Review of considerations for restoration of tule elk to the San Francisco Peninsula and northern Monterey Bay counties of California

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REVIEW PAPER

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Abstract

Successful translocations of tule elk (*Cervus canadensis nannodes*) have been conducted since the early 1900s, with their state population rising from a nadir of as few as three surviving individuals to about 500 when reintroductions began, and to over 5,700 by 2017. However, natural range expansion of extant populations is currently limited by heavily trafficked major highways and urban areas with dense human populations. We determined that the San Francisco Peninsula and northern Monterey Bay counties (the study area) offer 193,973 ha (479,308 acres) of protected open space, several orders of magnitude greater than coastal tule elk home range size. Habitat suitability is supported by abundant historical observer, museum, and archeological records of elk located in this region. The nearest elk population to the study area is in eastern Santa Clara County and has grown from 65 animals that were translocated to Mt. Hamilton in the Diablo Range from 1978–1981 to at least 90 in five–six separate herds counted by aerial and photographic surveys in 2019. United States (U.S.) Highway 101 and metropolitan San Jose remain barriers to western range extension. Translocation and/or construction of freeway over- and under-crossings may enable westward range expansion to a less arid region, contributing to increased resilience of tule elk to climate change, and bringing aesthetic, financial, and ecological benefits of this once native ungulate grazer to the area.

Key words: *Cervus canadensis nannodes*, historical ecology, Roosevelt elk, translocation, tule elk wildlife corridor, wildlife passage

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Introduction

Tule elk (*Cervus canadensis nannodes*), endemic to California, and one of three elk subspecies native to the State, were once numerous in the San Francisco Peninsula and northern Monterey Bay counties (McCullough 1965, 1969). Elk were extirpated from much of San Francisco Bay Area by 1850 (Everman 1915; McCullough 1969), with herds persisting in the North Bay’s Marin and Sonoma Counties until the 1870s (Harper et al. 1967). According to historical accounts, elk herds in the region were once large, numbering into the several hundred in the South Bay (Dane and Palóu 1935), North Bay (Harper et al. 1967), and East Bay (Bolton 1930a). Enumeration of historic elk herd size in the West Bay region is lacking. The nearest extant tule elk (*C. c. nannodes*) herds to the West Bay region reside in eastern Santa Clara County, the result of translocations of a total of 65 individuals to the Mt. Hamilton area 7 km east of U. S. Highway 101 in the Diablo Range from 1978–1981 (Phillips 1985). Most of these re-introduced elk rapidly dispersed, expanding their range to 5–6 herds in eastern Santa Clara County, and have now established herds in neighboring southern Alameda County, northern San Benito County, and western Merced and Stanislaus Counties. However, expansion of these eastern Santa Clara County elk herds to the west is hindered by U.S. Highway 101 and metropolitan San Jose, California. Either translocation, or creation of adequate wildlife under- and overcrossings of this freeway in Coyote Valley, the narrowest gap between the Diablo Range and Santa Cruz Mountains, would enable elk recolonization of extensive open space habitats in San Mateo, Santa Cruz, western Santa Clara, and northern Monterey counties, and may contribute to their persistence relative to climate change (Denryter and Fischer 2022).

Re-establishment of elk populations can provide significant potential aesthetic and ecotourism value, as well as multiple ecological benefits. Elk are charismatic megafauna whose appeal for wildlife viewing can generate significant revenues. At Oregon's Jewell Meadows Wildlife Area, where winter feeding stations are maintained at an annual cost of $200,000 to draw elk away from farmed lands, winter ecotourism receipts totaled $6.5 million annually (Donovan and Champ 2009). This revenue figure underscores the potential aesthetic value of elk and compares favorably to the non-consumptive economic value of another charismatic species, the bobcat (*Lynx rufus*), where wildlife viewing generated $305,000 to see a single bobcat in one winter season at Yellowstone National Park (Elbroch et al. 2017). Elk also provide a plenitude of ecological benefits. As California's native large grazers, elk can, like cattle, reduce grassland and scrub fuel loads, diminishing intensity of future fires. In a North American southern plains study of ungulate grazing after prescribed or natural fires, known as pyric herbivory, future fires had lower spread rates and flame heights were lowered three-fold (Starns et al. 2019). In another study at Tomales Point at Point Reyes National Seashore, tule elk helped to maintain open grasslands by decreasing shrub cover, while significantly reducing the abundance and biomass of a highly invasive exotic grass, *Holcus lanatus*, (Johnson and Cushman 2007). Tule elk are also an important browser which can facilitate seed dispersal and restoration of native blue oak (*Quercus douglasii*) and valley oak (*Quercus lobata*) savanna and woodland habitat (Phillips et al. 2012; Phillips 2013). Elk or elk calves are a preferred prey item for several native California predators, including puma (mountain lion) (*Puma concolor*), gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and black bears (*Ursus americana*) (Griffin et al. 2011). Lastly, elk carcasses are important to the diet of obligate and partial scavengers and may be of particular value to California condors (*Gymnogyps californianis*), that still rely today on supplemental feeding stations partly because of diminished ungulate megafauna populations (Walters et al. 2010).

The current study elucidates the history of and progress since the Mount Hamilton circa 1980 elk reintroductions, updating current population counts in the Santa Clara/Mt. Hamilton Elk Management Unit (EMU) via aerial and photographic survey. Area of protected open space habitat available to western range expansion from the eastern Santa Clara County elk herds is calculated and contrasted with reported tule elk home range sizes. We hypothesized that reported tule elk home range sizes requirements would negatively correlate with average annual rainfall. The archeological and historical observer evidence of elk in each of the study area counties are documented to confirm habitat suitability. Highway 101 bridge overcrossings and undercrossings in Coyote Valley are evaluated for their potential to enable safe passage of eastern Santa Clara County elk to the west, and new, more detailed standards for crossings measurements are recommended. Finally, the merits of recolonization with tule elk versus translocation of elk subspecies with broader genetic diversity are discussed.

Methods

Study Area

The study area (**Fig. 1**) was defined as the contiguous area spanning the San Francisco Peninsula counties of San Francisco, San Mateo, and Santa Clara, plus the northern Monterey Bay Area counties consisting of Santa Cruz, and that part of Monterey County west of Highway 101 and north of the Salinas River where it is crossed by U.S. Highway 101 in Salinas, California. These are the unceded lands of the Muwekma Ohlone (to the north of San Martin/Morgan Hill) and Amah Mutsun (to the south) present-day tribes.

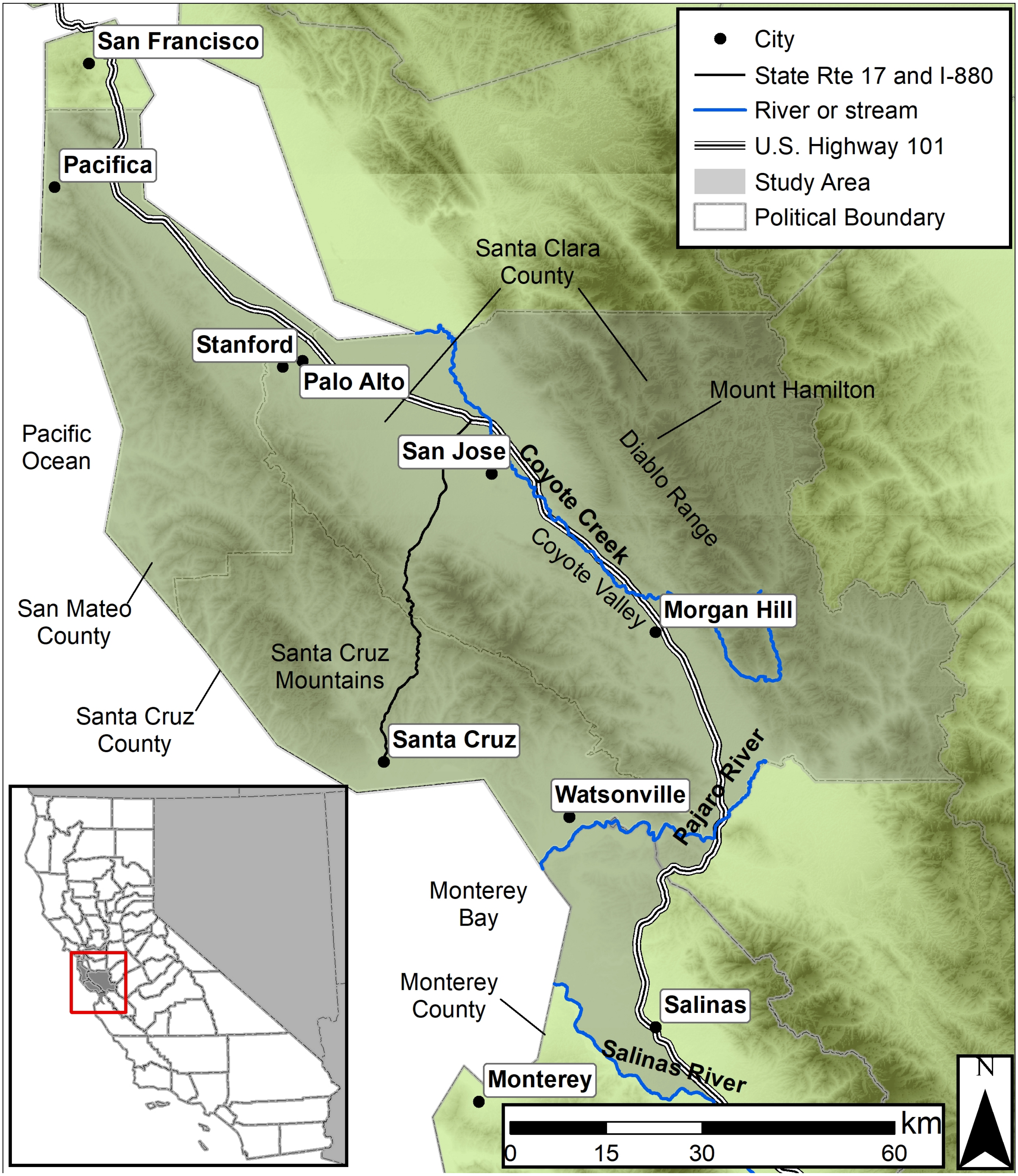

Figure 1. The study area (gray shading) illustrates the counties with protected open space lands available to westward expansion of elk, if enabled by crossings over and under of U.S. Highway 101. It is bordered by San Francisco County to the north, and the Salinas River in Monterey County to the south. It also includes the area of aerial survey of the existing elk herds in Santa Clara County east of the freeway in the Diablo Range. Green shading displays topographic relief, with lighter shading indicating lower elevations and darker shading indicating higher elevations.

The study area represents two Level III ecoregions with different biological diversities: California's Coast Range and parts of the Central California Foothills and Coastal Mountains ecoregion (Omernik and Griffith 2014; U.S. EPA 2013), and more specifically, the following Level IV ecoregions: Santa Cruz Mountains, San Mateo Coastal Hills, Leeward Hills, Monterey Plains and Terraces, Upper Santa Clara Valley and, east of Highway 101, the East Bay Hills/Western Diablo Range and Diablo Range (Griffith et al. 2016). The California Coast Range Ecoregion is characterized as a coastal fog zone with redwoods (*Sequoia sempervirens*) predominating in forests; the Central California Foothills and Coastal Mountains ecoregion is characterized by a Mediterranean climate with hot, dry summers and cool, moist winters, with predominant vegetation comprising chaparral, oak woodlands, and grasslands (U.S. EPA 2013).

Tabulation of protected open space in San Francisco, San Mateo, and Santa Cruz Counties for 2018 was obtained from the Conservation Lands Network 2.0 Report (Bay Area Open Space Council 2019). Protected fee and easement lands in Santa Clara County west of Highway 101 were calculated using geographical information system (GIS) mapping and excluded the Baylands as the latter are considered inaccessible to elk because of the urban San Jose metropolitan area. For the determination of protected open space in Monterey County, only the portion west of U.S. Highway 101 and north of the Salinas River from Salinas, CA to the coast was considered, as the Monterey, CA urban area is a likely barrier to elk range expansion to the south. In this restricted portion of northern Monterey County, we summed protected lands in the Elkhorn Slough State Marine Conservation Area, consisting of Elkhorn Slough State Marine Reserve, Coro Mojo State Marine Preserve, and Moss Landing State Wildlife Area (CA Parks 2021). Named reservoirs, which may serve as water sources and are generally surrounded by protected open space, were tallied for each county in the study area.

Historical and Archaeological Records Search for Elk in the Study Area

Archeological records of elk specimens for the study area were assembled via queries of the FAUNMAP (**http://www.ucmp.berkeley.edu/neomap/search.html**) for elk remains found in late Holocene archaeological sites, and Web of Science and Google Scholar searches using the key words: elk or Cervus, and county names. Museum records of elk in the study area were searched across all American museum collections participating in the Mammal Networked Information System (MaNIS) (**http://manisnet.org/**), the Arctos Multi-Institution and Multi-Collection Museum Database (**http://arctos.database.museum/**), and Integrated Digitized Biocollections (iDigBio) (**https://www.idigbio.org**) via Boolean searches. In addition, we contacted curators of mammal collections at museums local to the study area: the University of California Berkeley Museum of Vertebrate Zoology, and California Academy of Sciences (CAS). We also identified references from citations in other publications that reviewed the historic ranges of other California mammals (Zeiner et al. 1990; Schmidt 1991; Lanman et al. 2013). Further, we searched geographic place names using the United States Geological Survey (USGS) Geographic Names Information System (GNIS) (**https://geonames.usgs.gov/pls/gnispublic**) and toponomastic references (Gudde and Bright 2010; Durham 2001a, b).

Aerial and Photographic Surveys of the Alameda and Santa Clara-Mount Hamilton EMUs

On 6 November 2019, the California Department of Fish and Wildlife (CDFW) conducted aerial surveys for tule elk in the Santa Clara-Mount Hamilton and Alameda EMUs (**Fig. 2**). CDFW flew surveys in a Bell 407 Eagle HP helicopter with a pilot and three observers. Surveys were flown at transects spaced ~800 m apart, at a speed of 50–100 kph and altitude of ~30–60 m above ground level (and above maximum tree height in the survey area). The survey area was determined by stratifying survey areas within the Santa Clara-Mount Hamilton and Alameda Elk Management Units into strata with a high likelihood of detecting elk (i.e., based on elk telemetry data and historic surveys) and a low likelihood of detecting elk (e.g., areas with no recent records of elk; areas in non-preferred habitats of elk, etc.). During aerial surveys, observers recorded the number of elk observed in groups as well as the age and sex composition of groups (i.e., number of adult males, adult females, and calves) as previously described (Bush et al. 2021). Groups of elk were photographed, and numbers recorded during surveys were compared to photographs to confirm or correct data recorded during surveys.

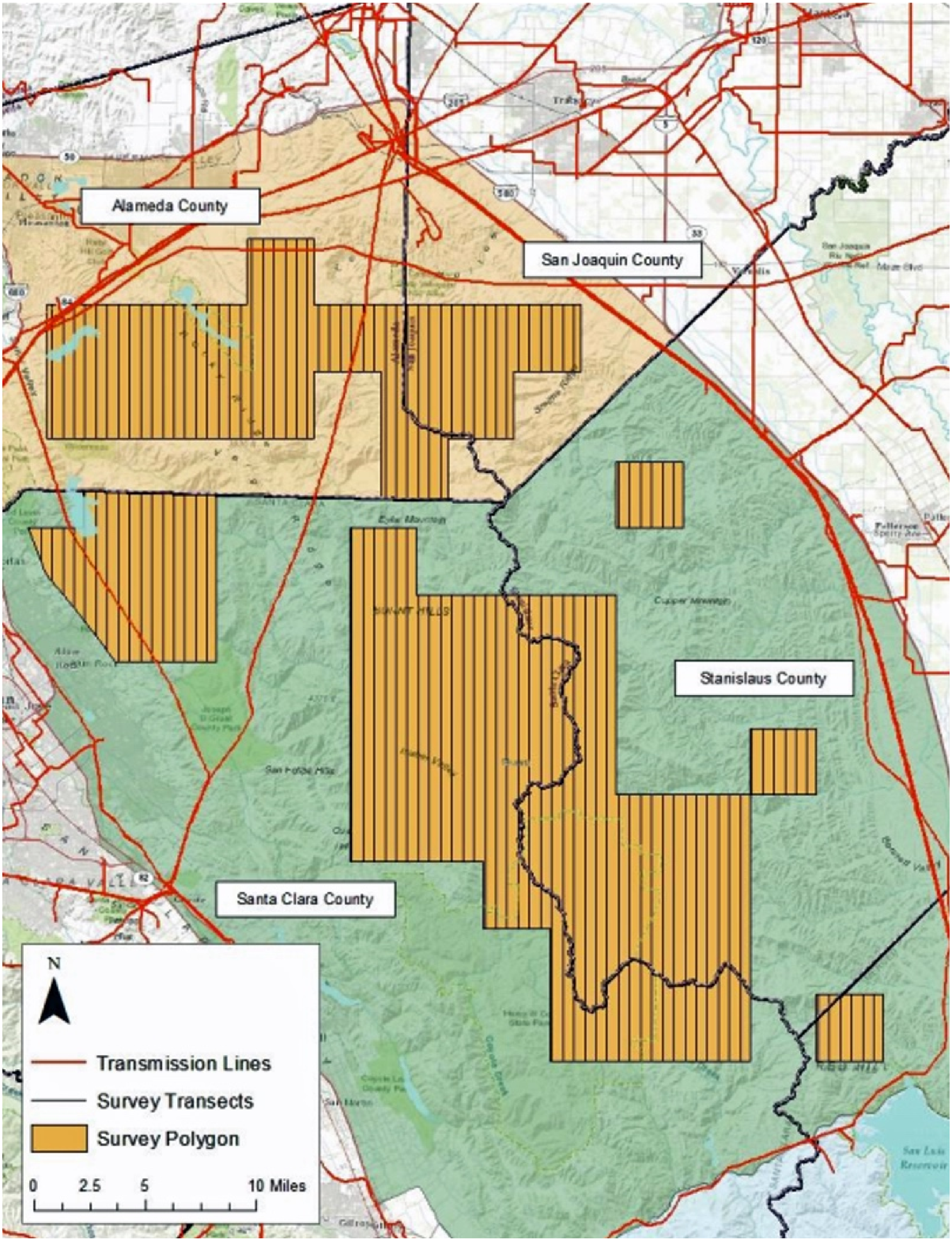
Alameda County
San Joaquin County
Stanislaus County
Santa Clara County
N
Transmission Lines
Survey Transects
Survey Polygon
0
2.5
5
10 Miles

Figure 2. Map of aerial survey areas in the Alameda and Santa Clara Elk Management Units in the Diablo Range in November 2019.

Evaluation of Potential Elk Under- and Overcrossings in Coyote Valley

Viaducts are defined as a special type of undercrossing characterized by a large bridge span over natural terrain (Smith et al. 2015; Denneboom et al. 2021). Other undercrossings beneath U.S. Highway 101 were defined as those passing over paved one- or two-lane roads. Culvert undercrossings were excluded from this study as unlikely to be utilized by elk. Openness ratios (OR) for viaducts and other undercrossings were calculated from a cervid's perspective, where width times height reflect the area of the aperture facing the animal, and length reflects the distance the animal would have to traverse to cross under the bridge. Thus, OR accounts for cervid avoidance of undercrossings and viaducts with narrow openings and a long tunnel distance to traverse, 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 of a lack of specific standardized methods for measurements of potential undercrossings, we implemented four more detailed and conservative guidelines:

1. If the bridge surface area was trapezoidal then the shorter of the two opposite widths was used.
2. If parallel northbound and southbound bridges were separated by less than a 25 m gap, then their combined undercrossing lengths were summed as if it was a single bridge.
3. Height for undercrossings were measured from floor to ceiling. However, when one side of the bridge was taller than the other, the shortest height was used, measured from the lowest level path along the floor.
4. If the floor of the undercrossing included a stream, as in both viaducts, then bridge height was measured from top of bank defined as the first definable break in 45 degree or greater bank slope, even when the stream was dry and passable as in winter.

For undercrossings, length and width of bridge spans were measured by tape measure and cross-checked against California Department of Transportation (CalTrans) internal management logs.

Two existing road bridges were evaluated for potential conversion from vehicle to wildlife overcrossings. First, the Santa Clara County Road Book was consulted for average daily traffic volume on the two roads crossing over U.S. Highway 101 (Freitas 2021). Next, because it is expected that cervids would avoid bridges that are too high, long, or narrow, a proposed "bridge effect" calculation (Reed and Ward 1985) of width times square root of height, divided by length (all in meters) was utilized and evaluated. Height for overcrossings was measured from road surface down to floor, utilizing a laser measure accurate to 1.6 mm at 50 m.

Results

Open Space in the San Francisco Peninsula and Northern Monterey Bay Counties Study Area

The total area of SF Peninsula and northern Monterey Bay counties is 687,195 ha (1,698,099 acres), of which 28.2% was undeveloped protected open space [193,973 ha (479,308 acres)] (**Table 1**). San Francisco County is excluded from the totals in **Table 1** as its open space is not contiguous/accessible by natural range expansion from San Mateo County.

Table 1. Total area, protected open space, and number of named reservoirs for counties, or portions of counties, in the study area in California.

County	Total Area	Protected Open Space	# Named Reservoirs
San Francisco County	12,147 ha	2,209 ha*	N/A
San Mateo County	191,918 ha	49,040 ha*	5
Santa Cruz County	337,734 ha	104,248 ha*	9
Monterey County (north of Salinas River/west of Highway 101)	29,257 ha	1,352 ha**	0
Santa Clara (west of Highway 101)	128,016 ha	39,333 ha	8
Total (excluding San Francisco County)	**687,195 ha**	**193,973 ha**	**22**

*(Bay Area Open Space Council 2019)
**(California Department of Parks and Recreation 2021)
Protected fee and easement lands in Santa Clara County west of U.S. Highway 101 and excluding the Baylands totaled 39,333 ha. In this area, two Special Districts, the Midpeninsula Region Open Space Preserves alone constitute 25,495 ha, all west of U.S. Highway 101, and the Santa Clara Valley Open Space Authority has preserved 10,117 ha, 3,947 ha being west of U.S. Highway 101.

Impact of Average Annual Rainfall on Reported Home Range Sizes for Tule Elk

Six reports of tule elk home range size were identified and plotted against average annual rainfall at each locale. Home range size (for both elk genders) trended towards a strong inverse (negative) linear correlation to average annual precipitation (Pearson's $r = -0.78$, $P = 0.067$), although it was not significant due to the limited number of studies ($n = 6$) (**Table 2**).

Table 2. Tule elk home range sizes reported for six different elk management units in California demonstrate strong inverse linear correlation to average annual precipitation.

Elk Management Unit (EMU)	Average Annual Rainfall	Average Home Range Size	Citation
Owens Valley[a]	10.2 cm	7,700 ha	Morrison et al. 2020
Carrizo Plain	22.9 cm	8,250 ha	Mohr 2020
Cache Creek	53.3 cm	5,100 ha	O'Connor 1988
San Luis Reservoir	26.3 cm	2,499 ha	Dziegiel 2021
Mt. Hamilton	59.9 cm	401 ha	Duncan 1988
Point Reyes	94.0 cm	217 ha	Cobb 2010

[a] The Owens Valley is outside historical tule elk range, but continues to be a productive tule elk population (Morrison et al. 2020)

Archeological, Museum and Historical Observer Records Searches

No elk place names were found in study area counties via USGS GNIS searches, except for an "Elk Glen Lake" in San Francisco; although the latter was not apparently related to the presence of elk. However, other toponomastic references identified place names clearly related to the historic presence of elk, as detailed below.

San Francisco County.—Historically, elk were present in San Francisco County, based on archeological evidence of elk remains in at least five different Native American shell mounds in San Francisco: at Hunter's Point, Fort Mason, Stevenson Street, Market Street, and Yerba Buena (Broughton 1994: McCrossin 1982). Perhaps the first historical observer record was from the De Anza Expedition on 23 March 1776. Bolton (1930b) wrote about the expedition's camp at Mountain Lake, near the southern end of today's Presidio: "Round about were grazing deer, and scattered here and there were the antlers of large elk." Also, when Richard Henry Dana, Jr. visited San Francisco Bay in 1835, he wrote about vast elk herds near the Golden Gate: on December 27 "…we came to anchor near the mouth of the bay, under a high and beautifully sloping hill, upon which herds of hundreds and hundreds of red deer , and the stag, with his high branching antlers, were bounding about…" (Dana 1840). However, it is not clear if Dana's observation pertained to the Marin County side or the San Francisco side of the Golden Gate Strait.

San Mateo County.—Elk was a "favored food" of the Ohlone People based on ethnohistoric and archeological evidence (Moratto and Singh 1981). In 1962, two historic period elk specimens were excavated from a coastal peat bog in Pacifica's historic Laguna Alta and housed in the University of California Berkeley Museum of Vertebrate Zoology (MVZ) (Pearl 1962; McCullough 1965). The California Academy of Sciences (CAS) also has an elk skull fragment collected in 1951 one mile inland from the mouth of coastal Purisima Creek 3.7 km south of Miramontes Point (California Academy of Sciences, specimen CAS MAM 9845). Additional coastal elk remains were found in at least five more late Holocene archeological sites in San Mateo County: SMA-113 (Quiroste Valley site) (Gifford-Gonzalez et al. 2013), SMA-115 (Montara State Beach site), SMA-118 (Bean Hollow State Beach site), SMA-244 (Butano Ridge site), SMA-97 (Año Nuevo Creek site) and SMA-218 (Año Nuevo State Reserve site) (Hylkema 1991). On the eastern or bay side of the San Francisco Peninsula, multiple elk remains were also unearthed at multiple archaeological sites (CA-SMA-263/CA-SCL-287) along San Francisquito Creek (Bocek 1988, 1992; Leventhal et al. 2010).

Santa Clara County.—In June 1776, Lieutenant Commander Don José Joaquín Moraga traveled through what we now know as the Santa Clara Valley on his way from the Presidio of Monterey to establish a mission in San Francisco. Moraga wrote: "In the great plain called San Bernardino… we descried in the distance a herd of large animals that looked like cattle, but we could not imagine where they belonged or from whence they had come…with horns similar in shape to those of the deer, but so large that they measured sixteen palms (3.4 m) from tip to tip… These animals [elk] are called *ciervos* in order to differentiate them from the ordinary Spanish variety of deer, here called *venados*, which also exist in abundance and of large size in the vicinity" (Dane and Palóu 1935). An Ohlone burial site (CA-SCL-128) on the Guadalupe River west of U.S. Highway 101 with radiocarbon dating to 1435 ± 30 years CE included an elk metapodial 150 mm long and was named *Róokoš Tiwoo Koro 'Ayttakiš* (Tule Elk Leg Woman) by the Muwekma Ohlone (Leventhal et al. 2015). General John Bidwell, of the 1841 Bartleson-Bidwell Party wrote: "In some of the fertile valleys, such as Napa and Santa Clara, there were elk literally by the thousand" (Hunt 1942).

Santa Cruz County.—Watsonville, California was originally the site of the Mutsun village *Tiuvta*, meaning "Place of the Elk" (Milliken 1988) related to *tiiwu*, meaning "elk" and "hunt elk" in the Mutsun language (Warner et al. 2016). Early Spanish explorers of California mistook elk for bison (*Bison bison*). Their sightings would have been elk since no other ungulate in the study area was as large or larger than cattle, and bison were only native historically in California's northeastern corner (Merriam 1926). Later, elk were also described by nineteenth century American hunters (Evermann 1915). They were also described in Santa Cruz County by Jilli (Cotoni) tribal group Awaswas Ohlone people (Milliken 1995), who utilized elk and lived on the Jarro Coast (El Jarro Point is north of Davenport, California) (Harrison 1892; Rolins 1925). Additionally, there is a historic place name "*Cañada del Ciervo*" (*ciervo* again is Spanish for *elk*) close to the boundary between Rancho de los Corralitos and Rancho San Andrés, near the present-day Larkin Valley Road. This "Elk Valley" was named by José Antonio Robles who rode down, roped, and killed elk there in 1831 (Clark 1986). Lastly, elk remains were found in at least five late Holocene archeological sites in Santa Cruz County, all coastal: SCR-9 (Bonny Doon site) and SCR-20 (Brown site) on the western slope of Ben Lomond Mountain, SCR-93 (Sunflower site) a coastal terrace on the north shore of the San Lorenzo River uphill from the Santa Cruz Beach in Santa Cruz, SCR-12 (At the Hill Above the River Site, named *Satos Rini Rumaytak* by the Muwekma Ohlone Tribe) (Starek 2013), and SCR-132 (Scott Creek site) 4 miles further inland (Hylkema 1991).

Monterey County.—In 1603, Spanish naval explorer Sebastián Vizcaíno discovered the port of Monterey, and noted elk at the mouth of the Carmel River in his January diary entry: "[there] were many cattle as large as cows although apparently they were harts, and yet their pelts were different,…and each horn was more than three yards long" (Vizcaíno 1603). Accompanying Vizcaíno to Monterey, was Father Antonio Ascensión, who described the Native Americans as wearing "elk-leather jackets" (Ascensión 1603). Elk were present not only on the Monterey County coast but also in the forests of the Santa Lucia Range. Lieutenant Pedro Fages of the 1769 Portolá Expedition established the Presidio at Monterey, again mistook elk for bison: "The slope of the Sierra which lies toward Monterey…there are many trees of great variety in good soil; there are wild buffaloes living in the depths of this forest" (Fages and Priestly 1919). On the same expedition, Miguel Costansó, described elk south of the mouth of the Pajaro River both on their way north on 6 October 1769 and south 25 November 1769 (Costanso and Teggart 1911). On the return south Costansó realized these were elk and not bison, writing: "With the object of examining the coast with minuteness and care, we rested at the *Laguna del Macho* ["one league" (5.6 km) south of the Pajaro River, which identifies the "*laguna*" as Elkhorn Slough]…the tracks which we had seen on the way to the port of San Francisco were not those of bison, but of very large deer, of an extraordinary appearance; [the scouts] had seen a herd of twenty-two near the shore. They said that these animals had high branching and heavy horns; that their color, from the breast to the chin, was white, the rest of the body a light chestnut, excepting the hind quarters, which likewise were white" (Costanso and Teggart 1911). Although Elkhorn Slough may have been named for its crooked, antler shape, most toponomastic references assert that it was named for the abundant elk horns found near the slough (Clark 1991; Gudde and Bright 2010). This is supported by findings at CA-MNT-229, an extensive shell midden situated on the south bank of Elkhorn Slough near the shore, where elk remains were dated from 200 BCE to 60 CE (Dietz et al. 1988; Jones and Jones 1992).

Aerial Survey of Diablo Range elk herds resulting from the 1978–1981 translocations to Santa Clara-Mt. Hamilton Elk Management Unit

As of November 2019, the California Department of Fish and Wildlife counted 90 tule elk during aerial surveys in the Santa Clara-Mt. Hamilton and Alameda Elk Management Units (**Table 3**).

Table 3. Minimum counts, by sex and age class, from aerial surveys of tule elk in the Santa Clara-Mt. Hamilton and Alameda Elk Management Units. Specific location information from surveys is considered sensitive and is withheld per California Department of Fish and Wildlife policy.

Group Number	Adult females	Calves	Adult Males	Total
1	4	0	2	6
2	2	1	0	3
3	1	2	3	6
4	7	7	5	19
5	0	0	1	1
6	0	0	3	3
7	0	0	2	2
8	0	0	1	1
9	0	0	1	1
10	0	0	4	4
11	0	0	2	2
12	7	3	0	10
13	17	6	2	25

Group Number	Adult females	Calves	Adult Males	Total
14	0	0	5	5
15	0	0	2	2
Total	**38**	**19**	**33**	**90**

These tule elk originated from four translocations of 65 total elk conducted annually from 1978–1981 to the San Felipe Ranch (owned by the Hewlett and Packard Families) on the western slopes of Mt. Hamilton along San Felipe Creek, tributary to Anderson Reservoir and the Coyote Creek watershed, and also to Grant County Park just to the south and also in the Diablo Range. From the Mt. Hamilton area of the Diablo Range in eastern Santa Clara County the nascent elk population has expanded to 5–6 herds across the 307,561 ha Santa Clara/Mt. Hamilton EMU, and established herds in neighboring counties north, managed as the Alameda EMU, and south managed as the San Luis Reservoir EMU (CDFW 2018; **Fig. 3**). The elk in these three EMUs originated with the Hewlett-Packard San Felipe Ranch 1978–1981 translocations and include herds at San Antonio Reservoir in Sunol, Alameda County to the north, to the San Antonio Valley Ecological Reserve near the Santa Clara County/Stanislaus County border to the east, to the Cottonwood Creek canyon and western San Luis Reservoir at the junction of Santa Clara, Merced, and San Benito Counties to the south, but no further west than U.S. Highway 101 in Coyote Valley at the foothills of the Diablo Range.

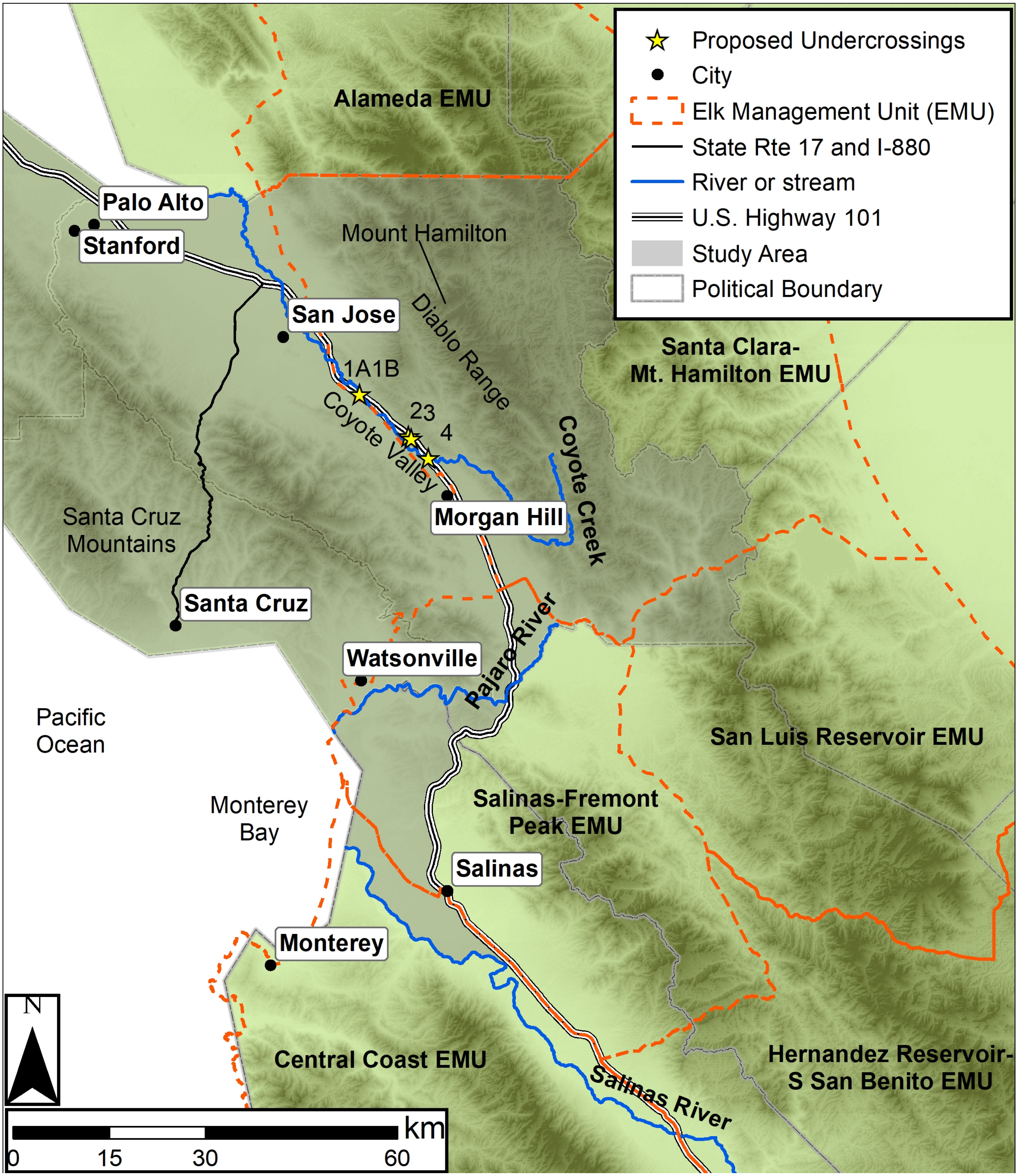

Figure 3. Map showing U.S. Highway 101 bisecting Coyote Valley, the narrowest gap between the foothills of Mt. Hamilton in the Diablo Range and the Santa Cruz Mountains. Undercrossings which could be modified to enable elk passage are 1A and 1B = Northwest Coyote Creek, 2 = Golf Cart Utility, 3 = Coyote Creek Golf Drive, 4 = Southeast Coyote Creek. Green shading displays topographic relief, with lighter shading indicating lower elevations and darker shading indicating higher elevations.

Assessment of Potential U.S. Highway 101 Wildlife Under- and Overcrossings for Elk in Coyote Valley

The Coyote Gap or Narrows at the north end of Coyote Valley is the narrowest gap between the foothills of the Santa Cruz Mountains and the Diablo Range and is only 0.6 km wide (Phillips et al. 2012; **Fig. 4**). Coyote Valley extends 10.5 km from the Coyote Gap in south San Jose in the north, to northern Morgan Hill in the south, and the 3,000 HA of the valley floor are bisected from northwest to southeast by U.S. Highway 101. As none of the 144 elk-vehicle collisions reported in California from 2016–2020 were on Highway 101 in the study area, it appears the traffic, noise, and/or fencing dissuades elk from crossing over this freeway (**Fig. 5**) (Shilling et al. 2021). Five undercrossings (UC), all beneath U.S. Highway 101 bridges, were identified as potentially suitable for tule elk passage (**Table 4**).

Figure 4. Aerial photo illustrates extensive, largely protected, open space lands extending west from Coyote Valley to the Pacific Ocean at top. U.S. Highway 101 runs horizontally at the base of the Diablo Range foothills at bottom. This freeway passes through the Coyote Gap or Narrows at Metcalf Road, the narrowest point separating the Diablo Range from the Santa Cruz Mountains' easternmost foothill, Tulare Hill (hill with crescent-shaped white scar, middle, far right). Courtesy Derek Neumann, Santa Clara Valley Open Space Authority.

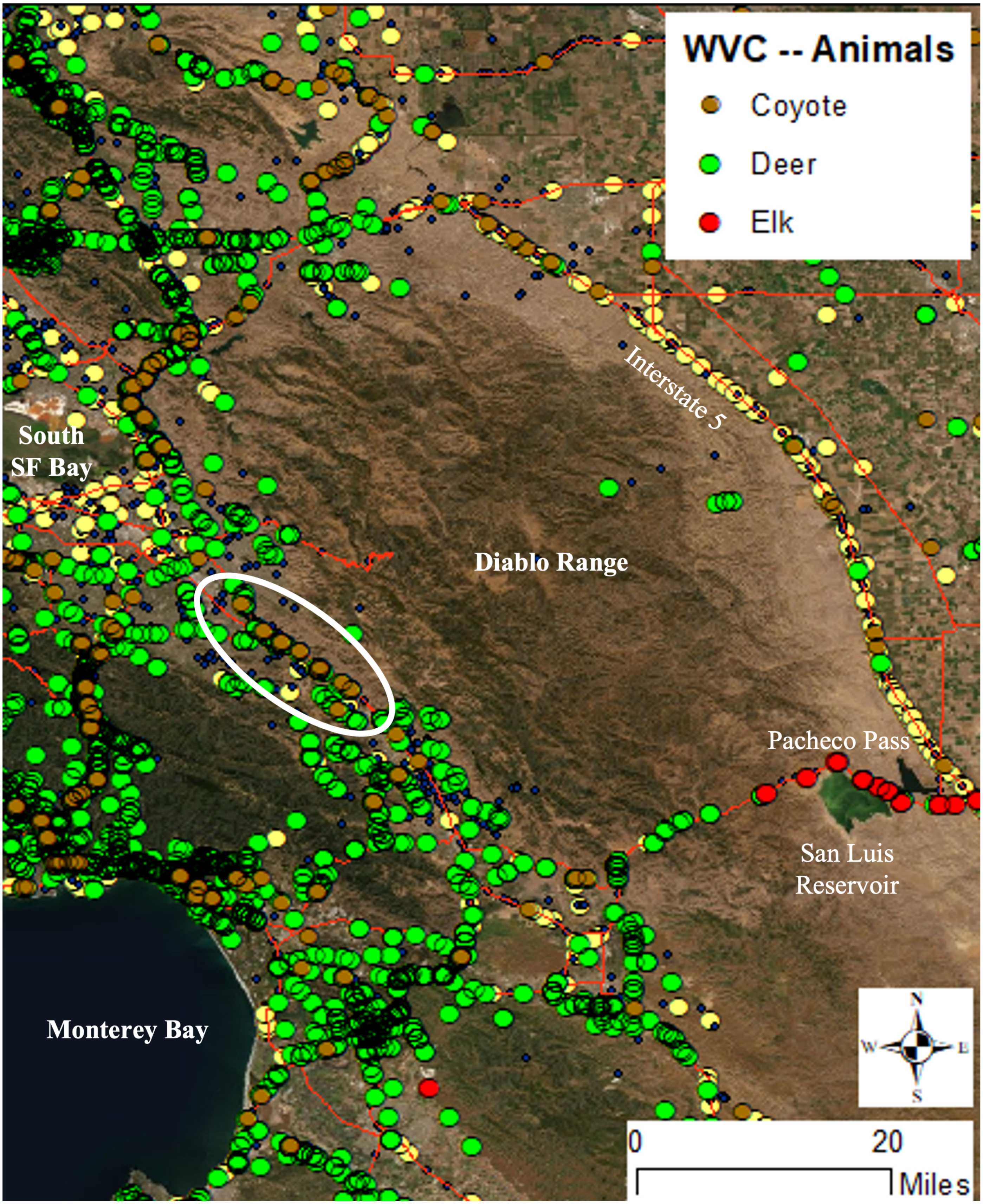

Figure 5. Map of elk, deer, and coyote wildlife-vehicle collisions (WVC) 2016-2020 inclusive. The Coyote Valley stretch of Highway 101 is identified, ironically, by the eight or nine coyote-vehicle collisions (brown circles) encircled by the white ellipse. In contrast, red circles mark numerous elk-vehicle collisions on Highway 152 at Pacheco Pass and San Luis Reservoir. The lone elk-vehicle collision seen in middle lower

map was on Old Stage Road east of Highway 101 and Salinas, California. Data and map courtesy of the California Roadkill Observation System and Road Ecology Center, University of California at Davis (Shilling et al. 2021).

Table 4. Calculations of Openness Ratios for potential Highway 101 undercrossings in Coyote Valley.

Coyote Valley U.S. Highway 101 Undercrossings (UC)	**Height**	**Width**	**Length to traverse undercrossings**	**Openness Ratio (OR) (> 1.5 is passable)**
Northwest Coyote Creek UC 1A	6.2 m	121.9 m	7.3 m	**102.6**
Northwest Coyote Creek UC 1B	4.7 m	85.3 m	36.9 m	**10.9**
Golf Cart Utility UC 2	4.6 m	22.9 m	49.9 m	**2.1**
Coyote Creek Golf Drive UC 3	5.8 m	51.8 m	43.2 m	**6.9**
Southeast Coyote Creek UC 4	7.1 m	125.0 m	43.4 m	**20.4**

Two of the undercrossings are viaducts, related to Coyote Creek passing under the freeway. The first of these two viaducts crosses beneath the junctures of north– and southbound Highway 85 and the freeway and is bordered by protected open space to the east (Basking Ridge) and the west (Coyote Creek Parkway County Park and Tulare Hill). It consists of two parts: one bridge span (Northwest Creek 1A UC) carries two lanes of northbound Highway 85 and is separated by 30 m (98.4 ft) from a second bridge span (Northwest Creek 1B UC) consisting of six combined lanes of Highway 101 and southbound Highway 85 which have a trapezoidal surface area. At the southeast end of Coyote Valley, the second Highway 101 viaduct (Southeast Coyote Creek UC) is located north of Morgan Hill's Burnett Avenue, the latter bordered by protected open space on both the east and west sides (Coyote Creek Parkway County Park) as well as the agricultural lands of Coyote Valley. A third undercrossing (Coyote Creek Golf Drive UC), is located where Coyote Creek Golf Drive/Scheller Avenue runs beneath Highway 101, in two parallel sections about 8 m apart (treated here as one single crossing structure). In contrast to these three undercrossings with very broad bridge spans, there is a potential fourth bridge undercrossing (Golf Cart Utility UC) south of Bailey Avenue and north of Coyote Creek Golf Drive, which is used as a golf cart underpass.

There are two U.S. Highway 101 overpasses in Coyote Valley. Bailey Avenue is heavily trafficked and therefore not suitable for conversion into a wildlife overcrossing. The other is the Metcalf Road bridge which has potential for conversion to a wildlife passage as it is lightly trafficked and not required for motor vehicle access to points east (which can be reached by Malech Road, a freeway frontage road from the Bailey Avenue exit) or west (which can be reached from Monterey Highway). The Metcalf Road overcrossing width is 7.6 m, height 14 m, and length 71.9 m, with calculated bridge effect equal to 0.56.

Discussion

Aerial surveys found that the expansion of the regional elk population since the 1978–1981 translocations to Mt. Hamilton has been modestly successful, with growth of 38.5% from 65 to at least 90 individuals in 2019. Because there were public reports of elk in measurement polygons that were not flown during surveys, the 2019 survey result should be regarded as a minimum count (i.e., there are likely additional elk in the EMUs that were not observed during aerial surveys; surveys to estimate elk abundance by correcting for imperfect detection (e.g., using mark-resight, sightability, distance sampling) have never been completed for these populations). Although the elk translocated to Mt. Hamilton have expanded widely to three neighboring counties to the north, east, and south of Santa Clara County, these neighboring counties were included in the aerial survey polygons as shown in **Fig. 2**. Although there is considerable unoccupied land in the Diablo Range, in recent drought years the elk have tended to cluster in regions with plentiful water supply such as San Antonio Reservoir in Alameda County and San Luis Reservoir in San Benito County and anecdotal reports suggest their distribution may be constrained by areas of poor-quality habitat. Much higher tule elk population growth rates have been reported for the Owens Valley and Point Reyes herds (McCullough 1969; Howell et al. 2002). Drought may have limited elk recruitment in the Diablo Range although the Owens Valley has an even more arid climate. Poaching may have limited population growth of elk in the Santa Clara/Mt. Hamilton EMU (Phillips 2013) and has resulted in extirpation of other translocated tule elk herds (Hanson and Willison 1983). Frequent elk poaching in California spurred development of a DNA sequencing tool to assist with forensic analysis of potentially poached tule elk remains (Jones et al. 2002). However, unconfirmed poaching reports in the Diablo Range are difficult to quantify. A comparison of elk population growth rates to the Pacheco State Park elk herd which has similar annual precipitation but highly active protection by rangers could help evaluate the impact of poaching in the Mt. Hamilton/Santa Clara EMU.

U.S. Highway 101 remains an impassable barrier to westward expansion of elk to the counties of the San Francisco Peninsula and northern Monterey Bay. These counties total 699,342 ha, of which 196,182 ha is protected open space largely connected by agricultural or unprotected forest lands. The quantity of open space lands available provide habitat areas exceeding tule elk home range requirements by several orders of magnitude. Home range size depends on habitat quality, gender, and is strongly related to average annual precipitation (McCullough 1969; Peek 2003). Our compilation of reported home range sizes from six different EMUs strongly negatively correlated with average annual rainfall (**Table 2**), suggesting that tule elk herds could be expected to require much smaller areas in the study area, as it is more coastal and less arid than the Santa Clara/Mt. Hamilton and other non-coastal EMUs. The study area west of Coyote Valley also offers a wide diversity of habitat types, which are preferred by elk (Huber et al. 2011; Didier and Porter 1999; Van Deelen et al. 1997). Based on the published literature and the findings above, we predict that the more coastal open space lands west of U.S. Highway 101 will provide superior forage, a better predictor of elk recruitment success than carnivore predation risk or weather conditions (Lukacs et al. 2018).

Museum specimens, historical observer records, ethnographic evidence, and/or late Holocene archeological specimens of elk were found in every county in the study area, further confirming that the region’s habitat was suitable for elk historically. Numerous large reservoirs across the San Mateo, Santa Cruz, western Santa Clara, and northern Monterey Counties provide adequate water supplies in the study area and may serve as important refugia for elk. Santa Clara County west of U.S. Highway 101 is relatively unique in its concentration of eight named reservoirs, each surrounded by protected County Parks lands. Westward expansion of elk towards the coast may be essential to resilience of tule elk populations as California’s climate becomes progressively warmer and more arid (Williams et al. 2020). Additionally, these areas appear to be climatically suitable for elk given middle-of-the-road emissions scenarios and thus could serve as important climate refugia for tule elk, particularly as the Santa Clara-Mt. Hamilton and Alameda EMUs are expected to be moderately vulnerable (i.e., likely to experience a decrease in abundance or range extent) to climate change by mid-century (Denryter and Fischer 2022).

As the narrowest point between the coastal Santa Cruz Mountains and the more interior Diablo Range, the Coyote Valley in Santa Clara County is the most cost-effective location for land preservation and wildlife crossing structures between these different ecoregions (Spencer et al. 2010; Phillips et al. 2012). However, it is bisected from north to south by U.S. Highway 101, the major barrier to westward expansion of eastern Santa Clara County elk populations. Coyote Valley is 6.5 km long from northwest to southeast, exceeding the minimum ideal width of 2 km for multispecies wildlife linkages (Penrod et al. 2006). Coyote Valley has been previously identified as critical to natural range expansion and enrichment of genetic diversity for numerous other native species [puma (Thorne et al. 2006; Penrod et al. 2013), bobcat (Penrod et al. 2013; Serieys and Wilmers 2019), American badger (*Taxidea taxus*) (Diamond 2010; Penrod et al. 2013)], and perhaps in future, to restored populations of pronghorn (*Antilocapra americana*) (Thorne et al. 2002).

Transportation infrastructure, such as U.S. Highway 101, is increasingly recognized as one of the major drivers of biodiversity loss worldwide (Benitez-Lopez et al. 2010; Polak et al. 2019). Enabling safe passage across these barriers can allow reversal of genetic introgression in “island” populations (Newmark 1987, Sawaya et al. 2014) and prevent wildlife-vehicle collisions (Van der Grift et al. 2013). Although large ungulates such as elk and pronghorn may occasionally use concrete-box culverts to cross beneath highways (Sawyer and Rudd 2005; Kintsch et al. 2021), the most common and effective undercrossing for large mammals appears to be open-span bridges that are, from an elk’s point of view, high and wide, of short “tunnel” length, with absent or minimal human activity, and distant from forest cover (Clevenger and Waltho 2005; Meese et al. 2009). A recent systematic review and meta-analysis of the literature for wildlife crossing structures for large mammals found that, for ungulates in general, viaducts (such as those at the northwest and southeast ends of Coyote Valley) are 2.9 times as more effective than overcrossings, and 3.6 times more effective than other undercrossings (Denneboom et al. 2021). However, in a five-year study more specific to elk use of five undercrossings and two overcrossings in Colorado, Rocky Mountain elk (*Cervus canadensis nelsoni*) were four times more likely to use an overpass than a non-viaduct underpass, although both were utilized (Kintsch et al. 2021). Although we could not locate references on limiting undercrossing openness ratios specific to tule elk, a review of a large German study (Olbrich 1984) indicated that red deer did not use underpasses with ORs less than 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). Regardless, ORs for all four existing freeway bridge span undercrossings exceed these undercrossing guidelines for cervids, including two viaducts with ORs of 20.4 and 102.6, one to two orders of magnitude greater than the minimum required OR of 1.5 for elk undercrossings. The adequacy of these openness ratios to facilitate elk use is supported by a recent sighting of two bull elk west of Highway 101, located only 0.5 km west of the southern Coyote Creek Highway 101 Undercrossing (UC 4) shortly after the initial submission of this manuscript (**Fig. 6**).

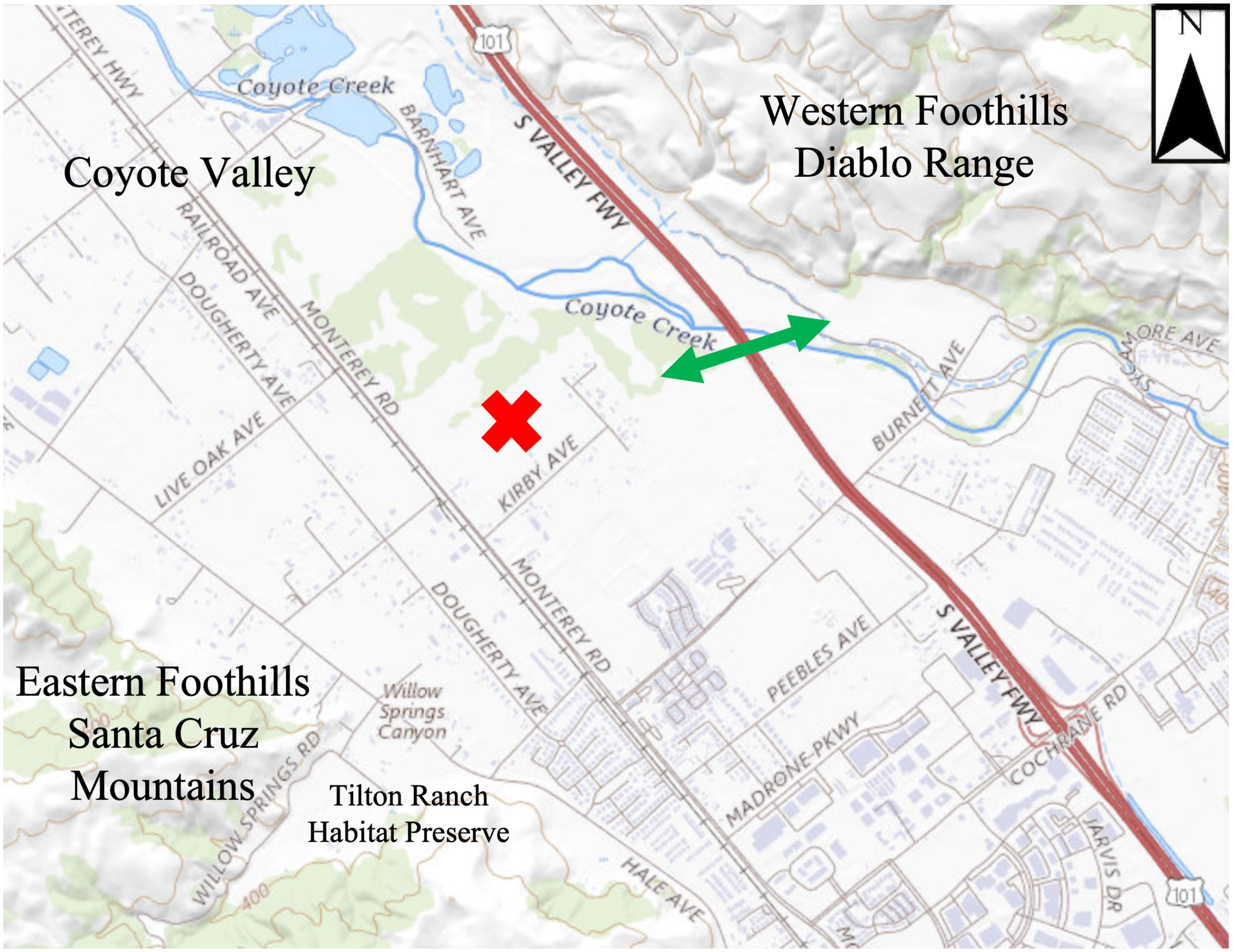

Figure 6. First elk sighting west of U.S. Highway 101 in the study area (marked by red "X") indicates that elk will use large viaduct undercrossings. Location is 0.5 km west of the large viaduct where Coyote Creek passes beneath the freeway in south Coyote Valley (marked by double-headed green arrow). Westward expansion of the existing eastern Santa Clara County tule elk herds could be facilitated by fencing and habitat modifications to four open-span bridge undercrossings and one potential overcrossing enabling safe passage of elk across U.S. Highway 101 in Coyote Valley. Minimum overcrossing widths of 50 m are recommended for elk (Clevenger and Huijser 2011), considerably wider than the 14.6 m width of Metcalf Road, although our bridge effect calculation of 0.56 exceeds reports for deer who crossed overpasses in Colorado with "bridge effect" indices of 0.34 and in Utah of 0.26 (Reed and Ward 1985). In addition, elk have successfully used the Parleys Summit wildlife overcrossing in Utah with a narrower width than the Metcalf Road bridge in our study area (13.1 m versus 14.6 m). Additionally, the Utah overcrossing is longer (97.2 m), passing over six lanes of Interstate 80 versus the 72.0 m length of the Metcalf Road bridge passing over four lanes of U.S. Highway 101 (Machemer 2020). The bridge effect calculation of the Parleys Summit wildlife overcrossing in Utah is 0.70, higher than Metcalf Road at 0.56. This is because of Parleys' greater height and appears to highlight a problem with the bridge effect calculation as even inclusion of the square root of height in the numerator is inconsistent with wildlife reluctance to use a bridge that is too high (Kintsch 2021). Problems with the bridge effect ratio may at least partially explain why this measure of ungulate overcrossing success has not been well validated for elk.

Before elk wildlife passages across U.S. Highway 101 are established or elk are translocated, plans should be established to minimize vehicle-animal collisions on other high-speed roads in the study area. Fencing is key to mitigation of animal-vehicle collisions and promotes ungulate use of wildlife passages by directing movements towards wildlife crossing structures (van der Grift et al. 2013; Denneboom et al. 2021). In addition, fencing at both freeway viaducts was noted to have gaps that could lead to elk-vehicle collisions and/or obstructed these large undercrossings, the latter hindering utilization by wildlife. Although Monterey Road, which also bisects Coyote Valley west of and parallel to U.S. Highway 101, is not likely a barrier to elk passage, it would become vulnerable to elk-vehicle collisions once elk can cross the freeway. Plans are already underway to implement wildlife crossing structures for multiple species at Monterey Road, including at the Tulare Hill-Metcalf Road intersection just west of the Metcalf Road bridge (Santa Clara Valley Open Space Authority 2019). Other human-elk conflict issues such as damage to fences and competition with livestock for forage should be reported to the California Department of Fish and Wildlife's Wildlife Incident Reporting (WIR) system and managed by established principles of adaptive management (Denryter and Heeren 2021). Stakeholder groups that work with the California Department of Fish and Wildlife also may be essential to ensure elk conservation and management are compatible with local conditions and needs.

Translocation of tule elk would be a less expensive option than building a *de novo* overcrossing over Highway 101 and also of conversion of the Metcalf Road bridge, however translocated elk without wildlife crossings back out of the Santa Cruz Mountains region would lead to further introgression in a genetically depauperate population. Tule elk suffered from a genetic bottleneck in the mid-1800s and have less genetic diversity than other elk subspecies (Meredith et al. 2007). Today's stock are all descended from a remnant population in the southern San Joaquin Valley which numbered as few as three individuals (Evermann 1915; McCullough 1969; Meredith et al. 2007). These elk were the founders of the entire tule elk translocation program since its initiation in California in the early 1900s (McCullough et al. 1996). Tule elk prefer open chapparal, interior grasslands, oak savanna, and coastal prairie habitat types (California Department of Fish and Wildlife 2018) and may not be well suited for the more densely forested Santa Cruz Mountains. However, Roosevelt elk (*C. c. roosevelti*) prefer the coastal forest habitat dominant in the study area, while also utilizing montane and bottomland grasslands, oak woodlands, coastal dunes, and wetlands (California Department of Fish and Wildlife 2018), all also available in the study area. The historical range boundary between tule elk and Roosevelt elk has been considered near the Sonoma-Mendocino Counties border based on morphological analysis of archaeological specimens (McCullough 1969). However, there is no biogeographical barrier at this putative boundary that would drive allopatric subspeciation, especially in a vagile species such as elk with good dispersal ability (Mayr 1963). In addition, some archeological specimens collected in the San Francisco Bay Area (Pacifica, San Mateo County, and Sunol, Alameda County), have been reported to have morphological features more typical of Roosevelt elk than tule elk (McCullough 1965; Leventhal et al. 2010; Leventhal et al. 2017). Further, there are reports of intergradation between tule elk and Roosevelt elk subspecies now that their ranges overlap in the Sherwood Valley, south of Laytonville, Mendocino County (Williams 2013). For all these reasons, it would be advantageous to ascertain whether the elk that originally inhabited the study area had broader genetic diversity than today's tule elk population in eastern Santa Clara County. A recent study validated the use of a panel of 96 nuclear DNA single nucleotide polymorphisms to differentiate the three elk subspecies in California (Rocky Mountain elk (*C. c. nelsoni*), Roosevelt elk, and tule elk) (Sacks et al. 2021). Before elk are translocated to the western San Francisco Bay region, it is recommended that ancient DNA sequencing of archeological specimens be utilized to determine whether the region's elk were genetically intermediate between Roosevelt and tule elk. Also, once elk either cross Highway 101 to the west or are translocated to the study area, genetic diversity should be assessed at baseline then at future intervals using validated tools (Sacks et al. 2016, Batter et al. 2021).

Limitations of the current study include the absence of well-established elk species-specific thresholds for openness ratios and bridge effect. Large ungulate species are often treated as a group regarding these structural measures, although elk may have different passage requirements than mule deer, bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), or pronghorn. Tools for evaluation of wildlife crossings need to be specific and standardized, then validated on a species-specific basis. Until now, methods for dimensional measurement of crossing structures have not been published with the detail required for bridges which are trapezoidal and not rectangular in area, divided versus undivided bridges, or for heights measured from undercrossing floors with uneven terrain or seasonal streams. The more detailed recommendations utilized here are conservative but require validation in future studies that monitor species-specific passage of wildlife crossings; thus, we recommend monitoring efforts involving establishment of trail cameras at proposed wildlife crossing sites before and after crossing projects are implemented. Lastly, structural dimensions should be regarded only as a minimum requirement for utilization of wildlife crossing structures (Meese et al. 2009). All four undercrossings in our study area have some human use that could lead to elk avoidance (Clevenger and Waltho 2005). During the daytime, people utilize Coyote Creek Trail which passes under both viaducts, and they use the golf cart undercrossing passage. Also, wildlife would have to share the Coyote Creek Golf Drive undercrossing with vehicular traffic, although it is minimal at night. In summary, minimal human presence, appropriate fencing, natural appearance of materials, ease of crossing terrain (e.g., undercrossing terrain that includes a wildlife path), low noise levels, and distance to forest cover are all contributing factors to successful elk passage beyond crossing dimensions (Clevenger and Waltho 2005). Telemetry of radiocollared elk could identify where the animals frequently confront the Highway 101 barrier and be useful to prioritize locations for improvement of undercrossings or construction of a *de novo* overcrossing (Bastille-Rousseau et al. 2018).

Since the early 1900s, ongoing work has protected open space lands in San Mateo, Santa Cruz, Santa Clara, and Monterey Counties (Yaryan et al. 2000), creating the opportunity to restore tule elk to an extensive region they inhabited historically. Connectivity to the study area offers superior habitat diversity and less aridity than their current location in the Diablo Range. The north end of Coyote Valley from Tulare Hill to Metcalf Canyon has been previously identified as a least-cost corridor between the Santa Cruz Mountains and the Diablo Range because it is so remarkably narrow (Penrod et al. 2013). The four existing undercrossings beneath U.S. Highway 101 barrier in Coyote Valley are dimensionally more than adequate for elk passage but will require fencing modifications to promote rather than hinder their use. However, daytime usage of these undercrossings by people may act as deterrents. For this reason and because recent elk-specific literature suggests a preference for overcrossings to undercrossings (Kintsch et al. 2021), we recommend that the lightly trafficked Metcalf Road bridge, located exactly at the Coyote Gap or Narrows, be converted to a wildlife overcrossing. Simple conversion at its current width would be radically less expensive than *de novo* construction of wildlife overpasses such as Parleys Summit Wildlife Crossing in Park City, Utah at $22 million (Machemer 2020) or Liberty Canyon Wildlife Crossing in Agoura Hills, California at $87 million (Solly 2019). Although translocation of elk to protected open space west of the freeway would be even less expensive than conversion of Metcalf Road bridge into a wildlife overcrossing, reintroduction alone without connectivity to the Diablo Range would ultimately lead to further genetic introgression in an elk subspecies already depauperate in genetic variation (Sacks et al. 2016). Furthermore, genetic introgression is already a problem for other wildlife species such as puma (Dellinger et al. 2020) in the biogeographically isolated Santa Cruz Mountains and coastal ecoregions. A century of protection of open space lands in the San Francisco Peninsula and northern Monterey Bay counties, combined with recent protection of agrarian and wild lands in Coyote Valley (Environmental Science Associates 2021), has set the stage for completion of safe passage for elk, as well as other species, across U.S. Highway 101 to and from the Diablo Range.

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