

RECONNECTING SMALL MAMMAL POPULATIONS IN THE CASCADE RANGE ACROSS AN INTERSTATE HIGHWAY: AN EARLY LOOK AT USE OF A WILDLIFE CROSSING STRUCTURE

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Abstract.—Expanding transportation corridors have fragmented ecosystems throughout the world, restricting the movement of organisms or acting as complete connectivity barriers. Wildlife crossing structures (WCS) can increase the permeability of roads by allowing animals to move safely between habitats. Small mammals are especially vulnerable to the effects of reduced connectivity because of their limited mobility; however, researchers have only recently begun to evaluate their use of WCS. This study was conducted at a newly constructed WCS under Interstate-90 near Snoqualmie Pass, Washington, in 2017. Our objective was to compare the small mammal species composition at the WCS and adjacent restoration sites to reference sites in the nearby forest. We also sought to evaluate how small mammals used installed habitat features (rock piles, brush piles, or fallen logs) to move through the WCS. We used live-trapping and remote camera-traps to assess small mammal communities. Our results indicated significantly fewer species, lower species diversity, and greater abundance of generalist species in and near the crossing structure than in the reference sites. Small mammals showed no preference for any particular habitat features across all sites but were more likely to be captured near a feature than in open areas. Two years post-construction, the WCS harbored half of the species found in the forest reference sites. We expect the number of small mammal species using the WCS to increase in the future as the habitat develops to support richer biodiversity and as additional species encounter the WCS.

Key Words.—community ecology; forest specialist; habitat fragmentation; habitat generalist; landscape connectivity; microhabitat; *Peromyscus*; road ecology

INTRODUCTION

Habitat fragmentation, urban sprawl, and expanding transportation networks have fractured ecosystems, restricting the movement of organisms across the landscape (Saunders et al. 1991; Forman and Alexander 1998; Goosem 2000; Dickson et al. 2005; Benítez-López et al. 2010; Buchmann et al. 2013). Traffic noise and lights cause many species to avoid crossing busy highways and connectivity is further reduced by mortality due to wildlife-vehicle collisions (Clevenger et al. 2003; Dodd et al. 2004; Glista et al. 2009; González-Galina et al. 2013). Transportation departments have recognized this rise in human-wildlife conflict and have responded by improving the safety of roads and prioritizing long-term monitoring (Clevenger and Waltho 2000; Clevenger 2012; Andrews et al. 2015). Reduced wildlife connectivity caused by roads at local and landscape scales can be mitigated by a variety of techniques, ranging from posting caution signs in high-risk wildlife crossing zones to constructing wildlife crossing structures (WCS; Hardy et al. 2003; Ford et al. 2009; Beckmann et al. 2012; Andrews et al. 2015; Huijser et al. 2016).

These methods for improving road safety for both drivers and wildlife can often be integrated into existing road construction projects (Clevenger et al. 2001a; Gurrutxaga and Saura 2014; Sawyer et al. 2016). For example, Interstate-90 (I-90) in Washington State bisects the Cascade Range and critical wildlife habitat corridors (Interstate 90 Snoqualmie Pass East Mitigation Development Team 2006). Near Snoqualmie Pass (elevation 921 m), the interstate experiences traffic

volumes averaging 31,000 vehicles on a typical day and > 58,000 vehicles on a busy weekend day (Washington State Department of Transportation [WSDOT] (US). 2016. 2016 Annual Traffic Report. Olympia (WA). Washington State Department of Transportation (US). Available from http://www.wsdot.wa.gov/mapsdata/travel/pdf/Annual_Traffic_Report_2016.pdf [Accessed 26 April 2018]). What began as a project to increase the number of lanes and make road safety improvements to accommodate increasing traffic volumes transformed into a collaborative conservation partnership with the added goal of improving the permeability of the interstate to wildlife (Interstate 90 Snoqualmie Pass East Mitigation Development Team 2006). As a result, Washington State Department of Transportation included 27 medium (2 m wide) to large (> 100 m wide) WCS (Mark Norman, pers. comm.) within the I-90 Snoqualmie Pass East Project (Wildlife Working Group 2008). About half of these have been constructed since 2008, with the remainder in planning stages. These WCS are designed to be effective not only for large mammals, but also for small mammals, fish, amphibians, and reptiles.

Small animals, with typically small home ranges and limited dispersal distances, are especially vulnerable to vehicle mortality and reductions in their ease of movement from habitat fragmentation and roads (Bowman et al. 2002; Jenkins et al. 2007; Barthelmess and Brooks 2010; Downs and Horner 2012; González-Gallina et al. 2013). Most wildlife crossing structures have been designed and tested for large-bodied, high-mobility species such as ungulates and large carnivores (Gloyne and Clevenger 2001; Clevenger and Waltho 2005), while studies have

only recently begun evaluating the effectiveness of wildlife crossing structures for small mammals (McDonald and St. Clair 2004; D'Amico et al. 2015; Martinig and Bélanger-Smith 2016) and other low-mobility species (Rytwinski and Fahrig 2011; Cunningham et al. 2014). Small mammals (< 5 kg; Bourlière 1975; Merritt 2010) serve important roles as both prey species and predators (e.g., consumers of plants and insects) and provide ecosystem services, such as seed and spore dispersal (Maser et al. 1978; Hayward and Phillipson 1979; Martin 2003; Pearce and Venier 2005). For example, in Pacific Northwest forests, Bushy-tailed Woodrats (*Neotoma cinerea*) and Northern Flying Squirrels (*Glaucomys sabrinus*) are two of the predominant prey species for the endangered Northern Spotted Owl (*Strix occidentalis caurina*; Bevis et al. 1997; Forsman et al. 2001; Cutler and Hays 2016). Some small mammals, such as Northern Flying Squirrels, serve as important dispersal agents for mycorrhizal fungi; loss of these dispersers can negatively affect the long-term function of coniferous forests, especially during recovery after large-scale wildfire or silviculture disturbance (Pyare and Longland 2001; Lehmkuhl et al. 2006).

Our objective was to evaluate small mammal use of one of the first completed WCS of the I-90 Snoqualmie Pass East Project. We aimed to determine which species of small mammals (target species < 1 kg) were using the WCS in its early post-construction stages and how they were moving through the structure. We compared the richness, diversity, relative abundance, community composition, and movement of small mammal species at the WCS to adjacent restoration sites and reference sites in nearby forest. We also evaluated the effectiveness of habitat features (fallen logs, brush piles, rock piles, and snags placed in the WCS and restoration sites) in providing cover for small mammals by testing the likelihood of capturing an animal at different habitat features. We hypothesized that in the early years after construction, WCS harbor only a subset of the surrounding small mammal assemblage that is able to inhabit recently disturbed habitats (Taylor 1999; Smith and Fox 2017), and habitat generalist species are more likely than forest specialist species to be the first to use a WCS. We predicted that the WCS would have lower species richness and lower diversity than the forest reference sites. The restoration sites would have intermediate species richness and diversity compared to the WCS and reference sites because they are closer to the forest edge and have more vegetation than the WCS (Monamy and Fox 2000; Clevenger et al. 2001b; McDonald and St. Clair 2004). We further hypothesized that small mammals are more likely to move along habitat features than in the open (Brehme et al. 2013; Ascensão et al. 2016). We therefore predicted that small mammals would be trapped more frequently in or near habitat features than in more open areas at our study sites. The main outcomes of our study are to provide early post-construction data for future assessments and to suggest specialized habitat restoration improvements for

small mammals at future WCS in the I-90 Snoqualmie Pass East Project and other connectivity projects.

METHODS

Study area.—We conducted our study along the I-90 transportation corridor in the Cascade Range of Washington State, approximately 4 km east of the Snoqualmie Pass summit near the lower Gold Creek Valley and upper end of Keechelus Lake. The mixed coniferous, mid-elevation forests were dominated by Western Hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and Western Red Cedar (*Thuja plicata*), with Vine Maple (*Acer circinatum*) and alder (*Alnus* spp.) in the forest understory. Riparian areas along streams and lakeshore habitats had interspersed patches of willow (*Salix* spp.) and cottonwood (*Populus* spp.) trees. The patchwork nature of land ownership around the Okanogan-Wenatchee National Forest, Interstate-90, railroad beds, Forest Service roads, and regulated reservoir levels were sources of considerable anthropogenic disturbance.

We compared the small mammal communities at five study sites: a WCS site, two restoration sites, and two forest reference sites (Fig. 1; Table 1). Our WCS was the

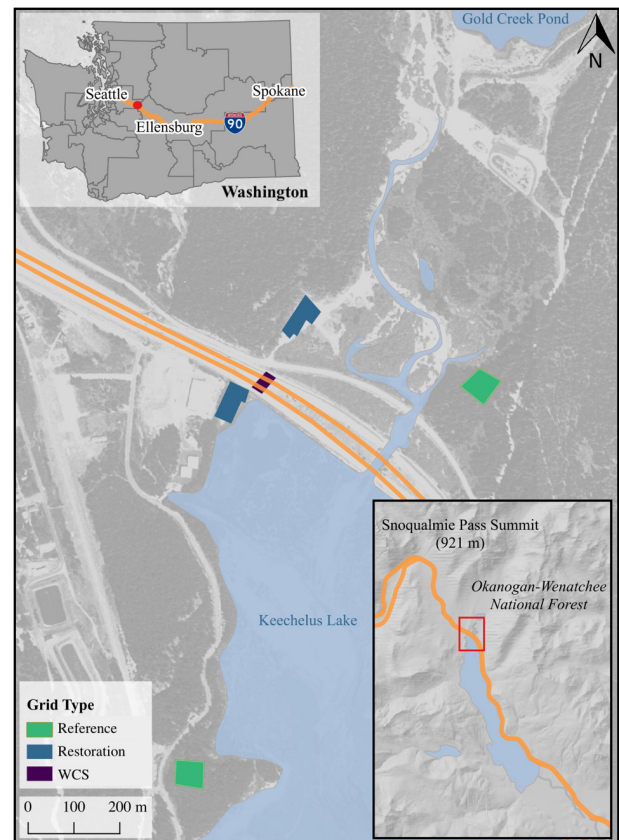


FIGURE 1. Northeastern portion of the Snoqualmie Pass East Project area and study area (black box in bottom inset) located along Interstate-90 in the Cascade Range of Central Washington State, USA, in summer 2017. The five study sites occurred north and south of I-90 and included the Hyak wildlife crossing structure (WCS).

Table 1. Location and description of study sites in the Cascade Range of Washington, USA, summer 2017: forest reference sites north and south of I-90, restoration sites north and south of I-90, and a wildlife crossing structure (WCS) under I-90. Habitat features included brush piles (BP), fallen logs (FL), rock piles (RP), and snags (S).

Site	Latitude	Longitude	Elev. (m)	Grid Area (ha)	Habitat Features Present			
					BP	FL	RP	S
Reference North	47.3910	-121.3797	772	0.36	x	x		x
Reference South	47.3844	-121.3892	777	0.36	x	x		x
Restoration North	47.3934	-121.3853	763	0.34	x	x	x	x
Restoration South	47.3915	-121.3874	771	0.35	x	x	x	x
WCS	47.3917	-121.3857	768	0.18		x	x	

Hyak wildlife undercrossing, constructed in 2013. The WCS with its 36-m span, soil floor, and solid concrete walls and ceiling allows wildlife to pass underneath I-90 (Fig. 2). In 2015, contractors added bark mulch over the soil, planted sparse ferns and herbaceous plants, scattered large logs throughout, and piled rocks along the interior walls (Fig. 2). At the time of the study, no fencing existed near the structure to guide animals to it or prevent them from attempting to cross the interstate. The two adjacent restoration sites had been previously cleared but were replanted with native trees and shrubs in 2015. Rock piles, snags, fallen logs, and brush piles were added to both sites as habitat features for wildlife. A paved Forest Service road separated the northern restoration site from the WCS. This site was a temporary wetland in early spring. The southern restoration site was directly adjacent to the southern entrance of the undercrossing. The two forest reference sites served as a baseline for expected small mammal species in the area. The northern reference was 200 m northeast of I-90 and southern reference was 800 m west of I-90 (Fig. 1). These second-growth forests had large-diameter conifers, well-developed canopies, and extensive woody debris on the forest floor and experienced occasional human recreation activity.

Live trapping.—At each site we installed a live-trapping grid. The general layout consisted of a 60 × 60 m (0.36 ha) grid with 49 stations in a 7 × 7 array

with 10-m spacing. We placed one Sherman live trap (Model LFATDG, H.B. Sherman Traps, Tallahassee, Florida, USA) at every station (49 traps per grid) and one Tomahawk live trap (Model 201, Tomahawk Live Trap, Hazelhurst, Wisconsin, USA) on alternate lines at 20-m intervals (16 traps). Two pitfall arrays, one upland and one lowland, each had one central 3.8 L (1-gallon) bucket and three peripheral buckets at the ends of 5-m galvanized wire mesh drift fence radiating from the center. We made slight modifications to the grid layout at the restoration sites due to spatial constraints, but the total number of traps was maintained. The WCS could accommodate only a half-size grid (30 × 60 m) with 28 Sherman traps, eight Tomahawks, and one central pitfall array.

We visually assessed the type of habitat feature that occurred within a 1-m radius of each grid station and categorized it as rock pile, log, brush pile, snag, or open. Rock piles were several layers of rocks at least 3 m high and at least 3 m in diameter. Fallen logs were at least 0.5 m in diameter, at least 1 m long, with a minimal degree of decomposition. Brush piles were at least 3 m in diameter and multilayered, with several branches of different sizes. Snags were standing dead trees or upright placed logs. We categorized as open any grid stations with habitat features smaller than the specified dimensions or without any habitat features.

We trapped each site for two consecutive nights in mid-July and again in late August 2017, for a total of 1,328



FIGURE 2. The Hyak wildlife undercrossing located at the Snoqualmie Pass in Washington State is an entirely terrestrial crossing structure with native plants, a wood-mulch floor, different sized fallen logs distributed throughout, and rock piles lining the western and eastern borders. (Photographed by Lindsay Millward).

trap-nights (number of traps set multiplied by number of nights traps were open). Bait for Sherman traps was a mixture of peanut butter, rolled oats, and molasses; for Tomahawk traps we used this mixture plus a piece of carrot. We added 8–10 live mealworms, a bottle cap filled with water, and a toilet paper roll (shelter) to each pitfall bucket to decrease shrew (*Sorex* spp.) mortality (Shonfield et al. 2013). We set traps in the late afternoon and checked them just before sunset and again in early morning to increase the likelihood of capturing diurnal, crepuscular, and nocturnal species. To avoid overheating animals, we closed all traps during the day.

We brought all captured animals in traps to a shaded processing area. For each individual, we identified the species, took standard measurements (weight, body length, tail length, hind foot length, ear length), recorded sex and age (juvenile, subadult, adult), and applied nail polish to the toes of one foot as a temporary mark. We used tail length to differentiate between adult Keen's Deer Mice, *Peromyscus keeni* (tail vertebrae length ≥ 96 mm), and Deer Mice, *P. maniculatus* (tail vertebrae length < 96 mm; Gunn and Greenbaum 1986; Zheng et al. 2003). We differentiated juveniles, subadults, and adult mice by weight and pelage color: juveniles weigh 13–16 g and have a solid grey pelage and adults weigh > 17 g and have a brown, coarse pelage (Healey 1967; Sullivan 1979; Van Horne 1982). Differentiating subadult deer mice is challenging and we made our best judgement calls in the field based on size and pelage (color and coarseness). We used an N165 injector needle (16 GA) to inject an 8 mm PIT tag (Biomark mini-HPT8, Boise, Idaho, USA) subdermally behind the head, roughly between the scapulae. We then released animals at the site of capture. Any individuals that died in the traps or during processing, we collected as specimens and stored in a freezer.

Remote camera traps.—We used remote camera traps (models RapidFire, Silent Image, Hyperfire, and Convert IR; Reconyx, Holmen, Wisconsin, USA) for a two-week period between July and October 2017 at each site to capture species that might not readily enter live traps. To avoid disturbance from researcher presence, we installed cameras at sites when we were not actively trapping. On each grid we placed four cameras per habitat feature (fallen log, brush pile, rock pile, and snag) at positions deemed most suitable for both camera position and concealment from potential theft. We mounted cameras within habitat features or facing them (depending on the feature) and did not use a scent lure (Glen et al. 2013). We set cameras to capture a burst of three or five images within a 5-sec interval when triggered by an animal, with a 30-sec delay between bursts (De Bondi et al. 2010). We counted images of the same species more than one hour apart as separate visitation events (Derugin et al. 2016). In cases where we could not identify the images to species, we placed it into a species group designation (e.g., woodrats, deer mice).

Data summary and statistical analysis.—We classified species recorded during the study as either habitat generalists or forest specialists (Appendix 1; Naughton 2012). We constructed species accumulation curves (Ugland et al. 2003) to verify sufficient sampling of the small mammal assemblage before further analysis. For each site type (WCS, restoration grids, reference grids) we calculated Shannon diversity index (H')

$$H' = \sum p_i \ln p_i$$

where p_i is the proportion of individuals found of species i , and Shannon's equitability (a measure of evenness; E_H)

$$E_H = H' / \ln S$$

where S is the number of species sampled (Magurran 1988; Heip et al. 1998). We determined species richness, or number of species sampled, for each site type by combining data from live-trapping and cameras. We used a Hutcheson t -test to compare species diversity between the restoration and reference sites (Hutcheson 1970). Because the sampling effort for the WCS (i.e., only one replicate) was not equivalent to the other sites, we did not include it in the t -test. For other comparisons, we standardized capture data (to account for fewer trapping stations in the WCS) as number of captures per 100 trap-nights (number of captures or camera-trap visitations divided by the number of trap-nights, multiplied by 100) or by comparing relative abundance (number of individuals divided by the total number of captures at each site; Mengak and Guynn 1987; dos Santos-Filho et al. 2006). We combined camera and live-trap data only to determine species richness at each site; otherwise, the two capture methods were analyzed separately.

We conducted all other statistical analysis using R 3.5.1 (R Core Team 2018). To evaluate habitat preference by small mammals, we used a Generalized Linear Mixed Model (GLMM) implemented with the glmmTMB package in R (v0.2.3; Brooks et al. 2017). The total number of individuals per trap station was modeled as a function of habitat feature (fallen log, brush pile, rock pile, open), trap type (Sherman, Tomahawk, pitfall), site type, and individual site, with site treated as a random effect (Hamilton et al. 2015). We used a log-link function and a Conway-Maxwell-Poisson distribution of error terms, due to significant underdispersion. We classified site type as either reference or combined restoration/WCS because the wildlife crossing structure was represented by only one site. Post-hoc, we replaced habitat feature with presence/absence of any habitat feature to produce our final model. We performed model validation via simulation using the DHARMA package in R (v0.2.0; Hartig 2018). Validation of our final model revealed no evidence of model misspecification (one-sample Kolmogorov-Smirnov test on the residuals, $D = 0.05$, P

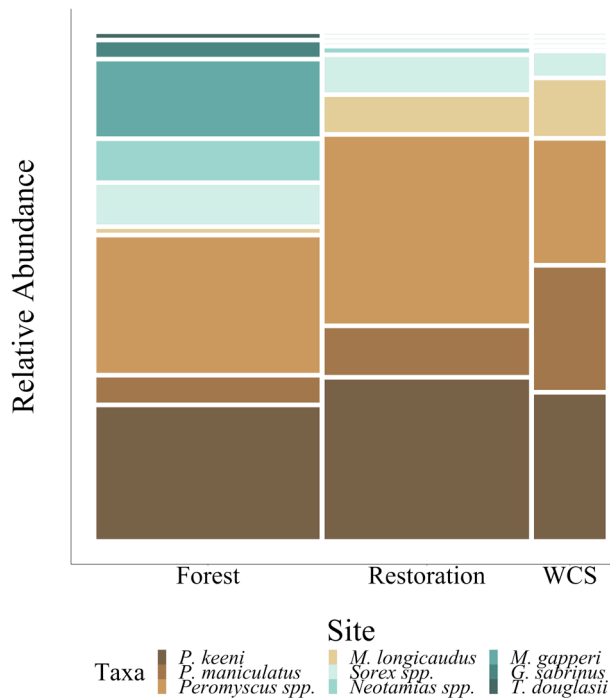


FIGURE 3. Mosaic plot of small mammal community composition at forest, restoration, and wildlife crossing structure sites in summer 2017 near the Snoqualmie Pass, Washington State. Relative abundance is the number of individuals of a particular species divided by the total number of individuals at each site. Column width represents the sampling effort. Generalist species are represented by shades of brown, while forest specialist species (Naughton 2012) are represented by shades of blue. (Appendix 1).

= 0.340). Following best practices outlined in Bolker et al. (2009), we estimated parameters by maximum likelihood laplace approximation and performed hypothesis testing of fixed effects with Wald Z tests. The overall significance of factors with more than two levels was assessed using a Likelihood Ratio test, followed by specific post-hoc pairwise comparisons via Wald Z tests using the `glht` function from the `multcomp` package in R (v1.4-10; Hothorn 2008) and the Tukey method to adjust for multiple testing.

To evaluate distance traveled by small mammals within a site, we calculated straight-line (i.e., minimum) distances between trapping stations for each individual that we recaptured on consecutive nights. We applied a General Linear Model executed with the `lm` function from the `stats` package in R 3.5.1 (R Core Team 2018) to model distance traveled in one night as a function of site, species, sex, and age. We used a power transformation of 0.7 on distance traveled to yield maximum conformation to a Gaussian distribution of error terms, as confirmed by model validation via simulation using the `DHARMA` package in R (v0.2.0; Harting 2018; one-sample Kolmogorov-Smirnov test on the residuals, $D = 0.09$, $P = 0.540$). We used F -tests for hypothesis testing of fixed effects.

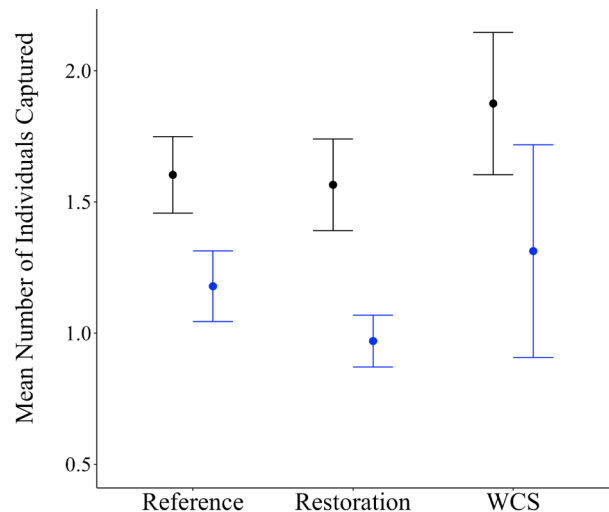


FIGURE 4. Mean (\pm standard error) number of small mammal individuals captured per 100 trap-nights at trap stations with habitat features present (black) and absent (blue) during 2017 at all sites near the Snoqualmie Pass, Washington State.

RESULTS

Live trapping.—Among the 472 total captures, we recorded 293 unique individuals and 10 species. Deer Mice and Keen's Deer Mice were the most frequently captured species, composing 69% of captures at the reference sites, 83% at the restoration sites, and 86% at the WCS (Figs. 3 and 4). The relative abundance of generalist species increased from the reference sites to restoration sites to the WCS, while the relative abundance of specialist species decreased (Table 2; Appendix 1). Compared to the reference sites, the WCS had substantially higher relative abundances of generalist Deer Mice (> 5 times as high; 6.9 vs. 1.2 individuals per 100 trap-nights), Keen's Deer Mice (1.5 times as high; 9.4 vs. 6.3 individuals per 100 trap-nights), and Long-tailed Voles, *Microtus longicaudus* (15 times as high; 3.1 vs. 0.2 individuals per 100 trap-nights). Within the WCS, several individuals were recaptured on different nights (one of five Long-tailed Voles, 17 of 39 deer mice). Two (of three) female Long-tailed Voles and three (of 18) female Deer Mice were reproductively active (pregnant, nipples prominent, or lactating).

Small mammal community composition.—Species accumulation curves leveled off, indicating sufficient sampling (Appendix 2). Species richness varied across the three site types (Table 3). Three species (Keen's Deer Mouse, Deer Mouse, and Montane Shrew, *Sorex monticolus*) occurred in all site types, and five other species (Cinereus Shrew, *Sorex cinereus*; Long-tailed Vole; Townsend's Chipmunk, *Neotamias townsendii*; Douglas Squirrel, *Tamiasciurus douglasii*; and Snowshoe Hare, *Lepus americanus*) occurred at both restoration and reference sites, but not at the WCS (Fig. 3). We captured

TABLE 2. Total number of trap-nights, recapture rates, and total number of captures per 100 trap-nights including number of individuals in parentheses at each site from live-trapping in 2017 near Snoqualmie Pass in the central Cascade Range of the central Cascade Range in Washington State. Habitat specialization (generalists and forest specialists) from Naughton (2012; Appendix 1).

Site Type	Trap Nights	Generalists	Forest Specialists	Total Captures	Recapture Rate
Reference	584	25.2 (11)	10.4 (2)	35.6 (13.0)	36%
Restoration	584	28.8 (9.9)	2 (0.4)	30.8 (10.3)	33%
WCS	160	43.1 (16.9)	1.3 (0)	44.4 (16.9)	38%

Southern Red-backed Voles (*Myodes gapperi*), Yellow-pined Chipmunks (*Neotamias amoenus*), and Northern Flying Squirrels (*Glaucomys sabrinus*) exclusively at the reference sites.

The reference sites had a significantly higher diversity than the restoration sites ($t = 4.382$, $df = 140$, $P < 0.001$). The abundances of species in the reference forest community were also distributed more evenly than in the restoration sites (Table 3; Fig. 3). The southern reference site had the highest evenness and highest diversity. The northern restoration site had the least even community, mostly dominated by Keen's Deer Mice, and the lowest diversity index.

Remote camera traps.—We documented 351 small mammal visitations (photo-captures of a species at least 1 h apart) from a total of 838 animal photographs over 761 trap-nights. Across all sites, 42% of visitations were deer mice, 36% were voles (*Microtus longicaudus* or *Myodes gapperi*), 8% were chipmunks, 5% were Douglas Squirrels, and < 10% were shrews, Snowshoe Hares, and Northern Flying Squirrels. We captured seven genera at the reference sites, six genera in the restoration sites, and three genera in the WCS. We captured Snowshoe Hares exclusively on wildlife camera, contributing to the overall species richness documented in the reference and restoration sites.

The total number of photo-captures per 100 trap-nights increased from the reference to restoration sites and WCS (Table 4). At both the WCS and restoration sites, the cameras captured more small mammals at rock piles than at other features. Across all sites, the cameras captured fewer individuals at snags than at other features.

Habitat features.—Based on live-trapping, small mammals collectively showed no significant preference

TABLE 3. Small mammal species richness and evenness (Shannon's equitability, E_H) from live trapping at sites in 2017 near Snoqualmie Pass in the central Cascade Range in Washington State. Combined reference and combined restoration are the combined richness and evenness of the north and south sites.

Site	Richness	E_H
Combined Reference	11	0.74
Reference North	9	0.63
Reference South	8	0.88
Combined Restoration	8	0.62
Restoration North	7	0.40
Restoration South	4	0.69
WCS	4	0.60

among habitat features (fallen logs, brush piles, rock piles, and open areas) across all sites (GLMM estimates assessed via likelihood ratio test, $LR = 5.183$, $df = 3$, $P = 0.160$). Captures of small mammals, however, were more likely at stations with a habitat feature present than at stations in open areas (Table 5; Fig. 4). Trap type was significant in both models because we captured significantly more animals in Sherman traps than either Tomahawk traps or pitfall traps (Table 5). Overall, capture rates did not differ between reference sites and restoration/WCS sites (Table 5).

Intra- and inter-grid movement.—The disproportionate composition of species with movement events (76 out of 84 events are deer mice) resulted in species being a significant predictor in our model ($F_{6,77} = 2.431$, $P = 0.034$). Therefore, we cannot confidently describe movement rates or trends between species. Of all species combined, neither site type ($F_{4,79} = 1.444$, $P = 0.230$) nor sex ($F_{1,82} = 0.208$, $P = 0.645$) was a significant predictor of distance traveled in one night within grids, but age was a significant factor ($F_{1,82} = 5.884$, $P = 0.018$), with adults of all species traveling farther than subadults/juveniles (estimated effect size of adult age = 6.2 m, 95% confidence interval = 0.6–14.6 m). Of the 84 total movement events that fit our criteria, 50% were adults and 52% were males. Small mammals moved on average 16.8 m (± 2.4) per night in the reference grids, 17.1 m (± 2.6) in the restoration grids, and 15.5 m (± 3.0) in the WCS site.

Movements of animals between sites were documented six times; all were deer mice. Five mice moved an average distance of 39 m from the WCS to the southern

TABLE 4. Average number of days a camera was deployed at a site, number of total camera-traps at a site, total number of trap-nights, and total number of captures per 100 trap-nights for each habitat feature category in 2017 near Snoqualmie Pass in the central Cascade Range of Washington State.

Site	Average Days	No. Camera Stations	Trap Nights	Total Captures per 100 trap-nights				
				Rock Pile	Brush Pile	Fallen Log	Snag	All Features
Reference	16	21	339	—	38.5	37.5	3.5	26.5
Restoration	14	21	294	75.9	53.6	42.9	14.3	54.8
WCS	16	8	128	115.6	—	28.1	—	71.9

TABLE 5. Fixed effect size estimates, 95% confidence intervals (C.I.), and Z and P values from a Generalized Linear Mixed Model where total number of small mammals captured in 2017 at each trap throughout the study period was modeled as a function of presence/absence of habitat features, trap type (Sherman, Tomahawk, pitfall), site type, and individual site, with site treated as a random effect. Effect sizes and confidence intervals are reported on the log scale. Asterisks (*) indicate significant effects, as assessed by Wald Z tests, using a Tukey correction for multiple testing. Comparisons are HF-NHF = habitat feature, no habitat feature, ST-TT = Sherman versus Tomahawk traps, ST-PT = Sherman versus pit-fall traps, TT-PT = Tomahawk versus pit-fall traps, and R-R&WCS = reference site versus restoration and wildlife crossing structure sites.

Comparison	Estimated Effect Size	95% C.I.	Z	P
HF-NHF	0.17	± 0.16	2.13	0.033*
ST-TT	2.01	± 0.44	8.88	< 0.001*
ST-PT	2.74	± 0.96	5.58	< 0.001*
TT-PT	0.73	± 1.05	1.36	0.342
R-R&WCS	0.05	± 0.17	0.63	0.530

restoration site. One female mouse traveled 136 m from the northern restoration site, across a Forest Service road, to the WCS.

DISCUSSION

The main objective of this study was to compare small-mammal species richness, composition, relative abundance, and movement at a WCS to adjacent restoration sites and nearby forest reference sites. Our data supported the prediction that the WCS would have lower species richness than both the restoration and reference sites, with the restoration sites having intermediate species richness. In addition to being exposed to noise, lights, and pollution caused by the highway, the WCS was < 2 y old at the time of this study and was in the early stages of habitat recovery with underdeveloped vegetation. This lack of habitat complexity likely contributed to the lower species richness and diversity we observed. For example, chipmunks prefer a thicker understory because it provides a source of food and cover from predators whereas Northern Flying Squirrels prefer a closed canopy but open forest floor that provides greater ease of movement (Carey 2000; Zwolak 2009; Rotholz and Mandelik 2013).

Several of the small mammal species recorded in our reference sites, but not in the WCS, such as the Yellow-pine and Townsend's Chipmunks, Douglas Squirrels, and Snowshoe Hares are forest habitat specialists. Habitat specialists can be key indicators for environmental changes because they are especially sensitive to any changes to their habitats, unlike their generalist counterparts that can use a larger variety of resources (Henrik 1994). Specialists may be more vulnerable than generalists to the effects of habitat fragmentation and road-effect zones because they are less tolerant of environmental changes and are less

likely to occupy the degraded habitat often found adjacent to roads (Umetsu and Pardini 2006; Barthelmess and Brooks 2010; Rotholz and Mandelik 2013). Most forest specialist small mammals require shrub or canopy cover and coarse woody debris for habitat, foraging, and safer movement (Carey and Harrington 1995; Gitzen and West 2001; Sollmann et al. 2015). Therefore, to be effective for the broadest spectrum of small mammal species, WCS that are large enough to accommodate habitat features should contain ample cover from predators, such as fallen logs and understory vegetation, to facilitate movement and improve connectivity (Kintsch and Cramer 2011; D'Amico et al. 2015; Schlinkert et al. 2016).

The species composition of small mammals varied among the site types we studied. Habitat generalists were the main inhabitants of the WCS. Similarly, only *Peromyscus* spp., among several small mammal species, were recorded passing through two WCS in Vermont 2–3 y post-construction (Bellis et al. 2013). Habitat degradation, such as forest clear-cutting and agriculture, alters the composition of small mammal communities, favoring open-habitat species such as Deer Mice and Long-tailed Voles (Zwolak 2009; Panzacchi et al. 2010). These species can thrive in early-successional, high-disturbance environments (Manson et al. 1999; Goosem 2000; Bissonette and Rosa 2009) like the recently restored areas and WCS in our study. Our forest reference sites, in contrast, supported a more even, diverse assemblage of species mostly consisting of closed-canopy, or mature forest, specialists.

The presence of high-quality habitat, such as natural substrate, natural light, habitat features, and plentiful vegetation, can encourage WCS use by small mammals (Ford and Fahrig 2008; McGregor et al. 2008; Hennessy et al. 2018). Our results showed an increased likelihood of captures when traps were located in or near any habitat feature (fallen logs, brush piles, rock piles) rather than in open or featureless areas. This apparent lack of preference for specific features may be linked to the high abundance of generalist species found in our surveys because Deer Mice and Long-tailed Voles are able to thrive in a broad variety of environmental conditions and habitat types. Our finding of more captures near habitat features aligns with other studies showing that Deer Mice are more likely to travel along logs and branches than on open ground (Graves 1988; Carey and Harrington 2001). Predators of small mammals, such as coyotes, have begun using the undercrossing (Josh Zylstra, pers. comm.), so movement across open areas may be risky and the protection offered by any habitat feature may be sufficient, at least for generalist species (Tallmon et al. 2003). As these restoration sites mature and the density of vegetation increases, we may begin to see species-specific habitat preferences and increased use by forest specialists (Smith et al. 2015). Captures of two forest specialists at our sites in 2018 (Southern Red-backed Vole in the WCS; Pacific Jumping Mouse,

Zapus trinotatus, at the northern restoration site) support this prediction.

A major drawback to our study design was that we evaluated the use of only one WCS; however, sampling effort within the WCS appeared sufficient (species accumulation curve approached an asymptote; Ugland et al. 2003). Additionally, the high abundance of Deer Mice caught in Sherman live traps may have biased the survey by physically limiting other species from being caught in the same traps. Remote cameras showed a lower relative abundance of Deer Mice, indicating the assemblage may have a more even composition than estimated by live trapping alone. The fewer camera trap-nights, camera-trap malfunction or poor placement, and inability to identify individuals prevented robust statistical analysis of our camera-trap data. The patterns observed from our remote camera-trap data provide an excellent opportunity for future studies. Movement patterns of small mammals near roads and within crossing structures, and health of individuals as an indicator of fitness at these sites of higher disturbance also merit further exploration (Sollman et al. 2015; Grilo et al. 2018).

This study is the first evaluation of wildlife use of crossing structures in the I-90 Snoqualmie Pass East Project. We expect that small-mammal richness and diversity will increase over the next several years as more species from the nearby forest discover and explore the WCS. Wildlife may require several years to adapt to WCS (Clevenger and Waltho 2005; Ford et al. 2009), and the number of animals discovering and using WCS often increases with time (Bond and Jones 2008; Gagnon et al. 2011; Soanes et al. 2013; van der Grift and van der Ree 2015). Development of the planted vegetation over time should also promote higher species richness and diversity in and near the WCS due to increased cover (McDonald and St. Clair 2004), food resources, and habitat complexity (MacArthur and MacArthur 1961; Bell et al. 1991).

Unlike large mammals with larger home ranges, such as Elk (*Cervus canadensis*) in the Cascade Range with 1,300–11,000 ha home range size (McCorquodale 2003), that likely use WCS primarily to move across the landscape, small mammals, which have smaller home range sizes (e.g., 0.1–0.4 ha for shrews, Hawes 1977; 0.4–4.0 ha for deer mice, Stickel 1968), may also be living largely within and adjacent to these newly created habitats. Our recaptures of individuals and captures of reproductive individuals within and adjacent to the WCS suggest that these small mammals are living in, rather than just passing through, the WCS. The availability of WCS is critical for improving connectivity between habitat patches separated by highways (Ford and Clevenger 2018). Therefore, designing WCS that contain high-quality, suitable habitat may be important to ensure these connectivity mitigation structures are effective at improving the permeability of the interstate to a variety

of small mammal species that reside in these forested mountain habitats.

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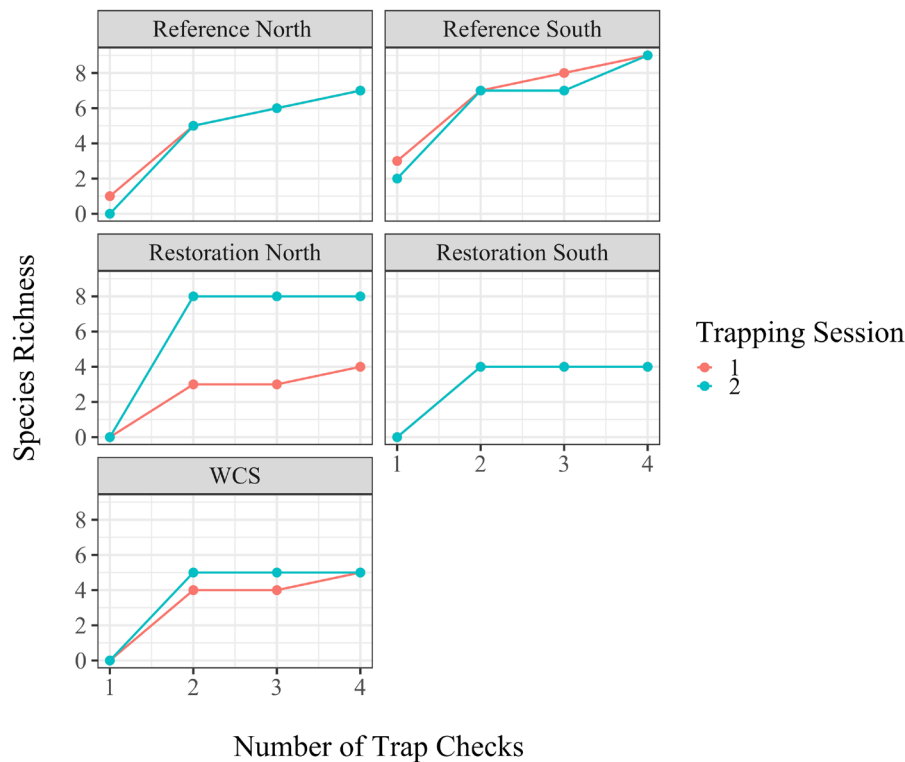
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ALISON SCOVILLE is an Associate Professor of Biology at Central Washington University, Ellensburg. After receiving a B.A. in Biology from Carleton College, Northfield, Minnesota (1997), she went on to complete a Ph.D. in Biology from Utah State University, Logan (2008). Her research lab group studies ecological and evolutionary genomics, with an emphasis on rapid evolution and conservation biology, in two model systems: *Mimulus guttatus* (Monkeyflower) and *Daphnia* (water fleas). She uses a combination of field work, molecular tools, and mathematical modeling. (Photographed by Kris Ernest).

APPENDIX 1. Scientific and common names of small mammal species recorded during the study, and their designation as habitat generalists (G) or forest specialists (S; from Naughton 2012).

Scientific Name	Common Name	Habitat Generalist or Forest Specialist
<i>Sorex cinereus</i>	Cinereus Shrew	S
<i>Sorex monticolus</i>	Montane Shrew	G
<i>Sorex</i> sp.	unidentified Shrew	
<i>Peromyscus keeni</i>	Keens's (Pacific) Deer Mouse	G
<i>Peromyscus maniculatus</i>	Deer Mouse	G
<i>Microtus longicaudus</i>	Long-tailed Vole	G
<i>Myodes gapperi</i>	Red-backed Vole	S
<i>Neotamias amoenus</i>	Yellow-pine Chipmunk	S
<i>Neotamias townsendii</i>	Townsend's Chipmunk	S
<i>Glaucomys sabrinus</i>	Northern Flying Squirrel	S
<i>Tamiasciurus douglasii</i>	Douglas's Squirrel	S
<i>Lepus americanus</i>	Snowshoe Hare	S

**APPENDIX 2.** Species accumulation curves or count of cumulative number of species from the start to the end of trapping, for each site as a reflection of trapping effort. Each site was trapped in two sessions during 2017 at sites near Snoqualmie Pass, Washington: once at the beginning of summer and again at the end of summer.