Western North American Naturalist

Volume 72 | Number 4 Article 13

2-8-2013

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Western North American Naturalist 72(4), © 2012, pp. 569–581

HOMING BEHAVIOR AND SURVIVAL OF PYGMY RABBITS AFTER EXPERIMENTAL TRANSLOCATION

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ABSTRACT.—Habitat fragmentation is hypothesized to influence movements of animals between isolated habitat fragments and to affect survival of animals moving between fragments. Translocation experiments can provide quantitative information on movements and survival. We assessed potential barriers to dispersal and survival of pygmy rabbits (*Brachylagus idahoensis*), a species of conservation concern that is hypothesized to be sensitive, after translocation, to fragmentation of its sagebrush habitats. We measured homing tendency and estimated survival of pygmy rabbits after short-distance (1–2 km) experimental translocations at sites in southeastern Oregon. We captured, radio-tagged, and translocated 59 pygmy rabbits across 3 landscape categories of habitat fragmentation. We used logistic regression to compare among landscapes the odds of homing, after accounting for sex and displacement distance of individuals. We used known-fate models in program MARK to estimate survival rates of rabbits after translocation. Fifteen percent of translocated pygmy rabbits successfully homed to within 150 m of their original capture locations. Individuals translocated across fragmented landscapes with patchy cover of big sagebrush were the most likely to home, whereas rabbits translocated across relatively continuous big sagebrush cover bisected by a road were least likely to home. We also found that pygmy rabbits that homed had higher survival rates than those that did not return to their home areas, and rabbits that settled near roads had lower survival rates than those that did not settle near roads. The proximity of the largest patch of big sagebrush also had a positive influence on the survival of rabbits after translocation. Our results indicate that fragmentation does not necessarily impede movements nor does it necessarily reduce survival.

RESUMEN.—Se hipotetiza que la fragmentación del hábitat influye los movimientos de animales entre fragmentos de hábitats aislados y que afecta la supervivencia de animales que se trasladan entre fragmentos. Los experimentos de translocación pueden proporcionar información cuantitativa sobre los movimientos y la supervivencia. Evaluamos las posibles barreras a la dispersión y la supervivencia de los conejos pigmeos (*Brachylagus idahoensis*), una especie que se intenta conservar y que se considera sensible a la fragmentación de sus hábitats de arbustos Artemisa, después de su translocación. Medimos la tendencia hogareña y estimamos la supervivencia de los conejos pigmeos después de translocaciones experimentales de corta distancia (1 a 2 km) en sitios del sureste de Oregon. Capturamos, marcamos con radiotransmisores, y translocamos a 59 conejos pigmeos a través de tres categorías de entornos de fragmentación del hábitat. Usamos una regresión logística para comparar las probabilidades de establecer su hogar entre los entornos luego de tomar en cuenta el sexo y la distancia de desplazamiento de los individuos. Usamos modelos de destino conocido en el programa MARK para estimar las tasas de supervivencia de conejos después de la translocación. El 15% de los conejos pigmeos translocados establecieron su hogar exitosamente a ≤150 m de sus ubicaciones de captura originales. Los individuos translocados a lo largo de entornos fragmentados con cubierta irregular de Artemisas grandes fueron los que más probabilidades tuvieron de establecerse, mientras que los conejos translocados a lo largo de cubiertas relativamente continuas de arbustos Artemisa grandes, bisectadas por una carretera, fueron los que tuvieron menos probabilidades de establecer su hogar. También encontramos que los conejos pigmeos que establecieron su hogar tuvieron una mayor tasa de supervivencia que aquellos que no regresaron a sus ámbitos hogareños, y que los conejos que se establecieron cerca de las carreteras tuvieron una menor tasa de supervivencia que aquellos que no se establecieron cerca de las carreteras. La proximidad del parche más grande de arbustos artemisas también tuvo una influencia positiva en la supervivencia de los conejos después de la translocación. Nuestros resultados indican que la fragmentación no impide necesariamente los movimientos ni reduce necesariamente la supervivencia.

Much of the big sagebrush (*Artemisia tridentata* ssp.) habitat in the Great Basin and Intermountain West of North America has either been lost, degraded, or fragmented due to agricultural conversion, energy development, grazing, invasive annual grasses, or altered wildfire regimes (Knick 1999, Miller and Eddleman 2001, Knick et al. 2003). These alterations of sagebrush habitat have coincided with the range contractions of pygmy rabbits (*Brachylagus idahoensis*), a sagebrush-obligate species that is endemic to the sagebrush-steppe

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ecosystem of the western United States (Green and Flinders 1980a, Weiss and Verts 1984, Verts and Carraway 1998). Populations of pygmy rabbits have declined across most of their range, and pygmy rabbits are a species of conservation concern (Hays 2001, Oregon Natural History Program 2004). The distribution of pygmy rabbit populations is naturally patchy and closely associated with tall, dense stands of sagebrush growing in deep, friable soils (Green and Flinders 1980b, Weiss and Verts 1984, Gabler 1997). Isolated local populations are naturally prone to periodic declines or extirpation (Weiss and Verts 1984) due to low and variable rates of survival (Wilde 1978, Sanchez 2007, Crawford et al. 2010). Consequently, long-term persistence of the species in any single locality may depend on recolonization via dispersing individuals (Fahrig and Merriam 1994).

The movements of the pygmy rabbit are considered relatively slow compared with other lagomorphs, which is a potential liability for pygmy rabbits when they move through open habitats (Sievert and Keith 1985, Lima and Dill 1990, Kotler and Blaustein 1995, Lagos et al. 1995). With the continued loss and fragmentation of sagebrush-steppe vegetation, suitable habitat for pygmy rabbits is becoming increasingly disjunct. This fragmentation has led to concerns about the vagility and ability of pygmy rabbits to cross between isolated patches of big sagebrush habitat (i.e., gap crossing; Dale et al. 1994) to maintain demographic and genetic connectivity (Orr 1940, Weiss 1984, Heady 1998, Estes-Zumpf et al. 2010). Radio-collared juvenile pygmy rabbits successfully crossed secondary roads and perennial streams during dispersal events in Idaho (Sanchez 2007, Estes-Zumpf and Rachlow 2009), but there has been little investigation into the influences of habitat fragmentation on the movements and gap-crossing ability of pygmy rabbits in other parts of their range.

Homing, the ability of an organism to return to its original home range after translocation, is well documented in some mammals (Chapman 1971, Schreiber and Graves 1977, Rogers 1988, Merriam and Lanoue 1990, Teferi and Millar 1993, Linnell et al. 1997), but it has not been well studied in pygmy rabbits (Green and Flinders 1979). The navigation mechanisms and physical obstacles an organism encounters during experimentally induced homing are similar to those faced during dispersal (Rogers 1988). In addition, the distances an animal is capable of traveling during homing may be comparable to the distances traveled during dispersal of juveniles (Bowman et al. 2002). Consequently, experimental translocations have been used to identify barriers to movement within fragmented landscapes for several species of small mammals (Savidge 1973, Merriam and Lanoue 1990, Clark et al. 2001, Bakker and Vuren 2004, McDonald and St. Clair 2004).

Our research was initiated to experimentally test the influence of habitat fragmentation on movements of pygmy rabbits after translocation by using telemetry to follow individual rabbits. We were interested in (1) the propensity of pygmy rabbits to home to their original capture sites (i.e., home range) and (2) whether survival of pygmy rabbits was influenced by their ability to home and by habitat features of the landscape they were moving across. We compared homing by pygmy rabbits after short-distance (1–2 km) experimental translocations across 3 categories of habitat fragmentation. Because pygmy rabbits are well adapted to use big sagebrush for forage, thermal protection, and cover from predators (Katzner and Parker 1998, Shipley et al. 2006), we predicted that individuals transported across landscapes with relatively continuous big sagebrush cover would have the highest rate of homing. Conversely, we also predicted that individuals taken across open, fragmented areas would have the lowest rate of homing. Linear landscape disturbances (i.e., roads) may influence movements of small mammals by acting as barriers and lowering survival rates (Oxley et al. 1974, Schreiber and Graves 1977, Fahrig and Merriam 1985, Richardson et al. 1997, Huijser and Bergers 2000). Consequently, we predicted that individuals transported across roads that bisect continuous big sagebrush would have a lower homing rate than those transported across similar habitat without roads but that they would have a higher rate of successful homing than those taken across open, fragmented areas with limited vegetative cover.

METHODS

Study Sites

All study areas were located in Lake and Harney counties of Oregon on lands administered

TABLE 1. Study regions, sites, and landscape features for assessing homing and survival of pygmy rabbits in southeastern Oregon. The Flint Hills, West Gulch, and Dixon Waterhole regions have 4, 3, and 1 site, respectively.

Study region[a]	Site	Landscape features[b]
Flint Hills	Flint Hills Valley	Contiguous big sagebrush cover
	Corn Lake Road	Linear landscape disturbance
	Hogback Road	Linear landscape disturbance
	Nasty Flat	Patchy big sagebrush cover
West Gulch	Burned	Patchy big sagebrush cover
	Unburned	Contiguous big sagebrush cover
	Lone Grave Mountain	Contiguous big sagebrush cover
Dixon Waterhole	Dixon Waterhole	Patchy big sagebrush cover

[a]The Dixon Waterhole and West Gulch regions were also used during a 2005 research project investigating survival, movements, and habitat selection by pygmy rabbits (Crawford 2008).
[b]Landscape category description: contiguous big sagebrush—possessing habitat characteristics (≥20% big sagebrush cover) adequate for potential occupation by pygmy rabbits; patchy big sagebrush cover—fragmented patches of big sagebrush; linear landscape disturbance—contiguous big sagebrush habitat bisected by a roadway.

by the Lakeview District of the Bureau of Land Management (BLM). We chose 3 regions with pygmy rabbit populations large enough for us to successfully trap adequate numbers of individuals for our research purposes. We divided these larger study regions into smaller sites based on the landscape characteristics that separated the capture and release sites of the translocated rabbits (Table 1). For more information and a map of the study areas, see Lawes (2009).

Capture, Handling, and Tracking

We trapped pygmy rabbits using Tomahawk #201 live traps (Tomahawk Live Trap Co., Tomahawk, WI) and we radio-collared rabbits with model RI-2DM VHF (7.1 g or 10.6 g) radio-transmitters (Holohil Systems Ltd. Carp, Ontario, Canada) from June to December 2008. We camouflaged unbaited traps with burlap, soil, and debris and placed them in burrow openings, runways, or frequently used sites. We varied the placement of traps and duration of trapping to increase trap success.

We weighed (g) and fitted individuals with VHF radio-transmitters at the capture sites. We measured and recorded the hind foot, ear, and total body lengths (mm), as well as the sex and age class (adult or juvenile) of each individual. We used a combination of weight and pelage condition to assign age class, and we ascertained sex through inspection of the genital region. We did not translocate any pregnant or lactating females or any individual weighing ≤250 g. We used uniquely numbered #1005-4 monel eartags (National Band and Tag Co., Newport, KY) as a permanent secondary marker. All individuals were translocated once.

We carried rabbits to release sites inside covered pet carriers (50 × 30 × 30 cm) or inside burlap-lined, covered Tomahawk traps to reduce handling stress during transport. At release sites, we placed carriers under the shade of a big sagebrush plant, opened the door, and allowed the rabbits to leave under their own will. All rabbits were released on the day of their capture during early morning hours (~2 h after sunrise). All rabbits translocated on the same day were released ≥200 m apart to reduce potential social interactions at release sites and to assure independence of movements as much as possible.

All release sites were within a 1–2 km radius ($\bar{x}$ = 1.14 km, SE = 0.03) from the capture site, which was within the median natal dispersal distance of pygmy rabbits in Idaho (Estes-Zumpf and Rachlow 2009). Direction of the release was chosen such that the big sagebrush conditions between the release sites and the capture sites met one of 3 categorical designations denoted as (1) contiguous big sagebrush habitat, (2) contiguous big sagebrush habitat bisected by a roadway, and (3) patchy habitat. Contiguous big sagebrush habitat was characterized by large, intact swaths of big sagebrush that possessed adequate shrub cover (≥20%) for potential occupation by pygmy rabbits. Patchy habitat was composed of disjointed fragments of big sagebrush located within a matrix of bunchgrass or little sage (*Artemisia arbuscula*) habitats (see Lawes 2009 for detailed description of sagebrush cover estimates, Appendix). Given the landscape scale of the study, we were constrained by the habitat conditions surrounding our capture sites, and thus random assignment of direction was not logistically feasible. However, the specific site of release was not predetermined, but chosen by the availability of big sagebrush cover after a 1-km minimum distance from the capture site had been reached. Attempts to recapture individuals were made either after they successfully returned to within 150 m of their initial capture site (i.e., homed) or after they settled in a new location for a 2-week period. Once recaptured, transmitters were removed and rabbits were released at the site of their initial capture. If an individual died, we visually examined the radio-collar, the physical remains, and the surrounding area to determine cause of mortality. We captured and handled pygmy rabbits with permission from the Oregon Department of Fish and Wildlife (Scientific Taking Permit #133-07) and in compliance with Oregon State University's guidelines for animal care and use (Permit #3744).

The aboveground activity of pygmy rabbits typically peaks during crepuscular hours (Larrucea and Brussard 2009), but individuals may be active anytime throughout a 24-h period (Heady 1998, Lee et al. 2010). As such, we concentrated releases and tracking efforts during crepuscular hours, but varied the timing of our observations to encompass the range of possible movement activity. Immediately after release, individuals were located every 15–30 minutes until their movement ceased. As a result, tracking typically continued for several hours postrelease, after which locations were acquired twice daily until the rabbits were recaptured. The number of days that pygmy rabbits were radio-collared during this study ranged between 1 and 74 d ($\bar{x}$ = 23.4 d).

Radio-collared pygmy rabbits were tracked using radio receivers with directional 3-prong or 2-prong antennas and handheld global positioning system (GPS) units (Garmin International, Inc., Olathe, KS) until individuals were visually observed or burrow location was identified. A concerted effort was made to not drive the rabbits around the landscape during tracking. Rabbits were frequently approached to within several meters without flushing, but if a rabbit was disturbed, we recorded an approximate location at the time of disturbance. For each observation, we recorded behavior of the individual, vegetative cover type, time, and location coordinates (Universal Transverse Mercator [UTM] referenced by the North American datum of 1927 [NAD27]).

GIS-Derived Habitat Characteristics for Survival Analysis

We created 3.14-ha circular habitat sampling areas centered at the UTM coordinates of the capture (n = 59) and release sites (n = 59) of translocated pygmy rabbits, using ArcGIS 9.3 to represent the available habitat at the home-range scale. Our habitat sampling areas were 2.7 times larger than the 1.16-ha mean annual home-range size estimate (95% fixed-kernel *LSCV*), but were about one-third as large as the maximum estimate of 10.46 ha from similar sites in southeastern Oregon (Crawford 2008). We also centered a circle at the midpoint between the capture and release sites to sample habitat at a landscape extent. These larger circular areas represented the regions through which pygmy rabbits navigated while returning to their original home ranges. We extracted habitat data by quantifying 1-m resolution aerial photograph raster layers, which were reclassified (0 = not big sage, 1 = big sage) based on color reflectivity. We used FRAGSTATS spatial analysis software to (1) quantify both the percentage of each sampled home range and landscape that was classified as big sagebrush (PLAND) and the percentage made up of the single largest patch of big sagebrush (LPI) and (2) provide a metric of big sagebrush patch isolation that is based on the area-weighted mean number of big sagebrush patches with edges within a 50-m radius of a focal big sagebrush patch at each scale (PROX_AM). We used the 8-cell rule, which includes adjacent pixels during calculations of patch size, to calculate our big sagebrush patches (McGarigal et al. 2002).

Homing Analysis

Logistic regression was performed using Proc GenMod (SAS Institute, Inc., Cary, NC) to compare the odds ratios of homing by radio-collared pygmy rabbits between the 3 habitat categories, after accounting for sex and the displacement distance of individuals. Statistical significance for all tests was set at α = 0.05. We assumed that individuals were captured within their core use areas and that those areas were near the center of their respective home ranges. As such, we considered an individual to have successfully homed if it returned to within 150 m of its original capture site. We defined failure to home as settling in a new location >150 m from the capture

TABLE 2. *A priori* hypotheses and models for testing the effects of various factors on survival rates of pygmy rabbits in southeastern Oregon, 2008.

Hypothesis description	Model
1. Survival rates differ among homing response	S(Homed)
2. Survival rates differ between rabbits that settled ≤100 m from a road and those that settled >100 m from a road	S(Road)
3. Survival rates differ among the weekly time intervals	S(t)
4. Survival rates are constant among homing responses, settlement distance, and weekly time intervals	S(.)
5. Survival rates decline linearly during the 5-week period	S(T)
6. Survival rates fluctuate quadratically during the 5-week period	S(TT)
7. Survival rates vary by the ordinal release date	S(Date)
8. Survival rates vary by a morphometric covariate	S(W/L)[a]
9. Survival rates vary by a habitat covariate(s)	S(H_i)[b]
10. Survival rates differ among homing responses and settlement distance	S(Homed * Road)
11. Survival rates differ among homing responses, settlement distance, and weekly time intervals	S(Homed * Road * t)
12. Survival rates differ among homing responses, settlement distance, and quadratically during the 5-week period	S(Homed * Road * TT)
13. Survival rates differ among homing responses, settlement distance, quadratically during the 5-week period, and by a morphometric covariate	S(Homed * Road * TT + W/L)
14. Survival rates differ among homing responses, settlement distance, quadratically during the 5-week period, and by the ordinal release date	S(Homed * Road * TT + Date)
15. Survival rates differ among homing responses, settlement distance, quadratically during the 5-week period, and by a habitat covariate	S(Homed * Road * TT + H_i)

[a]Weight/length (g/mm)
[b]H_i represents the potential effects of the percentage of the landscape in big sagebrush (PLand), the percentage of the landscape composed of the single largest patch of big sagebrush (LPI), or the area-weighted mean proximity index of big sagebrush patches at landscape and home-range scales.

site for 2 weeks (i.e., establishing a new home range) or dying before returning. A 150-m distance criterion was used because we were concerned that individuals might be hesitant to return to their exact capture burrows after disturbance. Estimates of pygmy rabbit home ranges are highly variable depending on the sex, season, geographic area, habitat quality, and estimation technique (Sanchez and Rachlow 2008). However, assuming a circular home range, the 150-m distance criterion for successful homing was within the maximum 95% fixed-kernel estimate of the annual home-range size calculated for pygmy rabbits on similar sites in southeastern Oregon (Crawford 2008). Lastly, given that predation risk could be a function of available shrub cover (Sievert and Keith 1985), we included mortality among the mechanisms responsible for unsuccessful homing.

Survival Analysis

We used known-fate models, which allowed for censoring, in Program Mark (White and Burnham 1999) to estimate the survival (S) of radio-collared pygmy rabbits for 5 weeks after they were translocated. All rabbits were entered into the data set on their initial capture date, and individuals were censored from the analysis after their recapture date or if they could not be located. We created a set of *a priori* candidate models based on biological hypotheses about potential influences on pygmy rabbit survival (Table 2). We modeled temporal variation in survival as constant throughout the 5-week period (.), varying weekly (t), linear through time (T), or quadratic through time (TT). We also hypothesized that *survival* could vary by the ratio of weight to total body length of the individual (a gross index of physical condition) or by the ordinal date of release, if the rabbit settled ≤100 m from a road or if the rabbit homed after translocation. In addition, we hypothesized that habitat variables might influence survival rates. We tested the effects of the percentage of the landscape in big sagebrush (PLand), the percentage of the landscape composed of the single largest patch of big sagebrush (LPI), and the area-weighted mean proximity index of big sagebrush patches at the landscape or home-range scales on the survival rates of pygmy rabbits.

We performed model selection using Akaike information criteria corrected for small sample sizes (AIC_c) using Program Mark (Burnham and Anderson 2002). We also computed the log-likelihood functions, AIC_c weights, and deviance for each model in program MARK

TABLE 3. Number of pygmy rabbits captured, radio-collared, and transported across 3 categories of habitat during research into homing ability and survival after experimental translocation in southeastern Oregon, 2008.

Landscape category	Habitat description[a]	Sex	*n*
Contiguous big sagebrush cover	Intact swaths of big sagebrush with a shrub cover ≥20%	♀	7
		♂	12
TOTAL			19
Patchy big sagebrush cover	Isolated patches of big sagebrush located within a matrix of bunchgrasses or little sagebrush	♀	7
		♂	12
TOTAL			19
Contiguous big sagebrush cover bisected by road	Linear landscape disturbance across intact swaths of big sagebrush with shrub cover ≥20%	♀	7
		♂	14
TOTAL			21
GRAND TOTAL			59

[a]Detailed estimates of percent big sagebrush groundcover are available in Lawes 2009.

(Burnham and Anderson 2002). We considered the model with the lowest AIC_c value as the best model, and any model within 2 ΔAIC_c values as competitive with the best model (Burnham and Anderson 2002). We calculated the ΔAIC_c values as the AIC_c value for the best model minus the AIC_c value of the *i*th model (Δi). We used AIC_c weights to gauge the strength of evidence for the top model versus the other models (Burnham and Anderson 2002). Rabbits were released to minimize social interaction, so we had no reason to suspect a lack of independence among the individuals. Further, we did not use $QAIC_c$ for model selection, and we assumed no overdispersion in the data ($\hat{c} = 1.0$) because we used individual covariates with known-fate data. We used the regression coefficients (β) and 95% confidence intervals for the various factors as evidence of an effect in the competing models. Additionally, we evaluated the precision of the estimates using the coefficient of variation (CV = [SE(S)/S] × 100).

RESULTS

Homing

Fifty-nine adult pygmy rabbits were captured and translocated; 21 (36%) were female and 38 (64%) were male (Table 3). Of these, 9 individuals (15%) successfully homed back to their original capture sites after translocation. We translocated 19 individuals across contiguous sagebrush habitat, and 11% (2 males) successfully homed back to their original capture sites. We translocated 19 pygmy rabbits across patchy habitat, and 32% (3 males, 3 females) successfully homed. We translocated 21 individuals across contiguous sagebrush habitat bisected by a road, but only 5% (1 male) successfully homed back to his original home range.

The fate of individuals that did not home varied. Nine mortalities of radio-collared pygmy rabbits were due to predation. Of these, 7 (78%) were translocated across contiguous big sagebrush habitat bisected by a road, one (11%) was translocated across contiguous sagebrush habitat, and one (11%) was translocated across patchy habitat. The number of days rabbits were radio-collared prior to predation ranged from 2 to 33 days ($\bar{x}$ = 13.67 days). Because of radio-collar failures, there were 2 individuals translocated across patchy habitat with unknown fates. The remaining 39 individuals (66%) did not return to their original home ranges, but settled into burrows at new locations. All but one individual was successfully recaptured and returned to its original capture location. This particular rabbit successfully homed to within 40 m of its capture site but evaded all subsequent recapture attempts.

There was no statistical evidence for an effect of sex ($\chi^2 = 0.04$, df = 1, $P = 0.836$) or displacement distance ($\chi^2 = 0.07$, df = 1, $P = 0.784$) on the proportion of individuals that successfully homed. However, there was support for an effect of habitat category ($\chi^2 = 5.87$, df = 2, $P = 0.053$). A comparison of the odds ratios after accounting for the sex of the individual and displacement distance indicated that pygmy rabbits were 9.6 (95% CI: 1.02–90.15) times more likely to successfully home across fragmented landscapes than landscapes with contiguous sagebrush habitat bisected by a road. Although not statistically significant, pygmy rabbits were estimated to be 4.5 (95% CI: 0.55–37.56) times more likely to successfully home across fragmented landscapes than they were across landscapes with

TABLE 4. Odds ratio estimates, standard errors, 95% confidence intervals, χ^2 values, degrees of freedom, and probabilities of χ^2 values for homing by pygmy rabbits after experimental translocation across 3 habitat categories in southeastern Oregon, 2008.

			95% CI[b]				
Comparison of landscape categories[a]	Estimates[b]	SE[b]	L_1	L_2	χ^2	df	Pr > χ^2
Patchy vs. bisected by road	9.58	10.96	1.02	90.15	3.90	1	0.048
Patchy vs. contiguous	4.56	4.91	0.55	37.56	1.99	1	0.158
Contiguous vs. bisected by road	2.10	2.85	0.15	30.12	0.30	1	0.585

[a]Landscape category descriptions: contiguous—large, intact area of big sagebrush; patchy—fragmented patches of big sagebrush; road—contiguous big sagebrush habitat bisected by a roadway.
[b]Estimates, SE, and 95% CI reported after back-transformation.

TABLE 5. Model selection results for the analysis of survival rates of pygmy rabbits that were translocated to areas outside of their home ranges in south central Oregon, 2008.

Model[a]	AIC_c	ΔAIC_c	AIC_c wt	K[b]	Deviance
S(Road * Homed * T + TT + Prox-l)	128.78	0	0.68	7	114.40
S(Road * Homed * T + TT + Date)	133.49	4.71	0.07	7	119.11
S(Road * Homed * T + TT + LPI-l)	133.63	4.85	0.06	7	119.26
S(Prox-l)	134.38	5.60	0.04	2	130.35
S(Road * Homed * T + TT + W/L)	134.94	6.16	0.03	7	120.56
S(Road * Homed * T + TT)	135.00	6.22	0.03	6	122.72
S(Road * Homed)	135.71	6.93	0.02	4	127.57
S(Road)	137.07	8.28	0.01	2	133.03
S(T + TT)	137.32	8.54	0.009	3	131.24
S(W/L)	138.10	9.32	0.006	2	134.06
S(Homed)	138.31	9.53	0.006	2	134.27
S(Date)	138.46	9.68	0.005	2	134.42
S(LPI-l)	138.58	9.79	0.005	2	134.54
S(.)	138.69	9.90	0.005	1	136.67
S(t)	138.76	9.98	0.005	5	128.56
S(LPI-h)	139.58	10.80	0.003	2	135.54
S(Prox-h)	139.60	10.81	0.003	2	135.56
S(Pland-l)	139.72	10.94	0.003	2	135.68
S(T)	139.95	11.17	0.003	2	135.91
S(Pland-h)	140.61	11.83	0.002	2	136.57
S(Road * Homed * t)	156.79	28.01	0	20	113.82

[a]Definition of variables: (.) time constant, (t) variable time effects, (T) linear time trends, (TT) quadratic time trends, (Homed) returned to within 150 m of capture site, (Date) ordinal date of release, (Road) settled within 100 m of a road, (W/L) ratio of weight (g) to length (mm), (LPI-l) index of largest big sagebrush patch at a landscape scale, (LPI-h) index of largest big sagebrush patch at a home-range scale, (Pland-l) percent of area as big sagebrush at a landscape scale, (Pland-h) percent of area as big sagebrush at a home-range scale, (Prox-l) area-weighted mean proximity index of big sagebrush patches at a landscape scale.
[b]Number of parameters

contiguous sagebrush habitat, and 2.1 (95% CI: 0.15–30.12) times more likely to successfully home after translocation across landscapes with relatively continuous big sagebrush cover than they were when moved across similar habitat that was bisected by a road (Table 4).

Survival

The best model [S(Road * Homed * T + TT + Prox-l)] indicated that survival rates of pygmy rabbits after translocation were affected by the proximity of roads to the areas the rabbits chose to settle in, the propensity of pygmy rabbits to home, a quadratic time effect, and the area-weighted mean number of big sagebrush patches with edges within a 50-m radius of a focal tall sagebrush patch at the landscape scale. There were no competing models within 2 AIC_c of this model (Table 5). The best model had an AIC weight of 0.68, which indicated that this model was approximately 10 times better than the second model [S(Road * Homed * T + TT + Date)] in the list. This second model indicated that survival rates were affected by the proximity of roads, propensity to home, a quadratic time effect, and the ordinal date of release. The best model was 9.9 AIC_c units better than the base model [S(.)] (no effects of roads, homing, time, or habitat characteristics), which indicated that the best model fit the data well. Pygmy rabbits that homed to their original site of capture did

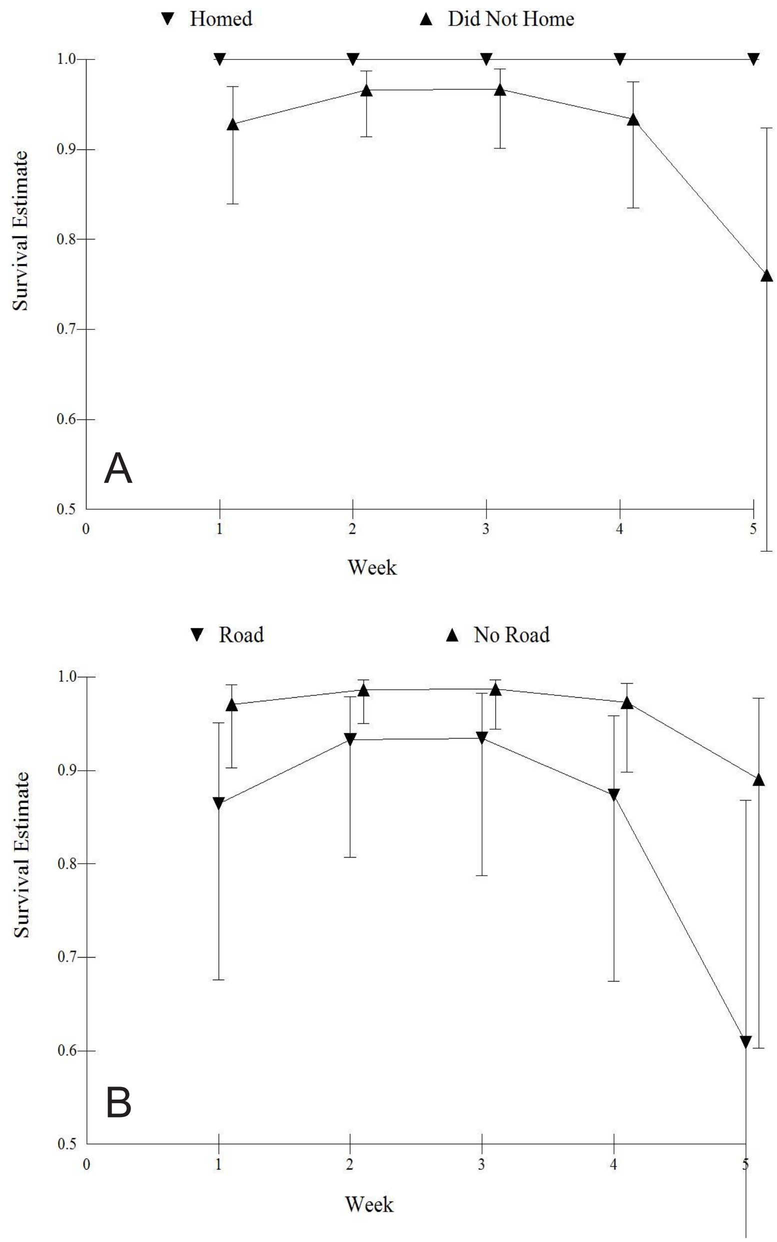

Fig. 1. Survival rates of pygmy rabbits that were translocated to areas away from their home ranges relative to their success at homing (A) and their success at settling near or far from roads (B) in south central Oregon, 2008.

not suffer any mortalities (S = 1.00, SE not computed) during the 5 weeks after translocation and release, and they had higher survival than rabbits that did not home (S = 0.62, SE = 0.13) (Fig. 1A). In addition, rabbits that settled close to roads had lower survival rates (S = 0.40, SE =0.17) during the first 5 weeks than those that settled farther from roads (S = 0.82, SE = 0.11) (Fig. 1B). Survival after translocation was higher during weeks 1–3, and then declined quadratically during weeks 4 and 5 for most rabbits.

Only one of the habitat covariates had a significant effect on survival of pygmy rabbits during the first 5 weeks after translocation and release. A higher proximity index at the landscape scale (Prox-l), which translates into lower sagebrush patch isolation, had a positive effect on survival (β = 0.0014, 95% CI: 0.0002–0.0003). There was some evidence that weight/body length ratios of pygmy rabbits as a crude measure of physical condition was important in the analysis, but the 95% confidence interval for this covariate overlapped zero (β = 2.25, 95% CI: –0.50 to 5.00), and the model that included this covariate was 6.2 AIC_c units lower than the best model. There also was some evidence that the percentage of the landscape made up of the single largest patch of tall sagebrush (LPI-l) was important, but the 95% confidence interval for this covariate also overlapped zero (β = 0.041, 95% CI: –0.015 to 0.098). There was no evidence that any of the other covariates were important in the analysis, because models that included them were >9.0 AIC_c units from the best model and were a poorer fit to the data than the base model with no effects [*S*(.)].

DISCUSSION

Habitat characteristics separating the capture and release sites appeared to be the most important factor influencing homing success of pygmy rabbits in our study. Out of all the groups, rabbits translocated across open, fragmented sagebrush habitat were the most likely to home, which was contrary to our original predictions. Homing in animals has been well documented for many taxonomic groups (for detailed review, see Joslin 1977, Papi 1992), and some studies on the homing ability of small mammals have reported differences in homing success as a function of the displacement distance and sex of translocated individuals (Stickel 1949, Griffo 1961, Bovet 1984, 1992). We did not detect these differences in pygmy rabbits during our study. The distances we translocated rabbits were not highly variable, however, and this lack of variability may have diminished the importance of displacement distance on successful homing. Similar to our results, there was no effect of sex on the probability of homing in experimentally translocated eastern chipmunks (*Tamias striatus*), nor was there an effect of the size of unsuitable habitat gaps (Bowman and Fahrig 2002). Contrary to our results, the highest homing success in 3 experimentally translocated species of murid rodents in Banff National Park, Canada, were in areas with continuous habitat (McDonald and St. Clair 2004). Schreiber and Graves (1977) also documented higher homing success in deer mice (*Peromyscus leucopus*) across continuous forest habitat than across a cleared powerline corridor.

Translocated pygmy rabbits in our study were observed using isolated burrows and using small patches (or individual shrubs) of big sagebrush, rabbitbrush (*Chrysothamnus* spp. and *Ericameria* spp.), and little sagebrush as hiding cover while moving across the landscape. These pygmy rabbits were also able to camouflage themselves on bare ground by lying flat on their bellies and putting their ears back close to their heads. One female that successfully homed in <24 h was observed crossing a nearly continuous 1-km expanse of low sagebrush in <15 min and successfully locating a large patch of continuous big sagebrush. Other individuals were also observed making shorter, straight-line movements between patches of big sagebrush that required crossing areas with little vegetative cover.

Although we did not compare movement speeds of pygmy rabbits in the various habitat conditions, Bakker and Van Vuren (2004) found that translocated red squirrels (*Tamiasciurus hudsonicus*) moved slower while crossing unsuitable habitat gaps and concluded that perceived predation risk was higher in those areas. Not only did individuals in patchy habitat have the highest probability of homing in our study, but the individuals that failed to home in that category moved the greatest distances from their release sites prior to settlement (Lawes 2009). These combined results suggest that for pygmy rabbits, familiarity with, or access to, higher-quality habitat in the fragmented landscapes may outweigh the predation risks associated with crossing large patches of inhospitable habitat. Given that recolonization of vacant habitat patches is likely necessary for pygmy rabbits to maintain genetic viability and viable population demographics (Estes-Zumpf et al. 2010), future investigation into the effects of habitat quality on the survival rates of pygmy rabbits would improve our understanding of the species' ecology.

Roads may have effects on small mammals either by acting as a physical barrier to movement (Clark et al. 2001) or by lowering survival rates (Oxley et. al. 1974, Schreiber and Graves 1977, Richardson et al. 1997, Huijser and Bergers 2000). As such, we considered predation to be one mechanism by which successful homing could be prevented during our study. Although we did not find the comparison of homing rates statistically significant between areas of continuous sagebrush and those bisected by a road, we found that rabbits that settled near a road after translocation had lower survival rates than those that settled farther from roads. This result was due primarily to the higher predation rates by coyotes on these individuals, and this effect on survival rates has important implications for the selection of sites for translocation of the species. Coyotes are known to use dirt roads as navigational pathways (Way et al. 2004), and their tracks were frequently observed along the roadways during our study, especially after snowfalls. Although none of our radio-collared pygmy rabbits were killed by vehicles, living in proximity to a roadway also puts individuals at risk of vehicle collisions (Trombulak and Frissel 2000).

The ecological effects of roads include altered local hydrology and vegetative growth patterns (Murcia 1995, Forman and Alexander 1998, Jones et al. 2000, Trombulak and Frissel 2000). These impacts may extend to >100 m on either side of a roadway, creating what has been referred to as a "road-effect zone" (Forman and Deblinger 2000). The earthen mounds associated with roadside ditches and berms created deeper soils and taller sagebrush along roadways in our study, which are habitat conditions attractive to pygmy rabbits. We observed rabbits settling along the roadways and documented lower survival rates for those individuals. If pygmy rabbits are indeed selecting these areas based on specific habitat cues (Stamps and Swainsgood 2007), then current road construction practices in some areas may be creating attractive habitat conditions in potentially unfavorable sites. These sites may function as an ecological trap (Battin 2004) and should be reevaluated.

To the best of our knowledge, this is the first study to estimate survival rates of mammals during the first few weeks after translocation. We found that pygmy rabbits that successfully homed to their original home ranges had higher survival rates than rabbits that did not home. This result was intuitive because rabbits that homed were likely more familiar with their home sites than those that did not home. However, we were surprised that such a small portion of the rabbits in our study found their way home after translocation. The explanation for this low homing success is unknown, so this aspect of the species' behavior needs further investigation. Lastly, the area-weighted mean number of big sagebrush patches with edges within a 50-m radius of a focal big sagebrush patch in the landscape (i.e., close proximity between patches of big sagebrush) had a positive effect on survival of pygmy rabbits after translocation. This result was also intuitive because big sagebrush communities are usually highly selected by the species (Green and Flinders 1980b, Gabler 1997, Heady and Laundre 2005). This result also has important implications for the selection of sites for translocation of the species. More studies on the survival rates of mammals after translocation are needed to understand if the patterns of habitat selection and survival rates observed in our study are similar to those observed in other species of mammals.

ACKNOWLEDGMENTS

We thank the Lakeview District of the Bureau of Land Management, the Oregon Department of Fish and Wildlife, the USDA Forest Service Silver Lake Ranger Station, Hart Mountain National Antelope Refuge, and the USGS Oregon Cooperative Research Unit for logistical support. We captured pygmy rabbits with permission of the Oregon Department of Fish and Wildlife (Scientific Taking Permit #133-07) and in compliance with Oregon State University IACUC guidelines (permit #3744). We thank the many technicians who helped us with the field work.

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Received 18 August 2011
Accepted 21 August 2012

APPENDIX. Mean and 95% confidence intervals of 8 landscape metrics calculated for each landscape category. Landscape metrics were calculated from 1-m resolution aerial photographs using ArcGIS and FRAGSTATS spatial pattern analysis computer programs.

Landscape metric[a]	Landscape category[b]	n^c	Mean	Lower 95% CL	Upper 95% CL
% Land classified big sagebrush[1]	Contiguous	19	39.56	35.62	43.49
	Road	21	41.85	36.63	47.07
	Patchy	19	16.42	11.98	20.85
Patch density[2]	Contiguous	19	144.59	131.42	157.75
	Road	21	149.16	126.39	171.93
	Patchy	19	123.02	108.07	137.97
Largest patch index[3]	Contiguous	19	15.78	13.09	18.47
	Road	21	17.64	14.12	21.15
	Patchy	19	3.85	1.87	5.83
Clumpiness index[4]	Contiguous	19	0.59	0.58	0.61
	Road	21	0.58	0.56	0.59
	Patchy	19	0.58	0.52	0.63
Connectance index[5]	Contiguous	19	2.07	1.21	2.92
	Road	21	3.26	3.04	3.48
	Patchy	19	3.19	3	3.38
Cohesion index[6]	Contiguous	19	99.41	99.28	99.55
	Road	21	99.17	98.73	99.62
	Patchy	19	90.03	83.89	96.17
Aggregation index[7]	Contiguous	19	75.42	73.52	77.33
	Road	21	75.48	73.26	77.69
	Patchy	19	63.57	56.73	70.4
Proximity[8]	Contiguous	19	8518	7326.3	9709.73
	Road	21	7963.7	5450.5	10477
	Patchy	19	1071.1	516.44	1625.84

[a]Landscape metric definitions:
[1]Percentage of the landscape that was classified as big sagebrush
[2]Number of big sagebrush patches per hectare
[3]Percentage of the landscape composed of the single largest patch of big sagebrush
[4]Proportional deviation of the proportion of big sagebrush adjacencies from that expected under a spatially random distribution
[5]Number of functional joinings between all patches of the big sagebrush within a 100-m distance criterion
[6]Physical connectedness of corresponding big sagebrush patches
[7]Frequency with which different pairs of big sagebrush patches appear side-by-side within the classified habitat circles
[8]Area-weighted mean number of big sagebrush patches with edges within a 50-m search radius of a focal big sagebrush patch.
[b]Landscape classification of the region between capture and release sites.
[c]Number of landscape extent circles.