

Road and highway undercrossings as potential critical linkages for California's elk populations

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RESEARCH NOTE

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California is the only North American state or province occupied by three elk (*Cervus canadensis*) subspecies: Roosevelt (*C.c. roosevelti*), Rocky Mountain (*C.c. nelsoni*), and tule (*C.c. nannodes*), the lattermost an endemic (Meredith et al. 2007; CDFW 2018). While less numerous relative to historic levels, all three subspecies have increased in abundance and distribution in recent decades due to management efforts (including human-mediated translocations of each), with 12,900 total elk estimated in 2018 (CDFW 2018). Within their distribution, California's elk occupy suitable habitat unevenly distributed both spatially and temporally, requiring maintenance of demographic and genetic connectivity to promote population persistence (Meredith et al. 2007; Batter et al. 2021). Maintaining and improving landscape connectivity for tule elk populations is of particular importance. All contemporary tule elk are descended from as few as three individuals and possess low levels of genetic diversity (Sacks et al. 2016; CDFW 2018). Although having rebounded to nearly 6,000 individuals to date, these genetically depauperate populations persist in a metapopulation format and, in the absence of connectivity, remain vulnerable to stochastic events that could lead to extinction of isolated populations (Newmark 1987; Crooks et al. 2017) or, at minimum, further inbreeding depression and lower fitness as well as reduced adaptability to changing environments (Williams et al. 2004; Frankham et al. 2017). Roosevelt and Rocky Mountain elk have greater genetic diversity compared to tule elk and are hybridizing near the north-central California-Oregon border (Williams et al. 2004; Meredith et al. 2007; Batter et al. 2021). However, their population abundance remains far below historic levels and they are also susceptible to effects of habitat fragmentation. Traffic infrastructure, particularly high-speed roads and highways, are primary drivers of habitat fragmentation and pose barriers to range expansion and linkages between populations of wildlife species in general, including elk (Clevenger and Waltho 2005; Ament et al. 2021). In fact, roads have been viewed as a major factor influencing landscape-scale elk distribution, with elk selecting habitat away from areas with high road densities and traffic levels (Rowland et al. 2004; McCorquodale 2013). High-speed roads and highways also cause dangerous elk-vehicle collisions (Tiedeman et al. 2019). Increases in temperature and aridity in California's climate are already challenging tule elk populations, highlighting the need for connectivity to cooler and more mesic habitats either at higher elevations, further north, or nearer the Pacific coast (Denryter and Fischer 2022; Lanman et al. 2022). Improved linkages that enable elk to safely cross roads could connect disjunct elk populations and enhance access to habitats more resilient to climate change. Recently, wildlife overcrossings have been constructed over major highways, such as over U.S. Highway 101 in southern California (Gustafson et al. 2022), to provide connectivity for large mammal species, although improvements to existing large undercrossings beneath traffic infrastructure may more cost-effectively enable safe passage. However, successful use of undercrossings by California's elk populations has not been well documented, and therefore may be underappreciated.

Wildlife crossing structures designed or retrofitted to provide safe passage for wildlife have been shown to reduce wildlife-vehicle collisions by up to 97% (Huijser et al. 2009) with one elk-specific study reporting that protective fencing to limit at-grade elk crossings and direct the animals to newly constructed crossing structures, combined with motorist alert signage activated by animal detection, reduced elk-vehicle collisions also by 97% (Gagnon et al. 2019). Costs of large wildlife-vehicle collisions in California have been estimated at \$1–2 billion from 2016–2020 inclusive, based on > 65,000 carcass observations reported to the California Roadkill Observation System

(CROS, <https://wildlifecrossing.net/california>; Tiedeman et al. 2019). The substantial costs of wildlife-vehicle collisions have been used to justify construction of *de novo* wildlife overcrossings over six-lane freeways in Utah and southern California costing \$22 and \$87 million, respectively (Barnick et al. 2022; Gustafson et al. 2022). Recent average cost estimates for *de novo* wildlife overcrossings of two- and four-lane highways are about \$6 million, vs. large fauna undercrossings nearly an order of magnitude less expensive at \$800,000. However, retrofitting of an existing bridge to serve as a wildlife overcrossing or improvement of an existing undercrossing exploitable by large mammals would be an order of magnitude less expensive than these amounts (Sijtsma et al. 2020).

Although there are occasional reports that large native ungulates may use narrow box culverts to cross beneath highways (Sawyer and Rudd 2005; Kintsch et al. 2021), most reports of elk using undercrossings occur at open-span bridge sites that are, from a cervid's perspective, high and wide, of short distance (length) beneath the road, with absent or minimal human activity, and distant from forest cover (Clevenger and Waltho 2005; Meese et al. 2009). Undercrossing openness ratios (ORs) are calculated as width times height divided by length (all in meters), as recommended for large-bodied mammals (Reed and Ward 1985; Clevenger and Waltho 2005; Meese et al. 2009). Because the OR calculation method referenced above lacks sufficient detail to account for variations in undercrossing infrastructure such as uneven floors with streams, divided roads, or non-rectangular bridge design, etc., we utilized the standard OR calculation along with recently proposed refinements to account for special case variations (Lanman et al. 2022). Although this approach requires ongoing validation, it found high OR ratios for two undercrossing structures that were subsequently successfully crossed by tule elk, each of two bulls, under U.S. Highway 101 in two different locations in Santa Clara County (Lanman et al. 2022; [Table 1](#)). The first were likely tule elk from extant herds in the Diablo Range, which crossed beneath U.S. Highway 101 in south Coyote Valley where Coyote Creek flows beneath the freeway (OR 20.4). The second may have been tule elk either from the Diablo Range or Gabilan Range, which crossed beneath U.S. Highway 101 where Tar Creek and the Union-Pacific Railroad pass beneath (OR 32.2). Although these reports were made by qualified observers, neither reflect repeated use of the undercrossings, nor were they confirmed by physical evidence such as scat, trail camera, or radio collar data.

Table 1. Observations of elk utilization of road/highway undercrossing structures by subspecies with locations, openness ratios, and level of evidence (roughly numbered from north to south in California [[Fig. 1](#)]).

Undercrossing structure #	Elk subspecies	Road/Highway	Stream/River	City, County	Openness Ratio	Documentation
1	Roosevelt	U.S. Highway 101	Prairie Creek	Orick, Humboldt	9.8	Expert observer, tracks, radio collar
2	Roosevelt	U.S. Highway 101	Smith River Overflow Bridge	Fort Dick, Del Norte	30.3	Radio collar
3	Roosevelt x Rocky Mountain ^a	Interstate 5 Northbound	Cottonwood Creek	Hilt, Siskiyou	12.3	Radio collar

Undercrossing structure #	Elk subspecies	Road/Highway	Stream/River	City, County	Openness Ratio	Documentation
4	Roosevelt x Rocky Mountain ^a	Interstate 5 Southbound	Cottonwood Creek	Hilt, Siskiyou	18.4	Radio collar
5	Tule	County Road 429	Tenmile Creek	Laytonville, Mendocino	13.2	Expert observer, radio collar
6	Tule	California State Highway 20	North Fork Cache Creek	Clearlake Oaks, Lake	21.4	Scat, trail camera, radio collar
7	Tule ^b	U.S. Highway 101	Coyote Creek	Morgan Hill, Santa Clara	20.4	Non-expert observer
8	Tule ^b	U.S. Highway 101	Tar Creek	Gilroy, Santa Clara	32.2	Expert observer
9	Tule	County Route G14/Jolon Road	Jolon Creek	Fort Hunter Liggett, Monterey	2.1	Expert observer, trail camera
10	Tule	County Route G14/Jolon Road	Unnamed tributary, Jolon Creek	Fort Hunter Liggett, Monterey	0.3	Expert observer, trail camera

^a Genetic assignment testing of elk in Siskiyou County suggested that populations were composed of both Roosevelt and Rocky Mountain elk and their hybrids (Meredith et al. 2007). Thus, we describe the elk population(s) here as Roosevelt x Rocky Mountain elk.

^b Two bulls only. All other observations were herds inclusive of bulls and cows.

To further explore the extent of road/highway undercrossings by elk, we interviewed CDFW and/or academic center biologists with experience studying California elk to gather evidence for use and characteristics of undercrossings within each subspecies' distribution ([Fig. 1](#)). Numerous incidences of elk using road infrastructure undercrossings are summarized below ([Table 1](#)). Notably, all had natural terrain floors mostly characterized by intermittent creeks, including the Smith River overflow channel which seasonally approximates a dry stream channel. The only exception was traversed by perennial Prairie Creek. Other undercrossing characteristics included: no human activity except the two undercrossings with a paved bicycle path beneath Coyote Creek in Coyote Valley; roads/highways had wire fences generally four feet in height; and seven undercrossings had no nearby forest cover and the other three had forest on both sides: Prairie Creek was situated in red alder (*Alnus rubra*) and Douglas fir (*Pseudotsuga menziesii*); Tenmile Creek in red alder and willow (*Salix* spp.), and North Fork Cache Creek in Fremont cottonwood (*Populus fremontii*) and willow.

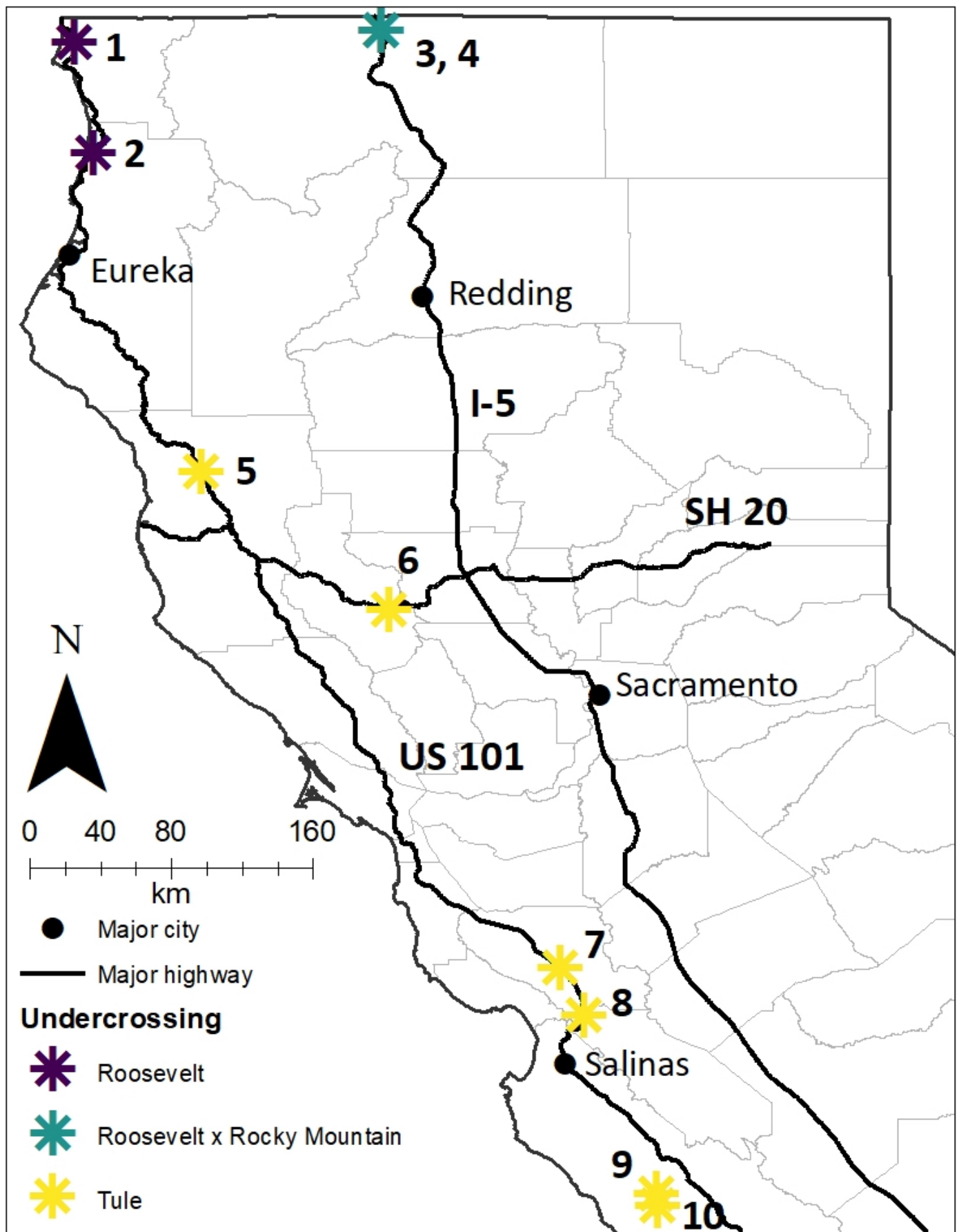


Figure 1. Undercrossing locations (*) color coded according to subspecies of the resident elk

population(s) documented utilizing the structures in northern and central California. Major highways include U.S. Highway 101 (US 101), Interstate 5 (I-5), and State Highway 20 (SH 20). Undercrossing structures include 1) US 101 Smith River Overflow Bridge, 2) US 101 Prairie Creek, 3) I-5 Cottonwood Creek Southbound, 4) I-5 Cottonwood Creek Northbound, 5) County Road 429 Tenmile Creek, 6) SH 20 North Fork Cache Creek, 7) US 101 Coyote Creek, 8) US 101 Tar Creek, 9) County Route G14 Jolon Creek North, and 10) County Route G14 Jolon Creek South. County boundaries are represented in light grey. Note: genetic assignment testing of elk in Siskiyou County (undercrossing structures 3 and 4) suggested that populations were composed of both Roosevelt and Rocky Mountain elk and their hybrids (Meredith et al. 2007). Thus, we describe the elk population(s) here as Roosevelt x Rocky Mountain elk. Based on over two years of repeated expert observations confirmed with trail cameras, a Fort Hunter Liggett tule elk herd in southern Monterey County is repeatedly utilizing a relatively small rectangular culvert where Jolon Creek, a tributary of the San Antonio River, crosses under County Route G14 (Jolon Road) ([Fig. 2](#)). Although the OR for the entire bridge span was 6.2, trail camera footage found that the elk only used the middle section – with OR of 2.1. At an even narrower culvert beneath Jolon Road nearby, trail cameras documented a tule elk herd utilizing a small, unnamed tributary of Jolon Creek – with OR of 0.3 ([Fig. 3](#)). Tule elk also repeatedly cross beneath County Road 429 west of Laytonville, Mendocino County using the Tenmile Creek bed (OR 13.2) based on expert observer and radio collar data. Another report documented tule elk using North Fork Cache Creek (OR 21.4) crossing beneath State Highway 20 east of Clearlake Oaks, Lake County, based on identification of scat, trail cameras, and radio collar data.



Figure 2. The Jolon Creek undercrossing beneath Jolon Road at Fort Hunter Liggett, Monterey County, CA, USA. Although the openness ratio of the entire bridge span was 6.2, trail camera footage found they only used the middle section—with openness ratio of 2.1. Note dry streambed natural terrain floor beneath middle section and lack of game trails under right and left sections (and fencing barrier at right section). (Taken 30 March 2022)



Figure 3. Trail camera (red arrow lower left) documented an elk herd following an unnamed tributary of Jolon Creek and utilizing this culvert at a second location beneath Jolon Road at Fort Hunter Liggett, Monterey County, CA, USA. With an openness ratio of 0.3, this is the smallest documented undercrossing regularly used by any elk species or subspecies. (Taken 12 July 2022)

Animals in a resident Roosevelt x Rocky Mountain elk herd (Meredith et al. 2007) near Hilt, California just west of Interstate 5 in Siskiyou County were radio collared and likely crossed repeatedly to the east of this freeway where Cottonwood Creek passes beneath. Although radio collaring alone does not definitely establish that elk crossed over or under Interstate 5, it is unlikely that elk would cross over this busy freeway (14,900 to 15,600 annual average daily traffic volume) and no elk-vehicle collisions from 2016-2020 inclusive were reported by the Road Ecology Center at University of California at Davis near this location (Shilling et al. 2021). This situation is similar to a previous report that U.S. Highway 101 is not crossed over by elk in Santa Clara County due to an absence of elk-vehicle collisions in contrast to records of such collisions on highways with less traffic in the same county (Lanman et al. 2022). Since Interstate 5 is a divided highway greater than 30 m apart, ORs were calculated separately for the northbound and southbound undercrossings. Elk herds were observed to the west of the southbound lanes at this location. Only one other potential crossing structure exists in the area, a railroad bridge overcrossing, but given its narrow width (8 m) and long length (114 m), elk would typically avoid an overcrossing with these “bridge effect” characteristics (Reed and Ward 1985; Clevenger and Waltho 2005).

Radio collar data, multiple expert observer records, and elk tracks further document that a Roosevelt elk herd, including bulls, cows, and calves, cross repeatedly beneath U. S. Highway 101 along Prairie Creek, 1.1 km north of Orick, Humboldt County, California (OR 9.8). Similarly, a Roosevelt elk herd is using a large undercrossing at the U. S. Highway 101 Smith River Overflow Bridge, (OR 30.3) nine miles north of Crescent City, Del Norte County, California. Successful passage was confirmed with radio collar data and crossing over this bridge would not be possible for elk given its 4.3 m elevation. As water passes beneath this bridge only when the Smith River overflows, it simulates a seasonally dry creek.

Utilizing highway undercrossings as linkages between elk populations represents a least-cost opportunity to improve wildlife linkages to increase genetic diversity and enable range expansion. This report adds to relatively scant elk species-specific literature regarding utilization of undercrossings. Except for citations referenced herein, most publications regarding effectiveness of wildlife undercrossings group deer (*Odocoileus* sp.) and elk together as “large ungulates” (Denneboom et al. 2021). California elk used undercrossings with OR mean (SD) 15.0 (\pm 10.1) and median (range) 16.7 (0.3 to 32.2). A recent systematic review and meta-analysis of the literature for wildlife crossing structures for large mammals found that, for ungulates in general, viaducts (defined as undercrossings with large bridge spans and natural terrain floors) are 2.9 times more effective than overcrossings, and 3.6 times more effective than other undercrossings (Denneboom et al. 2021). However, that meta-analysis lacked elk species-specific data. In a five-year study with elk-specific data on use of five undercrossings and two overcrossings in Colorado, Rocky Mountain elk were four times more likely to use an overpass than a non-viaduct underpass, but both were utilized (Kintsch et al. 2021). Although we could not locate references on the lowest threshold for undercrossing openness ratios specific to North American elk, a review of a large German study (Olbrich 1984) reported that Eurasian red deer (*Cervus elaphus*) utilized underpasses with ORs as low as 1.5 (Putman 1997), which is higher than the apparent minimum OR of 0.6 for considerably smaller American mule deer (*Odocoileus hemionus*) (Reed and Ward 1985). Thus, the current finding of Fort Hunter Liggett tule elk herd repeatedly using an undercrossing with an OR of 0.3 is the smallest OR reportedly utilized by any elk species or subspecies globally, the smallest subspecies-specific report for tule elk herds, and similar to the reported minimum OR for mule deer.

Although published elk-specific use of undercrossings is limited, and heretofore restricted to Rocky Mountain elk, building passage structures with directional fencing improved highway crossing rates, and achieved an 85% reduction in elk-vehicle collisions in Arizona (Dodd et al. 2006). In another study, traffic levels did not influence elk passage rates during below grade undercrossings (Gagnon et al. 2007). Even modest undercrossing success is likely to achieve the one migrant per generation threshold for maintenance of genetic diversity in Roosevelt and Rocky Mountain elk, and the one to ten migrants per generation threshold for populations with inbreeding depression, i.e., tule elk (Mills and Allendorf 1996). Although elk-vehicle collision records help to identify locations in need of over- and undercrossings, elk may be deterred from crossing busy highways with high noise and traffic levels such as busy federal highways (McCorquodale 2013, Lanman et al. 2022). Therefore, absence of collision data may lead to omission of high potential undercrossing sites where substantial vehicular traffic fragments areas of high-quality habitat.

Openness ratios are a key factor in identification of potential undercrossing linkages, but other factors including human activity, nearby vegetation cover, noise, and human development may also deter elk from using undercrossings (Clevenger and Waltho 2000). None of the undercrossings had shared human trails or paved surfaces except in Coyote Valley. Seven of ten undercrossing structures lacked nearby forest cover, although three were bracketed by forest (one in Roosevelt elk habitat and two in tule elk

habitat). Although a definitive conclusion is limited by this report's sample size, the presence of intermittent streams in highway undercrossings may be a key, yet previously underappreciated factor, favoring California elk selection of undercrossing sites.

Elk may be thought of as an "umbrella species" (Simberloff 1998) as undercrossings improved for elk passage would also benefit nearly all other native California mammals (Plumb et al. 2003; Sawyer, and Rudd 2005). In line with California's State Wildlife Action Plan's specific goal to maintain and improve wildlife corridors and genetic diversity (CDFW 2015), we recommend a comprehensive state-wide assessment of existing undercrossing sites that could improve connectivity and safe passage for elk beneath California's high-speed roads and highways. Once identified and prioritized, high potential undercrossing sites should be improved with directional and protective fencing, as failure to erect adequate fencing in association with passage structures limits effectiveness in reducing wildlife-vehicle collisions and promoting wildlife passage (Gagnon et al. 2019). Replacing paved undercrossings with natural substrate and reduction of nearby vegetation cover may further enhance elk crossing success rates. Lands adjacent to promising undercrossings should be protected via conservation easements or acquisitions, to minimize proximity of human activity. Before-after monitoring and long-term monitoring of the effectiveness of improved wildlife underpasses for elk and other species are key to adaptive management. Lastly, standardized and validated assessment of openness ratios and other key factors associated with successful elk passage should be iteratively studied to build on our findings and improve linkages between California's disjunct elk populations.

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