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Source: Journal of Mammalogy, 95(3) : 516-524

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/13-MAMM-A-187

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Journal of Mammalogy, 95(3):516–524, 2014

Home range size and habitat selection of reintroduced *Sylvilagus bachmani riparius*

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Effective restoration of threatened or endangered species requires understanding of basic ecological requirements such as habitat selection and home range needs. The endangered riparian brush rabbit (*Sylvilagus bachmani riparius*) occupies areas of dense, brushy cover along streamside communities in the San Joaquin Valley of California, but over 93% of this habitat has been lost to urban and agricultural development. We released over 325 captive-born rabbits at the San Joaquin River National Wildlife Refuge (Refuge) between July 2002 and July 2005, and we monitored 312 of these rabbits via radiotelemetry to assess spatial and habitat selection. Home ranges and core areas were similar among males and females, and were larger in the breeding season than during the nonbreeding season. Perhaps reflecting a growing population, home range estimates decreased in size over the duration of the study. Animals moved in response to a wildfire in July 2004, but home range area was similar in 90-day pre- and postfire periods. Of 1,143 possible dyads, 534 (47%) exhibited a mean of 86% overlap in 95% fixed-kernel home ranges. Overlap did not differ by dyad type (e.g., male–male), but was greater in nonbreeding than in breeding seasons; unlike home ranges, we did not detect any temporal changes in overlap as might be expected in a growing population. Riparian brush rabbits exhibit scale-independent habitat selection, disproportionately favoring thick understory cover such as sandbar willow mixed with dense shrubs (blackberry, roses). Refuge managers have promoted escape cover and flood refugia at strategic locations throughout the Refuge; our results concur that these are important habitat elements in the niche of riparian brush rabbits.

Key words: fixed kernel, habitat selection, home range estimation, home range overlap, *Sylvilagus bachmani riparius*

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DOI: 10.1644/13-MAMM-A-187

Riparian brush rabbits (*Sylvilagus bachmani riparius*; RBR hereafter) occupy areas of thick, brushy cover along rivers and tributaries in the Central Valley of California (Williams et al. 2008) and are listed as endangered both by the state of California (CDFW 2008) and the federal government (USFWS 2000). By the mid-1980s, primarily because of habitat destruction, the riparian forest within the range of RBR had been reduced to a few small and widely scattered fragments, totaling about 2,100 ha (Williams et al. 2002, 2008). Currently, 2 extant populations of RBR are known, and both are small and at risk of extinction from demographic and/or environmental stochasticity (especially flooding, wildfire), and possibly from competition with desert cottontails (*S. audubonii*—Williams and Basey 1986; Williams 1988; USFWS 1998).

Controlled propagation and reintroduction is an increasingly useful method in conservation and restoration of threatened and endangered species, and, recognizing the urgent threats faced by RBR, we initiated a controlled propagation and reintroduction program at the San Joaquin River National Wildlife Refuge (Refuge hereafter) in November 2001. General recommendations, such as use of "soft" versus "hard" releases (sensu Bright and Morris 1994) and releasing large numbers of animals near the core of the species range, may increase the likelihood of successful reintroduction (Fischer and Lindenmayer 2000), but understanding the ecology of target species, including demography, behavior, reproductive biology, spatial ecology, and habitat associations (Kleiman 1989, 1994; Wolf et al. 1996), are central to reintroduction efforts (Morrison 2002). Unfortunately, spatial and habitat requirements of RBR

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have not been studied, and inferences from related subspecies are limited.

Reflecting their common name, brush rabbits generally favor dense shrub cover and brambles, presumably for protection from predators (Chapman 1974; Chapman and Litvaitis 2003). In the Central Valley of California, Williams and Basey (1986) concluded that frequently flooded secondary successional communities were less likely to be inhabited by RBR (Williams and Basey 1986), but discovery of another population led Williams et al. (2002) to suggest that the species might prefer patchy, secondary successional communities to overgrown climax riparian communities. Given these somewhat ambiguous results, conservation managers in this region require clarification of spatial requirements and habitat selection by this subspecies.

In addition to biotic factors such as predation, abiotic disturbances may be important threats to brush rabbits, and during this study our study site experienced 2 major disturbances. In July 2004, a wildfire (the Pelican Fire) burned 588 ha of the Refuge, including the primary release locations and approximately 53% of the available high-quality habitat for brush rabbits (Phillips et al. 2005). In March 2005, unusually large reservoir discharges on the Merced and Tuolumne rivers resulted in flooding of riparian habitat. Flooding occurred again in May and June 2005 due to melting of an above-average snowpack in the Sierra Nevada.

Brush rabbits generally have small home ranges (HRs), and males have larger HRs than females (Connell 1954; Shields 1960; Chapman 1971); however, because this developing population is unlikely to have reached carrying capacity, we predicted that neither HR nor core areas (CAs) would differ between males and females. We also predicted that HR size would be larger than that reported from more established populations of *S. bachmani* (again reflecting limited density dependence in this young population). We predicted that HRs would differ in breeding and nonbreeding seasons, reflecting either reduced activity by females (e.g., engaged in maternal care) or greater movements by males seeking mating opportunities. We predicted that animals would move in response to habitat loss due to wildfire, but we had no a priori rationale for expecting HR area to change. Limited data precluded assessment of spatial responses to flooding (although our expectations would be similar to those for wildfire). To understand habitat needs (and to provide useful management advice) we assessed selection of available habitats. We expected HRs to include differential cover by dense shrubby or bramble vegetation, and that movements within HRs would exhibit similar selectivity.

Materials and Methods

Study area.—The Refuge is located on the San Joaquin River approximately 18 km west of Modesto in Stanislaus County, California (37°36′54″N, 121°12′47″W). Much of the Refuge property was previously leveled and cultivated for irrigated agriculture. A levee system separates the formerly cultivated portions of the Refuge from adjacent areas of brushy and riparian habitat. The land between the levees and the San Joaquin River was dominated by native California blackberry (*Rubus ursinus*), willows (*Salix* spp.), mugwort (*Artemisia douglasiana*), and wild rose (*Rosa californica*). The northeastern portion of the property was occupied primarily by perennial pepperweed (*Lepidium latifolium*) with lesser contributions by other weed species.

Recognizing the importance of refuge habitat, and simultaneous to reintroduction of RBR, Refuge managers planted 344 ha of riparian habitat and revegetated 6,584 linear meters of levees with riparian habitat to provide escape cover and foraging habitat for rabbits. They also built 30 (8 large, 22 small) flood refugia mounds at strategic locations within the Refuge. Each mound includes a belt of dense vegetation ("green riprap;" pers. comm. to P. A. Kelly from K. Forrest, Manager, San Luis National Wildlife Refuge Complex, United States Fish and Wildlife Service) along its base to prevent potential erosion associated with scouring flood flows and to provide additional escape cover (Lloyd et al. 2013; River Partners 2013).

Reintroduction and telemetry.—In our controlled propagation program we captured a new cohort of breeding animals from the wild population each year to produce progeny for reintroduction. Captive-bred rabbits were reared in large outdoor enclosures in suitable habitat and over 3½ years 476 offspring were produced within the breeding enclosures; 325 rabbits were reintroduced to unoccupied habitat within their historic range (Williams et al. 2008; Hamilton et al. 2010). Elsewhere we report on the success of this reintroduction effort (Williams et al. 2008) and subsequent survivorship of reintroduced rabbits (Hamilton et al. 2010).

We fitted 312 reintroduced rabbits with radiocollars (Model M1750, Advanced Telemetry Systems, Isanti, Minnesota) weighing approximately 13 g (2% of mean body weight; range 1.3–3.3%), with a battery life of 7 months to 1 year, and with mortality sensors to alert us if they remained motionless for $\geq$ 6 h. All handling procedures were approved by the University of California, Davis Animal Use and Care Administrative Advisory Committee, and met guidelines recommended by the American Society of Mammalogists (Sikes et al. 2011, 2012).

Triangulation during daylight hours was affected by radio-interference, compromising our ability to get good null signals and reliable telemetry locations. This, in combination with logistical challenges (e.g., staffing, ease of access to all parts of the Refuge), mandated that we restrict telemetry to evening periods (1–2 h before sunset and extending until 4–5 h after dark). Hence, results presented here refer to activity and space use during this time period; although we believe these are justifiably extrapolated to general activity and space use, this must be done with some caution.

Initially, we tracked radiocollared rabbits using 2-element "H"-style directional antennas and portable receivers. Signals were followed to determine the patch or clump of brush each individual was using and the animal's position was estimated

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to within a few meters and recorded in Universal Transverse Mercator coordinates (Garmin global positioning system [GPS] III or GPS V receiver, accurate to $\leq$ 20 m). Because reintroduced rabbits dispersed more widely than expected, local pinpointing became prohibitive; thus, beginning in September 2002 we monitored individuals using 5-element precision direction-finding arrays (Model RA-NS, Telonics, Inc., Mesa, Arizona). To acquire location information, bearings were taken simultaneously by 2 technicians. We used hand-held radios to ensure near-synchronous collection of bearings (within 10 min) and we discarded those with intersection angles $< 45°$ or $> 135°$. Researchers also recorded time, weather conditions, and signal quality (weak, medium, or strong) for every bearing. Successive bearings on collared individuals were separated by at least 1 h to minimize autocorrelation (Swihart and Slade 1985). We determined rabbit locations with a custom-designed extension (Jenness Enterprises 2002) to ArcView geographic information system (GIS; ESRI 2002). To minimize error polygons and reduce error associated with bearing accuracy, researchers recorded all bearings from 1 of 11 fixed stations.

We evaluated technician error by recording bearings on carcasses ($n = 89$, actual location not known to technician) before their collection. Once the carcass was located, we recorded the position with a GPS receiver for comparison with the position estimated by telemetry (Bond et al. 2001). The distance between telemetry stations and dead rabbits ranged from 39 to 598 m, and telemetry error averaged 5.5° and 47 m ($SD = 4.9°$ and 38 m).

We defined breeding as 1 December–31 May and the nonbreeding seasons as 1 June–30 November (Mossman 1955), and we applied incremental area analysis in a beta version of Ranges 7 (Kenward et al. 2003) to determine the number of locations needed to reliably estimate HRs (Odum and Kuenzler 1955). We used a total of 4,982 locations to calculate seasonal (breeding/nonbreeding) 95% HRs and 50% CA for 101 individuals (translocated = 50 F, 38 M; native-born = 7 F, 6 M) using Ranges 7 (Kenward et al. 2003). These individuals were monitored for 3 years (1 December 2002–30 November 2005) and collars were replaced as necessary; median (*SD*) duration of monitoring was 285.6 (221.1) days for males and 286.8 (146.2) days for females. We estimated HR area using both minimum convex polygon (MCP—Mohr 1947; Jennrich and Turner 1969) and fixed-kernel methods (FK—Worton 1989). MCP was chosen to facilitate comparisons between earlier studies, and results are available in Hamilton (2010); we will not discuss MCP estimates further here. For FK estimates we used the reference value as the smoothing parameter (Kenward et al. 2003). In addition, we estimated pre- and postfire geometric centers of each animal's HR and, using the Distance tool in ArcView, compared the distance between these activity centers to evaluate the amount of range shifting in response to this event. Data were assessed for normality using the Shapiro–Wilk statistic and visual confirmation of histograms. HR and CA size estimates were log-transformed to meet assumptions of analysis of variance (ANOVA). Because data on individual rabbits in subsequent years were unlikely to be independent, we were cautious in the analyses and conservative in interpretation of these data. To account for potential nonindependence, we assessed differences in HR and CA size between sexes, seasons, and years with a mixed-model ANOVA in SAS (Proc Mixed—SAS Institute Inc. 2008). The model had fixed effects for year, season, and sex, included all possible interactions, and contained an additional random effect for individual rabbits (nested within sex). We used a Satterthwaite approximation for calculating error degrees of freedom and a variance component (independent and additive) structure for the error terms (Satterthwaite 1946).

For each pair of animals (α and β) we calculated an index of mean overlap (OI; Minta 1992):

$$\mathrm{OI} = \sqrt{\left(\left[\frac{\text{HR overlap}}{\mathrm{HR}_\alpha}\right] \times \left[\frac{\text{HR overlap}}{\mathrm{HR}_\beta}\right]\right)},$$

where HR overlap was the area (m^2) of overlap between the respective HRs. Overlap was calculated for 95% FK HRs, and had a potential range of 0 (no overlap) to 1 (100% overlap). Although this is a relatively simple metric (Kernohan et al. 2001; Fieberg and Kochanny 2005), we believe it is both sufficient and reasonable for an introduced population in which individuals likely are not experiencing typical density-dependent influences and have not approached local or regional carrying capacity. We calculated seasonal (breeding, nonbreeding) overlap for the 534 dyads (157 female–female [F:F], 285 male–female [M:F], 92 male–male [M:M]) that exhibited HR overlap. Sixty dyads that overlapped in more than 1 season exhibited very little change in overlap between seasons (OI changed < 0.04). Nonetheless, to be conservative, we compared overlap among our full data set ($n = 534$ dyads) as well as on a restricted data set containing only the first occurrence of those dyads that overlapped in multiple seasons ($n = 464$ dyads; 134 F:F, 250 F:M, 80 M:M). Because transformation failed to normalize data in either set we applied nonparametric tests. Differences in OIs were evaluated with Kruskal–Wallis tests for dyads and Mann–Whitney *U*-tests for seasonal comparisons. We used Spearman rank correlation to test potential associations between subsequent seasons and the decline in the proportion of overlapping dyads over time. These tests were conducted in Statistica (Statsoft Inc. 2002); all analyses used a critical value of $P = 0.05$, although we interpret $P < 0.10$ as representing strong trends that may be ecologically important.

Habitat associations.—We acquired satellite images taken before and after the wildfire, and aerial photography after the fire, to estimate the distribution of vegetation and potential habitat for rabbits present on the Refuge before and after this event. We classified habitats into 7 categories on the basis of specific habitat components believed to be important to RBR (e.g., predator avoidance), including plant communities and structural elements. Habitat classes were ground-truthed in the field by 2 technicians, and both multispectral satellite imagery and GIS were used to calculate the distribution and extent of

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Table 1. Habitat categories used in assessing associations by riparian brush rabbits (*Sylvilagus bachmani riparius*), and the available area within each classification (in hectares and as a percentage of the total San Joaquin River National Wildlife Refuge) during pre- and postfire intervals.

Habitat class	Description	Prefire	Postfire	
		ha (% cover)	ha (% cover)	% Change
Dense riparian	Closed canopy and very dense understory. Wild rose, California blackberry, willows, box elder (*Acer negundo*), cottonwood (*Populus fremontii*), valley oak (*Quercus lobata*).	85.2 (11.4)	47.6 (15.1)	−44.1
Oak woodland	Closed canopy, fewer understory shrubs, greater quantities of grass. Valley oak, creeping wild rye (*Leymus triticoides*), Santa Barbara sedge (*Carex barbarae*), wild rose, California blackberry.	54.6 (7.3)	30.4 (9.6)	−44.3
Willow / shrub	Dominated by sandbar willow (*Salix exigua*) and mixed with dense shrubs (California blackberry, wild rose).	142.4 (19.1)	60.4 (19.1)	−57.6
Open grassland	Open spaces at the base of tall grassy vegetation. Perennial pepperweed, Johnson grass (*Sorghum halepense*), mugwort, evening primrose (*Oenothera elata*), Great Valley gumweed (*Grindelia camporum*).	221.6 (29.7)	38.6 (12.2)	−82.6
Dense grassland	Dense mat of vegetation with less open space at the base for travel. Black mustard (*Brassica nigra*), sweet clover (*Melilotus* sp.), rip-gut brome (*Bromus diandrus*), creeping wild rye, prickly lettuce (*Lactuca serriola*), horseweed (*Conyza* sp.).	113.3 (15.2)	25.5 (8.1)	−77.5
Bare ground/short grasses	Bare ground or vegetation (forbs, grasses) measuring 15–30 cm.	29.1 (3.9)	15.2 (4.8)	−47.8
Wetlands	Marshlands consisting of smartweed (*Persicaria* sp.), cattail (*Typha* sp.), bulrush (*Scirpus* sp.), etc.	4.9 (0.7)	3.5 (1.1)	−28.6

each habitat class in the area of the Refuge used by RBR (Table 1; see Phillips et al. 2005 for details of spectral analyses).

We assessed proportions of habitat use using compositional analysis at 2 spatial scales (second- and third-order—Johnson 1980) to determine a ranking of habitat use (Aitchison 1986; Aebischer and Robertson 1992; Aebischer et al. 1993; Smith 2004). Second-order selection refers to placement of the HR by individuals or social groups within the geographic range, whereas third-order selection refers to habitat features used within the HR (Johnson 1980). Because patterns of habitat selection were similar at both scales, we only present second-order results here; details on third-order selection are presented in Hamilton (2010). We analyzed seasonal habitat selection (breeding versus nonbreeding) and we applied log-ratio compositional analysis to compare use versus availability of habitat types. Compositional analysis was run using Compos Analysis software (Smith 2005) in association with Ranges 7. We defined available habitat by proportional representation across the study area, and "used habitat" by the proportional representation of these habitats within 95% FK HRs. We also assessed habitat selection within CAs (50% FK). To avoid division by zero, we assigned a small value for use (0.001) in habitat types that were available but not used by rabbits (Aebischer et al. 1993). We used randomization tests to determine the significance of Wilk's lambda and of *t*-values; these results were used to generate a simplified matrix of ranks where higher rank number corresponded with a greater selection for that habitat type. Randomizations were based on 1,000 iterations (Smith 2005, 2006).

Results

HR, CA, and catastrophic abiotic influences.—Incremental area analysis indicated that $\geq$ 15 locations were required to reliably characterize RBR HR; whereas most studies require higher sample sizes, this reflects the limited vagility of RBR as well as their dependence on patches of shrubs (see below). FK HRs varied by season and year, but not by sex (Table 2). HRs were larger in the breeding season than in the nonbreeding season (1.97 ha [95% confidence interval $\{CI\} = 1.73–2.23$] versus 1.60 ha [95% $CI = 1.41–1.80$]) and in 2003 than in 2004 and 2005 (2003, 2.11 ha [95% $CI = 1.75–2.51$]; 2004, 1.73 ha [95% $CI = 1.53–1.94$]; 2005, 1.53 ha [95% $CI = 1.31–1.78$]). No interactions were significant (Table 2). FK CAs were larger in the breeding season but did not differ by sex or year, and no interactions were significant (Table 2). During the nonbreeding seasons, FK CAs were relatively consistent in size over the 3 years, although breeding-season CAs showed a trend toward decreasing size over time. Male FK CAs were roughly constant in size over the 3 years, whereas those for females showed a trend toward decreasing size over time.

Twenty-two rabbits (11 males and 11 females) were in or adjacent to the Pelican Fire of 2004. Although FK HRs for these animals differed between sexes (male = 1.86 ± 0.79; female = 1.56 ± 1.36 [mean ± *SE*]; $F = 7.20$; $d.f. = 1, 40$; $P = 0.0106$), they exhibited no changes between 90-day periods before versus after the fire (prefire = 1.49 ± 0.81; postfire = 1.92 ± 1.33; $F = 0.002$; $d.f. = 1, 40$; $P = 0.9658$). Both sexes responded similarly to the fire (fire × sex interaction; $F = 1.04$; $d.f. = 1, 40$; $P = 0.3125$). Rabbits near release enclosure 2, which was surrounded by fire but did not burn, showed greater shifts in the geometric centers of their HRs than rabbits near release enclosure 1, which was not directly affected by fire (shifts were 76.59 ± 2.84 m, $n = 9$ versus 23.28 ± 0.93 m, $n = 13$; $t = –4.03$, $d.f. = 20$, $P = 0.0006$).

Spatial overlap and habitat use versus availability.—Analysis of the complete data set revealed no trend in HR overlap between dyad types (Table 3; Kruskal–Wallis $H =$

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Table 2. Mixed-model analysis of variance results for the effect of sex, season, year, and all potential interactions on the fixed-kernel home range and core area sizes of riparian brush rabbits (*Sylvilagus bachmani riparius*) at the San Joaquin River National Wildlife Refuge. Significant effects are in bold font. Note that PROC MIXED applies a restricted maximum-likelihood-based estimation routine and consequently does not provide sums of squares.

Fixed-kernel	Effect	*d.f.*	*F*	*P*
Home range	Sex	1, 97	2.84	0.0949
	Season	**1, 100**	**8.45**	**0.0045**
	Sex × season	1, 100	0.70	0.4041
	Year	**2, 144**	**3.68**	**0.0275**
	Sex × year	2, 144	2.11	0.1249
	Season × year	2, 102	2.11	0.1268
	Sex × season × year	2, 102	1.88	0.1573
Core area	Sex	1, 98.1	1.38	0.2425
	Season	**1, 101**	**16.43**	**0.0001**
	Sex × season	1, 101	1.13	0.2898
	Year	2, 145	2.27	0.1067
	Sex × year	2, 145	2.38	0.0965
	Season × year	2, 103	2.68	0.0730
	Sex × season × year	2, 103	1.26	0.2894

4.59, $d.f. = 2, 531$; $P = 0.1005$), but overlap was greater in the nonbreeding season than in the breeding season ($U = 27{,}654$, $z = -3.11$ $d.f. = 1, 532$; $P = 0.0019$). We obtained similar results when we evaluated the restricted data set that included only the 1st season of data for dyads that persisted over multiple seasons; there were no significant differences in overlap between dyad types (Kruskal–Wallis $H = 4.55$, $d.f. = 2, 461$; $P = 0.1028$) and mean overlap was greater in the nonbreeding season than in the breeding season ($U = 19{,}300$, $z = -3.51$ $d.f. = 1, 462$; $P = 0.0004$). Finally, for the complete data set, there was no indication that the proportion of dyads exhibiting overlap at release enclosures 1 and 2 changed over time (as might be expected with a growing population; $r_S = -0.03$, $d.f. = 8$, $P = 0.5144$).

Within the study area, compositional analysis indicated that rabbits established HRs nonrandomly (all $\chi^2 > 40$, $d.f. = 5$, $P < 0.001$) and they exhibited very clear patterns of habitat selection (Table 4). In both the breeding and nonbreeding seasons rabbits favored willow/shrub habitat, exhibiting secondary selection for open grassland and dense riparian, which were favored over oak woodlands, dense grasslands, and wetlands (in that order). In general, rabbits appeared to avoid oak woodland, dense grassland, and especially wetland habitats.

Habitat selection in CAs was similar to that exhibited for HRs, with the sole qualitative exception that wetlands and dense grasslands shifted in relative importance (Table 4). In general, CA habitat selection reinforced patterns observed for HRs, with willow/shrub and either open grasslands or dense riparian selected in preference to other habitats; wetlands and dense grasslands were consistently the least favored habitats.

Discussion

At the San Joaquin River National Wildlife Refuge, HRs and CAs of riparian brush rabbits were larger in the breeding season than in the nonbreeding season but did not differ across years or sex. We noted a trend for smaller breeding-season CAs among female rabbits over the 3 years of this study, which could reflect gradual "filling" of space as population density increased (although further data are required to confirm this hypothesis). In contrast, however, we detected no parallel trend in overlap of HRs, although these did overlap more in the nonbreeding season than in the breeding season; in concert with seasonal changes in HR and CA this suggests some level of seasonal territoriality, with greater spatial isolation during the breeding season. RBR disproportionately use early-successional habitats such as willow/shrub over late-successional habitat such as grassland or woodlands. Finally, rabbits shifted in response to a catastrophic wildfire but their HRs remained similar in size.

Flooding at the Refuge had a negative influence on survivorship (Hamilton et al. 2010), and whereas initial observations suggested that the Pelican Fire had not greatly affected rabbits other than shift the geometric centers of their HRs, we subsequently noted (February 2005) that most rabbits near release pens 2 and 1 ($21/24 = 88\%$ and $13/21 = 62\%$) had died of undefined causes (Hamilton et al. 2007), suggesting that postfire mortality may be greater than reflected in results presented here. Although it seems reasonable to infer that similar HR area before and after the Pelican Fire reflects similar habitat quality, we did not test this, and given the dependence of brush rabbits on dense cover it may be that even the modest

Table 3. Mean (± *SD*) overlap index (OI) for male and female brush rabbits (*Sylvilagus bachmani riparius*) at the San Joaquin River National Wildlife Refuge. Dyads are designated as FF (female–female), FM (female–male), and MM (male–male).

	Release enclosures combined							
	FF		FM		MM		Dyads combined	
Season	Mean OI	*n*	Mean OI	*n*	Mean OI	*n*	Mean OI	*n*
Breeding 2003	0.83 ± 0.09	14	0.86 ± 0.10	26	0.88 ± 0.07	7	0.85 ± 0.09	47
Nonbreeding 2003	0.86 ± 0.10	35	0.91 ± 0.06	30	0.93 ± 0.03	5	0.89 ± 0.09	70
Breeding 2004	0.82 ± 0.12	19	0.86 ± 0.09	53	0.85 ± 0.12	27	0.85 ± 0.11	99
Nonbreeding 2004	0.85 ± 0.10	51	0.88 ± 0.09	109	0.88 ± 0.11	41	0.87 ± 0.10	201
Breeding 2005	0.85 ± 0.12	13	0.85 ± 0.10	29	0.78 ± 0.12	6	0.84 ± 0.11	48
Nonbreeding 2005	0.87 ± 0.08	25	0.84 ± 0.14	38	0.85 ± 0.11	6	0.85 ± 0.12	69
Total	0.85 ± 0.10	157	0.87 ± 0.10	285	0.87 ± 0.11	92	0.86 ± 0.10	534

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Table 4. Ranked variable sequence (most to least used; higher rank number corresponds with a greater selection for that habitat type) for proportional habitat composition of riparian brush rabbit (*Sylvilagus bachmani riparius*) home ranges versus the study area, core areas versus home range, and locations versus 95% fixed-kernel home-range estimates. A significant difference between 2 consecutively ranked variables is indicated by >>>. The variables water and barren/short grass were omitted from this analysis. Br and Nonbr refer to breeding and nonbreeding season, respectively. Sample sizes for the breeding season were 73 (both sexes), 32 (males), and 41 (females); for the nonbreeding season they were 94, 39, and 55, respectively.

Comparison	Season	Habitat preferences
Study area versus home ranges	Br	Willow/shrub >>> Open grassland > Dense riparian >>> Oak woodland > Dense grassland > Wetlands
	Nonbr	Willow/shrub > Open grassland > Dense riparian >>> Oak woodland > Dense grassland >>> Wetlands
Core areas versus home ranges	Br	Willow/shrub >>> Open grassland > Dense riparian >>> Oak woodland > Wetlands > Dense grassland
	Nonbr	Willow/shrub >>> Open grassland > Dense riparian >>> Oak woodland > Wetlands > Dense grassland

spatial shift could have resulted in elevated exposure to predation or other mortality factors.

Home ranges reported here are considerably larger than those reported previously for brush rabbits; whereas Connell (1954), Shields (1960), and Chapman (1971) estimated HRs as 0.14–0.57 ha, our estimates are well in excess of 1–2 ha. Differences in these estimates could reflect study methods (including field methods and HR estimators) or different habitat, and as such we hesitate to make strong inferences from these comparisons. For example, Connell (1954) studied brush rabbits in chaparral, which is very different from the riparian shrub habitat studied here. Both Shields (1960) and Connell (1954) assessed HR area with livetrapping, which is now known to bias estimates of HR (Hayne 1949; McShea and Gilles 1992). Shields (1960) trapped 5 ha in coastal northern California over a 16-month period, whereas Connell (1954) sampled 4.6 ha over 14 months in coastal hills near Berkeley, California. Chapman (1971) used radiotelemetry, but rabbits in his study carried transmitters for a mean of only 48 days and a maximum of only 137 days. Additionally, he collected only 20–30 locations per animal over a much shorter timescale (approximately 6 days) than in this study. Hence, we believe that our data are robust relative to these studies. Half a century ago, Connell (1954:392) noted that brush rabbits are "one of the commonest game mammals" in chaparral habitat of California, "yet surprisingly little has been published on its natural history." Although our results help to strengthen our understanding of this species, they also underscore the need for further comparative field research.

An alternative hypothesis for the larger HRs documented here is that this is a growing population that has not been influenced greatly by density-dependent competition (see below). This may be reasonable for a population in the 1st year following reintroductions. Similarly, Zoloth (1969) speculated that population density might influence brush rabbit foraging ranges; he reported that the density of brush rabbits at his study site on Año Nuevo Island, California was almost 3 times that of Shields (1960) and twice that noted by Orr (1940) within a hedge in San Francisco, and that rabbits on Año Nuevo Island appeared to forage within smaller ranges than did brush rabbits reported by Shields and Orr. Zoloth (1969) argued that high-quality habitat on Año Nuevo Island contributed to higher densities of rabbits and decreased foraging ranges because resources and escape cover were more readily available. Activity ranges of rabbits in locations with lower-quality cover and forage were more consistent in size with those observed by Shields (1958) and Connell (1954) for mainland populations (Zoloth 1969). Further work on carrying capacity and the relationship between density and foraging activities would be productive.

Connell (1954) and Shields (1960) reported that HRs of male brush rabbits tended to overlap, whereas those of females overlapped less or not at all; however, Shields (1960) observed unsystematic overlapping of HRs and found that no animals maintained ranges that were completely isolated from other individuals. In our study, males and females demonstrated similar overlap with neighbors of either sex, but overlap differed significantly between breeding and nonbreeding seasons. It is unclear if these results reflect brush rabbit social structure or are an artifact of the landscape. Over one-half of dyads (53%) exhibited no overlap at all, suggesting that rabbits may not have saturated the habitat and supporting our speculation (above) that observed patterns may reflect a relatively young population. Alternatively, in situ recruitment may have led to greater overlap in subsequent years than suggested by our data (because we collared few native-born rabbits). Our telemetry observations are not fully consistent with the 1st scenario. Many rabbits were documented dispersing long distances shortly after release enclosures were opened, possibly indicating that these areas were saturated, thus causing individuals to spread throughout the refuge; alternatively, this may have reflected movements of naïve rabbits exploring a novel landscape. Because we were able to collar and monitor only a small portion of native-born rabbits that we identified ($n = 13$ of 174), we could not comprehensively survey populations in subsequent years, and we are unable to assess the viability of the 2nd hypothesis. Additionally, the release protocol may have affected OIs because the majority (~85%) of releases occurred during nonbreeding seasons. Of these releases, over half ($n = 177$; ~52%) took place in a single season (nonbreeding 2003). Moreover, animals that were released from enclosure 2 may have been precluded from normal movement patterns by a slough channel that carried irrigation runoff in the summer. A levee and short grass field bordered this release enclosure along the western edge and the slough encircled the other 3 sides. At all release sites, and particularly at enclosure 2, it is likely that large influxes of individuals resulted in high OIs as animals

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initially were concentrated near the reintroduction site. Consequently, a longer monitoring horizon may be required to observe unbiased levels of overlap among established residents.

As noted above, Williams and Basey (1986) inferred that frequently flooded secondary successional communities were less likely to be inhabited by RBR. However, at that time the only site known to be occupied was Caswell Memorial State Park, which had been subjected to long-term fire suppression and flood control, resulting in mature plant communities with few successional species and a relatively low number of brush rabbits. In contrast, results from the Refuge indicate that RBR selectively establish HRs and CAs with disproportionate quantities of willows/shrubs and tall woody perennial vegetation. Dense riparian vegetation, herbaceous nonnative annual grassland, oak woodlands, and wetlands were used less often in the placement of HRs and CAs, even though they were available. Reinforcing these patterns, habitat selection by brush rabbits was similar at all spatial scales analyzed.

The early successional vegetation that RBR appears to favor may be disproportionately prone to catastrophes as demonstrated by the July 2004 wildfire and the spring 2005 flooding. The Pelican Fire burned 588 ha of the Refuge, including the primary release locations and much available habitat for RBR. Perhaps surprisingly, HR size was not significantly affected by the wildfire and we detected no effect on habitat use. Among radiocollared individuals, only 3 fire-related mortalities and few injuries were discovered in the weeks following the event. The seemingly minor influence of this event likely reflects the spatial distribution of the fire, which did not burn approximately 42% of willow shrub habitat and 66% of dense riparian habitats, particularly along slough channels; these likely provided escape cover and forage for existing rabbits. However, as noted above a large proportion of rabbits near both release pens had expired within about 7 months of the fire (Hamilton et al. 2007). Several studies have documented direct mortality or physical injuries to cottontail species following natural or prescribed fires (Chew et al. 1959; Komarek 1969; Erwin and Stasiak 1979; King et al. 1991), and Simpson (1972) argued that the proximal cause may be postfire crowding and possibly functional responses by predators; at his site, for example, predators foraged exclusively within remnant cover after prescribed fire in Georgia due to the increased concentration of available prey (Simpson 1972). We were unable to detect direct negative effects of crowding following the July 2004 wildfire since most of our radiocollared rabbits were located in riparian habitat that was not burned. A small number of animals was not documented after the fire, but they were not radiocollared so their fate could not be determined. Two individuals in unburned riparian habitat dispersed soon after the fire, possibly in response to local crowding.

Flooding also is an important disturbance at the Refuge, and although survival of translocated rabbits decreased by ~30% during the March 2005 event (Hamilton et al. 2010), we lack data to assess the effect of flooding on HR and CA sizes. It seems likely that RBR will move under flooding conditions (as seen in swamp rabbits, *S. aquaticus*—Zollner et al. 2000), but the extent to which their "cognitive landscape" includes knowledge of escape routes and flood refugia (or if they simply move "uphill") is not known. In either case, however, these observations comprise a call for protected escape routes and refugia above flood levels.

Insights from this study may be limited by the fact that the population most likely is well below carrying capacity. Although we have no information on the density that might correspond to carrying capacity in this system, we assume that rabbits will approach this relatively soon as long as sufficient resources are available to allow for the population to persist. Powell and Mitchell (2012) make a compelling case for the importance of multiple metrics when evaluating HRs; we concur that particularly in the case of an endangered species that appears to exhibit limited habitat preferences, further efforts to understand the ecology and management needs of this taxon would benefit by incorporating additional metrics such as energetic cost and reward, predator risk ("landscape of fear"), and the distribution and availability of movement corridors. Brush rabbits are particularly dependent on dense vegetation (Chapman and Litvaitis 2003), but they clearly move between and among patches of such habitat; as such they provide an interesting species for further effort on how best to integrate movement corridors into assessments of HRs. Our observations in response to both the Pelican Fire and the floods of 2005 suggest that conservation management of RBR will require sufficient escape and refuge habitat, and assume that these animals learn the spatial distribution of such habitat elements. These provide ample fodder for further applied research on this species.

The broader context of this study lies in the historic fragmentation and loss of key habitat; riparian habitat in the Central Valley has been reduced by 93–98% (Katibah 1984; Dawdy 1989), and remaining habitat must be managed carefully to maximize conservation potential (Eubanks 2004; Darby and Sear 2008; Hanak et al. 2011). On the basis of data reported here, habitat management should focus on maintaining disturbance regimes to promote early successional vegetation, especially scouring floods or mechanical means to promote periodic renewal of patches of successional willow species. Additionally, restoration and maintenance of other native shrub lands, especially those dominated by *Rubus* spp., *Rosa* spp., and shrubby trees such as box elder (*Acer negundo*) and tall perennial early successional vegetation, would provide important habitat for RBR. Landscapes containing greater quantities of early successional, dense shrubby vegetation should be prioritized for reintroductions or conservation. However, because such habitat also poses risks in terms of fire and flooding we recommend establishment of additional refugia from catastrophic events. Although we were unable to evaluate the effect of flooding on the spatial dynamics of monitored rabbits, the potential for significant effects on rabbit populations (Hamilton et al. 2010) suggests that measures to mitigate flood risk should be a component in management plans for this and ecologically similar species.

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Acknowledgments

This work (trapping, handling, radiotelemetry, and reintroduction) was conducted under permits and Memoranda of Understanding issued to DFW and PAK by the United States Fish and Wildlife Service and the California Department of Fish and Wildlife. Funding for this cooperative project has been provided by many agencies and programs: United States Bureau of Reclamation (Conservation Program; Habitat Restoration Program; South Central California Area Office in Fresno), CALFED (Sacramento–San Joaquin Delta water-quality program between the State of California and the United States Federal Government), United States Fish and Wildlife Service (San Luis National Wildlife Refuge Complex, Burned Area Emergency Response, Sacramento Fish and Wildlife Office, Pacific Southwest Region Office), and the California Department of Fish and Wildlife ESA Section 6 program. We thank members of the Riparian Mammals Technical Group for ongoing funding, discussion, advice, and logistical and other support. Additionally, we thank the California Departments of Water Resources and Fish and Wildlife for their critically important logistical support of the breeding program and the California Department of Parks and Recreation for ongoing support. We are grateful to the veterinarians of the UC Davis Wildlife Health Center and Veterinary Medical Teaching Hospital, particularly K. Gilardi and S. Larsen, for their care and expertise. We also thank River Islands, LLC, especially S. Dell'Osso, for allowing us to capture RBR on their property to use as brood stock in the controlled propagation program. For their many hours of hard work and their dedication to this project, we thank the past and present members of the riparian brush rabbit team and the California State University, Stanislaus—Endangered Species Recovery Program, particularly L. P. Hamilton, M. Lloyd, and E. Williams. We are very grateful to R. Kenward for providing a beta version of Ranges VII.

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Submitted 30 July 2013. Accepted 20 December 2013.

Associate Editor was Lisa A. Shipley.

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