	76.07	0.00	0.00	2	876.62
{S (.)}	882.83	78.27	0.00	0.00	1	880.82
{S (total length)}	883.80	79.24	0.00	0.00	2	879.78
{S (ear length)}	883.85	79.29	0.00	0.00	2	879.83
{S (weight)}	884.01	79.45	0.00	0.00	2	879.99
{S (age)}	884.10	79.54	0.00	0.00	2	880.09
{S (T)}	884.39	79.83	0.00	0.00	2	880.38
{S (foot length)}	884.51	79.95	0.00	0.00	2	880.50
{S (mass : length ratio)}	884.65	80.09	0.00	0.00	2	880.64

[a] Variable definitions: time effects modeled as constant (.), variable time effects (t), linear time trends (T), quadratic time trends (TT), study site (area), and sex (sex).
[b] Number of parameters.

improve the fit to the data compared to S (.). In addition, the 95% *CI*s for the regression coefficients for these covariates all overlapped 0 substantially.

Based on model S (area * sex + t), annual survival rates from September 2005 to August 2006 varied from 0.003 (*SE* = 0.003, 95% *CI* = 0.000–0.023) for males at Dixon to 0.173 (*SE* = 0.066, 95% *CI* = 0.078–0.342) for females at Spaulding (Table 4). These estimates were very precise because all coefficients of variation (*CV*) were <10% and varied from 2.3% to 6.6% (Table 4). Female rabbits had greater annual and monthly survival estimates than males on all study sites except Fish Creek (Table 4). Evidence existed for a significant difference between sexes ($\hat{\beta}$ = 0.746, *SE* = 0.043, 95% *CI* = 0.663–0.829) based on model S (sex). The extremely low survival rates for males at Dixon and higher rates for females at Spaulding and West Gulch appeared to be responsible for the significance and inclusion of the sex parameter in the best model. In addition, male and female survival rates for Spaulding and West Gulch sites were higher than those for Dixon and Fish Creek (Fig. 3). Monthly survival rates varied from 0.328 (*SE* = 0.085, 95% *CI* = 0.186–0.509) for males on Dixon in May 2006 to 0.988 (*SE* = 0.012, 95% *CI* = 0.916–0.998) for females on Spaulding in June 2006. Survival rates of male and female pygmy rabbits were low during November 2005–January 2006 and April–May 2006.

Predation.—Pygmy rabbits were subject to high levels of mortality due to predation during this study, because 265 (88.9%) of 298 radiomarked individuals were killed by

TABLE 4.—Survival rates, *SE*s, 95% *CI*s, and coefficients of variation (*CV*s in %) from model S (area * sex + t) for 241 pygmy rabbits on 4 study sites in southeastern Oregon and northwestern Nevada from September 2005 to August 2006.

Group	Sex	n	Annual survival estimate	SE	95% CI Lower	95% CI Upper	CV
Dixon	♂	36	0.003	0.003	0.000	0.023	6.6
	♀	29	0.067	0.040	0.020	0.202	3.3
Fish Creek	♂	26	0.056	0.037	0.015	0.190	3.4
	♀	30	0.040	0.026	0.011	0.138	3.6
Spaulding	♂	28	0.083	0.046	0.027	0.229	2.9
	♀	36	0.173	0.066	0.078	0.342	2.3
West Gulch	♂	20	0.100	0.064	0.027	0.309	2.9
	♀	36	0.152	0.059	0.068	0.304	2.3

predators from June 2005 to April 2007. We were able to identify the predator species for 133 of the 265 (50.2%) mortalities. Usually, we were unable to identify the predator species responsible for rabbit mortality when only the radiocollar and scant remains were found (37.1%). Coyotes (*C. latrans*; 19.6%) and various raptors (18.5%) were the most commonly confirmed predators of radiomarked pygmy rabbits. Northern harriers (*C. cyaneus*), golden eagles (*Aquila*
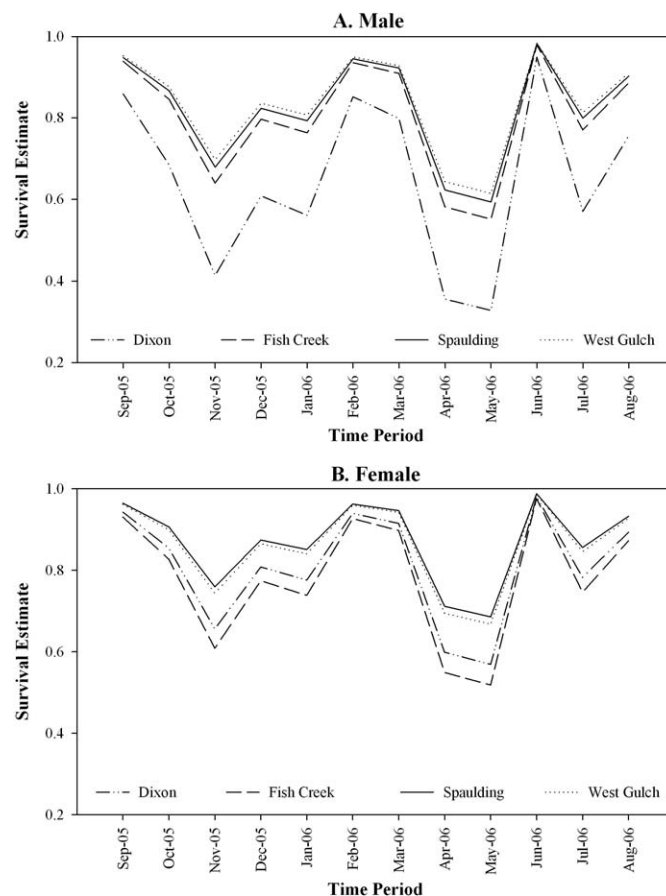
FIG. 3.—Monthly survival rates of A) male ($n = 110$) and B) female ($n = 131$) pygmy rabbits from model S (area * sex + t) on 4 study sites in southeastern Oregon and northwestern Nevada from September 2005 to August 2006.
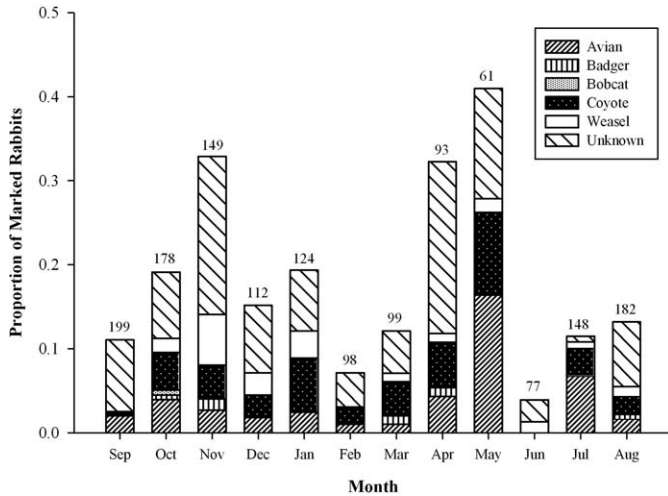
FIG. 4.—Proportion of radiomarked pygmy rabbits killed by predators by month on 4 study sites in southeastern Oregon and northwestern Nevada from June 2005 to April 2007. Numbers of rabbits radiomarked each month are listed above the columns.

chrysaetos), and owls were observed on the study sites and likely killed pygmy rabbits; however, direct predation by these raptors was not documented, and it was difficult to identify the species of raptor responsible from the scant remains that were usually available. Other common predators included weasels (*Mustela* spp.; 9.8%) and badgers (*T. taxus*; 2.3%), and a bobcat (*L. rufus*; 0.4%) killed 1 rabbit.

A comparison of the proportion of radiomarked rabbits killed monthly by predators revealed 3 noteworthy patterns (Fig. 4). Coyotes were a relatively consistent predator of pygmy rabbits throughout the year. In contrast, the proportion of rabbits killed by weasels was greatest during the late fall and winter, October–January. Finally, the relative number of rabbits killed by avian predators was variable throughout the year but highest in May during the spring migration of these raptors. Different predators were responsible for 2 periods of low survival (Fig. 3) on the 4 study sites (Fig. 4). From November 2005 to January 2006 weasels and, to a lesser extent, coyotes were the most common predator of radio-marked rabbits, in addition to being the most common predator on the Dixon site during this study. In April and May 2006 avian predators were responsible for the majority of the mortality, in addition to being the most common predators on the Fish Creek and Spaulding sites during this study.

DISCUSSION

Survival rates of radiomarked pygmy rabbits varied among study sites, sexes, and months in a parallel pattern in our study, which generally supported our initial hypotheses. In contrast, we found no evidence of an effect of physical condition (mass : length ratio) on monthly survival rates; therefore, rabbits killed by predators were not likely in poor condition, so mortality was related to other factors. Mean mass : length ratios of adults fluctuated throughout the year and variation was high (Fig. 2). Adult female rabbits had greater mass : length

ratios in the late spring and summer than in winter and early spring. Only 3 of the females captured during this time period were suspected pregnant, so this was not the reason for increased mass : length rates during this season. Additionally, mass : length ratios of adult males were lowest during the spring and early summer, possibly due to increased movements during the breeding season (Crawford 2008). Survival estimates in our study did not vary by age class. All radiomarked pygmy rabbits weighed >250 g; therefore, survival estimates did not include the high mortality rates of juveniles during the 2 months following emergence from their natal burrows (Estes-Zumpf and Rachlow 2009).

Survival of pygmy rabbits was notably low in our study. Although we cannot completely rule out the possibility that radiocollars affected survival, we did use weight and the mass : length index of physical condition as individual covariates in the analyses and found that they were not significant. When whole caresses were recovered, analyses of stomach contents indicated that individuals had been eating. We also found no evidence that radiocollars caused any physical damage to the rabbits or resulted in increased mortality. Annual survival of radiomarked pygmy rabbits in the Lemhi Valley in Idaho ranged from 0.07 to 0.45 (Sanchez 2007), which is within the range of our estimates. Consequently, we concluded that radiocollars did not make rabbits more vulnerable to predation in our study.

Strong evidence was found that survival varied among months, with the lowest survival occurring from November 2005 to January 2006 and April to May 2006. These 2 periods of low survival likely were associated with an increased likelihood of pygmy rabbits encountering predators, especially weasels during the winter and raptors in the spring. Similarly, Sanchez (2007) and Wilde (1978) documented low survival among pygmy rabbits in Idaho in late winter and early spring. In Idaho, mortality of pygmy rabbits peaked in the spring and might have been associated with increased foraging by both avian and terrestrial species (Sanchez 2007). Mate searching and elevated agonistic behavior during the breeding season could place additional stress on individuals (Gross et al. 1974). Furthermore, timing of lowest survival is not consistent among leporids. Low periods of survival for eastern cottontail (*Sylvilagus floridanus*) during winter have been documented (Bond et al. 2001; Trent and Rongstad 1974). However, populations of brush rabbit (*Sylvilagus bachmani*) had decreased survival from September to March (McKay and Verts 1978). In our study the highest survival occurred during September 2005, February and March 2006, and June–August 2006. Similarly, survival rates for pygmy rabbits in Idaho were highest (100%) in summer and early fall (Wilde 1978).

Annual survival of pygmy rabbits was highly variable among study sites and sexes. Similarly, Sanchez (2007) reported that annual survival for pygmy rabbits in the Lemhi Valley of Idaho was influenced greatly by study site. Differences in predator abundance, grazing management strategies, and vegetative characteristics could have been responsible for differences in annual survival rates among our

study sites. Vegetative characteristics, however, did not vary appreciably among study sites (Crawford 2008), so we saw no indications that differences in vegetation might have been the cause, although such factors can be influential at the scale of home range of an individual. With respect to cattle grazing, study sites where grazing was allowed had the highest (Spaulding, $S = 0.173$) and lowest (Dixon, $S = 0.003$) annual survival rates. The Spaulding site received minimal grazing pressure from livestock during fall 2005 and 2006 gathering events, whereas evidence of livestock grazing on the Dixon site was prominent when it was used from June to September 2006. Additionally, annual survival rates on Sheldon National Wildlife Refuge, where cattle grazing was not permitted but grazing by feral horses was sporadic, were relatively low (Fish Creek, $S = 0.040$–0.056). We did not measure forage utilization or any direct influence of cattle grazing on habitat quality, so we cannot make any conclusions about the effects of grazing on survival of pygmy rabbits. Although other studies have suggested that domestic grazing can influence shrub cover and soil compaction by trampling and understory grass cover via foraging (Gahr 1993; Knick 1999; Thines et al. 2004), these direct impacts need further study. We strongly suspect that the differences in survival rates among our study sites were a result of differences in predator densities or use of the sites because predation was the major cause of mortality.

Female pygmy rabbits had considerably higher annual and monthly survival than males on 3 of our 4 study sites. Lower annual survival rates for male rabbits could be associated with a greater risk of predation due to greater movements and larger home ranges of males (Crawford 2008), particularly during the breeding season as males search for estrous females. In contrast, annual survival rates of wild (Sanchez 2007; Wilde 1978) and reintroduced (Westra 2004) pygmy rabbits in Idaho did not vary by sex. In other leporids variation in survival between sexes was not consistent. In California, *S. bachmani* had unequal survival between sexes (Connell 1954); however, *S. floridanus* in Mississippi (Bond et al. 2001) had equal survival rates for males and females.

Pygmy rabbits in our study had annual survival rates ranging from 0.003 to 0.173 ($SE = 0.003$–0.066), which were low but generally consistent with the few studies on this species. *CV*s for all area * sex combinations were all <10% (Table 4) indicating that our sample sizes were adequate to estimate annual survival rates. Annual survival of pygmy rabbits in Idaho was 12% (Wilde 1978). Westra (2004) reported higher annual survival rates of 32% for pygmy rabbits reintroduced in Idaho, which might have benefited from availability of artificial burrows. Further, mean annual survival rates of radiomarked pygmy rabbits in Idaho varied widely for each sex (male $S = 0.07$–0.45; female $S = 0.09$–0.44— Sanchez 2007). Survival rates for *B. idahoensis* generally were below the range of estimates of annual survival for other leporids, although different estimation methods make comparisons difficult. Studies in southwestern Wisconsin, east-central Illinois, and Mississippi estimated annual survival rates of *S. floridanus* to be ~20% (Bond et al. 2001; Rose 1977; Trent

and Rongstad 1974). Low estimates ($S = 0.04$) of annual survival also were reported for black-tailed jackrabbits (*Lepus californicus*) in southeastern Idaho (French et al. 1965).

Although population densities of pygmy rabbits can fluctuate dramatically among years, Green and Flinders (1980a) suggested that evidence for multiannual cycles was lacking for pygmy rabbits. Although our survival analysis represents 1 year of monitoring, examination of these data suggests that pygmy rabbit populations can undergo dramatic declines in successive years. A subsequent pygmy rabbit investigation on our study sites in summer of 2007 indicated low abundances (T. Lawes, Oregon State University, pers. comm.). Trap success during our study in summer 2005 (0.005 rabbits/trap hour) was considerably higher than during summer 2007 (0.002 rabbits/trap hour). Therefore, the extremely low survival rates observed in our study were likely from declining populations. Similarly, Weiss and Verts (1984) observed a marked decrease in pygmy rabbit activity and abundance at 66% of their occupied sites 1 year later, which suggested that populations were susceptible to rapid declines and local extirpation. Pygmy rabbit populations may function as metapopulations (Hanski and Gilpin 1991); declining populations with low survival rates may be maintained over generations by immigration from local increasing populations with higher survival rates. In Canada, similar declines in trapping efficiency were documented for cyclic populations of snowshoe hares (*Lepus americanus*— Keith and Meslow 1968; Meslow and Keith 1968).

Although we were able to identify predator species for only 50.2% of moralities, radiocollars with scant but fresh rabbit remains also were frequently recovered (37.1%), which suggested that predation was responsible for a high percentage of the unknown deaths. Many of the carcasses from undetermined predator species might have been scavenged by another predator after death, making it difficult to identify the species responsible for mortality. Additionally, it was virtually impossible to identify the specific species of raptors responsible for mortality unless they were observed killing or consuming rabbits. Although it was possible that some individuals could have died from disease, malnutrition, or something other than predation, our monitoring intervals were relatively short (4 or 5 times per week) and few intact carcasses were found. Consequently, we concluded that predation was the primary cause of mortality.

Predators of pygmy rabbits during this investigation were coyotes, weasels, badgers, bobcats, and avian species including northern harriers and owls, which were similar to those from other studies of pygmy rabbits (Gahr 1993; Sanchez 2007; Wilde 1978). Different predators were responsible for 2 distinct periods of high predation and low survival of pygmy rabbits in our study. Based on snow tracking, predation by weasels in our study was most common during winter months (November 2005–January 2006) when they moved from burrow to burrow searching for and killing rabbits. Similar weasel predation was noted on pygmy rabbits in Idaho (Wilde 1978). In contrast, avian predators were

responsible for the majority of mortality of radiomarked rabbits in April and May 2006 during spring migration. Gahr (1993) reported only 2 instances of confirmed predation on radiomarked pygmy rabbits, both by avian predators in May and August. Coyote predation was relatively consistent throughout our study. Coyotes and badgers preyed upon some individuals by digging through and destroying pygmy rabbit burrows, which was similar to coyote predation on pygmy rabbits in Idaho (Wilde 1978).

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APPENDIX I

Monthly sample sizes of radiomarked pygmy rabbits used to estimate survival on 4 study sites in southeastern Oregon and northwestern Nevada from September 2005 to August 2006. Total represents the number of radiomarked pygmy rabbits used to estimate survival for each group (study site and sex) across all months.

Group	Sex	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Total
Dixon	♂	14	12	9	6	3	5	6	4	4	5	9	8	36
	♀	13	10	8	6	7	11	11	10	8	7	10	9	29
Fish Creek	♂	9	12	12	7	6	12	11	9	4	2	5	8	26
	♀	11	15	14	9	9	12	11	11	3	3	5	8	30
Spaulding	♂	9	12	9	8	9	12	11	11	7	11	11	9	28
	♀	13	17	17	14	14	16	13	13	10	13	13	12	36
West Gulch	♂	8	8	6	6	6	4	6	9	6	3	5	6	20
	♀	17	21	21	14	14	12	13	15	10	8	10	13	36
Monthly total		94	107	96	70	68	84	82	82	52	52	68	73	