The historical range of beaver in the Sierra Nevada: a review of the evidence

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The North American beaver (Castor canadensis) has not been considered native to the mid- or high-elevations of the western Sierra Nevada or along its eastern slope, although this mountain range is adjacent to the mammal's historical range in the Pit, Sacramento and San Joaquin rivers and their tributaries. Current California and Nevada beaver management policies appear to rest on assertions that date from the first half of the twentieth century. This review challenges those long-held assumptions. Novel physical evidence of ancient beaver dams in the north central Sierra (James and Lanman 2012) is here supported by a contemporary and expanded re-evaluation of historical records of occurrence by additional reliable observers, as well as new sources of indirect evidence including newspaper accounts, geographical place names, Native American ethnographic information, and assessments of habitat suitability. Understanding that beaver are native to the Sierra Nevada is important to contemporary management of rapidly expanding beaver populations. These populations were established by translocation, and have been shown to have beneficial effects on fish abundance and diversity in the Sierra Nevada, to stabilize stream incision in montane meadows, and to reduce discharge of nitrogen, phosphorus and sediment loads into fragile water bodies such as Lake Tahoe.

Key words: beaver, California, *Castor canadensis*, Cascade Range, Central Valley, historical distribution, Nevada, range, Sierra Nevada

The currently recognized historic range of the North American beaver (Castor canadensis) surrounds the Sierra Nevada to the west, north, and northeast, but the California Department of Fish and Game (CDFG) (Williams 1986, Zeiner et al. 1990) considers that mammal to be native only to the Central Valley, the Pit, McCloud and Klamath River drainages of far northern California, and the lower Colorado River in the extreme southeastern corner of the state. As far as could be ascertained, this determination is based on monographs by early twentieth century zoologists Joseph Grinnell (Grinnell et al. 1937:636) and Donald Tappe (1942), who concluded that beaver were not historically extant at elevations above 305 meters (1,000 feet) on the western slope, nor on the eastern slope, of the Sierra Nevada. Both authors recognized that abundant suitable habitat existed for beaver in the Sierra Nevada, but Tappe (1942) hypothesized that the rocky canyons of the Sierra foothills served as a barrier to migration from the Central Valley to the lower gradient streams of the middle to higher elevations of that mountain range. Neither Grinnell et al. (1937) nor Tappe (1942) clarified how beaver came to be distributed above the high gradient stream barriers that commonly occur in every other significant North American mountain range from the northern treeline in Arctic Canada to northern Mexico (Morgan 1868:31-32, Naiman et al. 1988).

As beaver approached extirpation in California, they were afforded full protection in 1911 (Tappe 1942). In 1921 Grinnell et al. (1937:703) estimated the statewide population of California Golden beaver (*C. canadensis subauratus*) at 1,000 individuals that were confined to the lower Central Valley, primarily in the Sacramento-San Joaquin River Delta. By 1925, limited trapping again was allowed, but this rapidly depleted the population to the point where full protection was again mandated in 1933. By the time of Tappe's (1942) monograph, he estimated only 1,300 beavers remained in California.

Reports by zoologists in the first two decades of the twentieth century appear to conflict with the later reports of Grinnell et al. (1937) and Tappe (1942). Stephens (1906:97-98) described "the Pacific beaver" as ranging from "Alaska to central California east to and including the Sierra Nevada and Cascade Mountains" and added, "In most parts of California the presence of beavers is only made known by the stumps of the trees and saplings that they have cut." Bryant (1916) noted that, "The beaver of our mountain districts has been entirely exterminated and there are but a few hundred survivors to be found along the Sacramento, Colorado and San Joaquin Rivers."

Both Grinnell et al. (1937) and Tappe (1942) based their assertions on interviews of then contemporary trappers or rangers working for CDFG or U.S. Forest Service, and a limited review of the then available historical trapper accounts. Information gaps were likely since mountain men were not punctilious diarists, and often their exploits were not recorded in writing until several decades after their trapping expeditions (Novak 1987). Trapping records also may have grossly underestimated harvest of beavers; in one study 44% of California's licensed trappers failed to file reports (Williams 1986). Such underreporting may have been deliberate in order to conceal profitable hunting grounds. More importantly, the trappers and rangers that were contemporaries of Grinnell et al. and Tappe recorded observations at a time when beavers had been nearly extirpated from California, and approximately one hundred years after fur trapping had commenced in the state. For example, James Ohio Pattie caught beavers on the lower Colorado River in 1827, Jedediah Smith trapped the San Joaquin, Sacramento, Trinity and Klamath watersheds in 1828, and Peter Skene Ogden led the first Hudson's Bay Company fur brigade across the northeast corner of California during 1826-1827 (Hensley 1946, Warner 1966). Ogden's orders

included the creation of a "fur desert" south and east of the Columbia River that, theoretically, would so deplete the region of fur-bearing mammals that westward American migration by those in pursuit of beavers would be stifled (Dolin 2011:292). In less than 20 years, the Hudson's Bay Company had decimated beaver populations in California to the point where, after 1843, they ceased sending "hunting parties in that direction" (Nunis 1968:169).

Hensley (1946) provided a detailed summary of government-sponsored beaver translocation programs from 1923 to 1945, and noted that this effort was to "extend the range of California beavers in nonagricultural areas throughout the State, not only for the purpose of producing a valuable fur crop, but with the hope that all advantage may be taken of the water storage, erosion control and aesthetic values that may be derived from the presence of properly located beaver colonies." Therefore, any evidence used to support the historic presence of beavers on either the east or west-facing slopes of the Sierra Nevada must predate 1923.

The objective of this review is to challenge long-held assumptions that beaver did not range historically into elevations above 305 meters on the western slope of the Sierra Nevada, or along the eastern slope of that mountain range. Strong evidence has recently confirmed their historical presence at 1,637 meters and higher elevations in the Sierra Nevada (James and Lanman 2012), well above the 305 meter altitudinal limit promulgated by Grinnell et al. (1937) and Tappe (1942). This discovery was based on a novel approach utilizing radiocarbon dating of wood excavated from two different, recently exposed ancient beaver dams in the upper Feather River watershed in eastern Plumas County, and dates periodic occupancy of the site by beavers between AD 580-1850 at one site, and to 1820 at a second site (James and Lanman 2012). This review complements that physical evidence with an expanded review of historical records of occurrence by other reliable observers and additional indirect evidence including ethnographic information, reviews of geographic place names, historical newspaper accounts, and evaluations of habitat suitability.

MATERIALS AND METHODS

We searched for physical specimens of beaver obtained prior to 1923 in all museum collections participating in the Mammal Networked Information System (MaNIS) and the Arctos Multi-Institution and Multi-Collection Museum Database via Boolean searches. In addition, curators of mammal collections were contacted at the California Academy of Sciences, Los Angeles County Museum of Natural History, Moore Laboratory of Zoology, Museum of Vertebrate Zoology, San Diego Museum of Natural History, Santa Barbara Museum of Natural History, National Museum of Natural History (NMNH), and the UCLA Dickey Collection. Web of Knowledge, Google, and Google Scholar were used to search for historical fur trapper records and ethnographic evidence of beaver. FAUNMAP (http://www. museum.state.il.us/research/faunmap/aboutfaunmap.html) was queried for C. canadensis remains found in archaeological sites. We also contacted six county historical societies and five college libraries for relevant source material. References were also identified from citations in other publications that reviewed the historic range of other California mammals (Schmidt 1991, Bockstoce 2005:61-71). Historical newspaper accounts were searched at the Library of Congress digitized "Historic American Newspapers" (1836-1922) (http:// chroniclingamerica.loc.gov/), the California Digital Newspaper Collection (1847-present) (http://cdnc.ucr.edu/cdnc), and Newspaper Archive (1847-present) (http://newspaperarchive. com/). Geographic place names were searched using the Geographic Names Information

System (GNIS) and toponomastic references (Gudde 1998, Durham 1998). Elevations of stream mouths were obtained from GNIS and the USGS National Map Viewer.

Evidence was ordered into three categories of decreasing reliability. Physical evidence of beaver such as radiocarbon dates from beaver cuttings and physical specimens in museum collections was considered definitive, followed by documented historical records of beaver by reliable observers such as scientists, trappers, or rangers, in accordance with the classification scheme of Aubry et al (2007). Lastly, newspaper accounts, ethnographic information, geographic place names, and evaluations of habitat suitability were considered to be supportive of more reliable lines of evidence if used judiciously.

RESULTS

The FAUNMAP query located no *C. canadensis* remains in archaeological sites in the Sierra Nevada. Also, the search for U.S. museum specimens collected prior to 1923 for the genus "*Castor*" yielded no specimens from Sierra Nevada counties. However, five specimens identified as *C. c. shastensis*, dating to 1892 or 1893, were located in the National Museum of Natural History. Their provenance was from the Pit River in Shasta County and its Hat Creek tributary, the latter having its origin in the Lassen National Forest where the northern Sierra Nevada and the southern Cascades blend together. Of note, only one other California beaver specimen prior to 1900 was located in any U.S. museum, also at the NMNH. That specimen is from Santa Clara County, and was collected in 1855. In California, no museum contained any beaver specimen predating 1906. Although the California Academy of Sciences was founded in 1853, all but a single cartful of its collections were destroyed in the 1906 San Francisco earthquake and subsequent fire. The mammal collections of other natural history museums in California began post-1904 (Table 1).

TABLE 1.—California's major natural history museums, the year founded, and the year that the mammal collection was initiated, or restarted in the case of the California Academy of Sciences following the 1906 San Francisco earthquake.

Institution	Year Founded	Year Mammal Collection (Re-) Initiated
California Academy of Sciences	1853	1906
Los Angeles County Museum of Natural History	1910	1910
Moore Laboratory of Zoology	1950	1933
Museum of Vertebrate Zoology (Berkeley)	1908	1908
San Diego Natural History Museum	1874	1904
Santa Barbara Museum of Natural History	1916	1916
The UCLA Dickey Collection	1910	1910

The first well-documented overland fur trapping parties entered interior California from the northern portion of the Central Valley (drained by the Sacramento River, historically known as the Bonaventura) and from the southern and southeastern Central Valley (drained by the San Joaquin River, then known as the south fork of the Bonaventura). Trappers also approached the Sierra Nevada from the east by following the Humboldt River through

Nevada. The Hudson's Bay Company fur brigades from Fort Vancouver, Washington were the first major trapping expeditions to arrive in the Sacramento Valley, while westbound American mountain men first trapped in the vicinity of the San Joaquin River. Hudson Bay's Peter Ogden Snake River expedition during 1826-1827 was also the first to trap the northeastern edge of California, taking about 1,500 beaver from the Klamath and Pit rivers in two months (Warner 1966). Jedediah Smith, leading an American trapping expedition, crossed the Colorado River into California's Mojave Desert in 1826 and entered the San Joaquin Valley from the south. Smith trapped northward to the American River, then left eleven men on the Stanislaus River to trap the streams while the remainder of his party made a winter crossing of the Sierra Nevada to resupply at the summer rendezvous to be held at Bear Lake, located on the border between present day Idaho and Utah (Smith et al. 1992:19).

Quantitative records of beaver take on the upper reaches of the tributaries of the Sacramento and San Joaquin rivers were not located, but the fact that these rivers were trapped to their source is documented in an 1837 order from Dr. John McLoughlin, Chief Factor of the Hudson's Bay Company in Oregon, to fur trapper Michel Laframboise: "The valley, itself, with the numerous streams flowing into it, from the surrounding mountains have all been visited and their stores of Beaver considerably reduced. Feather River...is the only known exception, its source remains still unexplored..." (Nunis 1968:159). This record suggests that beaver in southern and central Sierra Nevada rivers were nearly depleted, if not extirpated, by 1837. Another Hudson's Bay Company report, by Peter Ogden in 1831, also mentions trapping to the sources of the streams of the San Joaquin River: "on the South Branch of the Boveantura which I trapp'd from its sources to its discharge in the Gulf of St. Francisco I was fortunate in securing 1000 Beavers" (Ogden and Scaglione 1949). Jonathan Warner's account of the American trapping party led by Ewing Young in 1832 provides a third line of evidence that Sierra Nevada rivers were trapped to their headwaters, as he described trapping along the Kings River "up to and some distance into the mountains and then passed on to the San Joaquin River, trapped that river down to canoe navigation in the foothills, where a canoe was made..." (Warner 1907). The easiest place to cross between the two rivers would have been their headwaters high in the Sierra Nevada, which are only two miles apart (Figure 1). Williams (1973:9) also interpreted the Young-Warner party as having trapped on the upper Kings River, noting that they "had been trapping fur-bearing animals at the headwaters of the Kings River about the same time that the Walker party was descending the Merced River".

In 1906, trapper Roy De Voe reported trapping beaver on the Kern River in the southern Sierra around 1900, making camp at its confluence with Rattlesnake Creek (elevation 2,007m) and last seeing beaver sign at Funston Meadow (elevation 1,974m) in 1946 (Townsend 1979). There is also an 1845 record that John Sutter, the founder of the first Anglo-American community in the Central Valley, sent his fur trappers into the Sierra: "This Year I pay a considerable Amount of my debts, the half to the Hud. Bay Compie., a good Amount to the Russians. Mr. Thompson and others I shall be abble to pay them at least half in furs. It is no doubt my Trappers are doing well this time. I[n] the Month of September I fit out the Canoes for the Rivers, lakes and Bay, and a small party in the Mountains where Lieutt fremont passed. There are yet plenty of Beaver and never disturbed by trappers" (Larkin and Hammond 1952:282). John Charles Fremont had crossed Carson Pass and descended to Sutter's Fort along the South Fork of the American River in February, 1844 (Graham 2000:98).

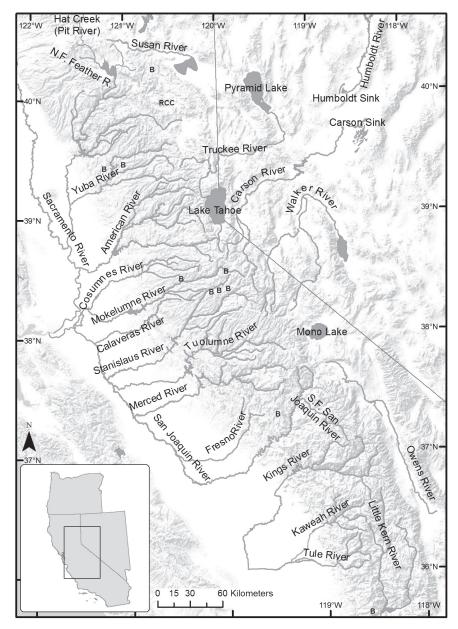


FIGURE 1.—The Sierra Nevada extends from the Susan River in the north to the Kern River watershed in the south. Locations of current and historic beaver place names in watersheds of the Sierra Nevada, California and Nevada, USA, were sourced from the USGS GNIS, and are marked as "B". Red Clover Creek, the site of radiocarbon dated nineteenth century beaver dam wood in two locations, is marked as "RCC". This figure also highlights the proximities of several selected watersheds: Pit River's Hat Creek tributary, which is considered southern Cascades but whose headwaters are 0.5 km from Feather River headwater tributaries in the Sierra Nevada; the Humboldt River Sink and the Carson River Sink; and the South Fork San Joaquin River (S. F. San Joaquin River) whose headwaters are 2 km from the Kings River headwaters and represent the likely trapping route of Jonathan Warner and Ewing Young in 1832. Beaver lived historically (and today) in the Pit River and Humboldt River, and there are no physical barriers to beaver colonization of Sierra Nevada watersheds from these locations.

Although it contradicted a key thesis of his monograph, Tappe (1942:8) confirmed that beaver were present historically on the upper Kings River when he stated, "Beavers were apparently not uncommon on the upper part of the Kings River as late as 1880. Mr. Andrew D. Ferguson, a retired game warden now (1940) living in Fresno, reports that the last fresh beaver cuttings seen by him on this stream were noted in 1882-83. According to him, beavers were scattered all along the Kings River prior to this...".

In the northern Sierra Nevada, Tappe (1942:20) himself observed beaver in 1940 at three widely separated points: below Silver Lake on Bridge Creek and the Susan River in Lassen County, and along Indian, Thompson and Wolf Creeks in Plumas County. Because the nearest of these locations was >64 kilometers (airline) from the nearest known (1934) beaver translocations at Rowland Creek, and because he judged several abandoned dams to be older than 1934, Tappe judged that it was "most probable" that these were native beaver.

The Humboldt River flows westerly nearly to the eastern slope of the Sierra Nevada, terminating in shallow lakes in the Humboldt Sink, about 40 miles east of the termini of the Truckee and Carson Rivers. Peter Skene Ogden (1910:394), on a Hudson's Bay Company expedition to the terminus of the Humboldt River, wrote in his diary on 15 May 1829, "In no part have I found beaver so abundant. The total number of American trappers in this region at this time exceeds 80. I have only 28 trappers... The trappers now average 125 beaver a man and are greatly pleased with their success." Although Ogden is credited with mapping the Humboldt River to its terminus, his report is important as it reveals that otherwise unrecorded American fur trapping parties were already there and had hunted westward at least to the Humboldt Sink on the eastern edge of the Sierra Nevada. Indeed, as his next entry on 17 May notes, "large tracks of pelicans seen indicate a lake."

An American trapper, Stephen H. Meek, set his traps in the Truckee River on his way to discovering Lake Tahoe in 1833 (Mason 1881:58). High precipitation creates a hydrological connection between the Humboldt Sink and nearby Carson Sink (Figure.1) on average about once every twelve years, thereby connecting the undisputedly beaver-rich Humboldt River to the Carson River watershed of the eastern slope of the Sierra. In fact, James "Grizzly" Adams reported catching beaver in the Carson River (Hittell 1861:250) in 1854: "In the evening we caught a fine lot of salmon-trout, using grasshoppers for bait, and in the night killed half a dozen beavers, which were very tame." In a much later record Tappe (1942), in a footnote in his monograph, relates the account of an eyewitness who said beaver were plentiful on the upper part of the Carson River and its tributaries in Alpine County until 1892, when they fell victim to heavy trapping. That footnote provides a third contradiction of Tappe's (1942) thesis that beaver were not native to the Sierra Nevada, as he wrote: "It seems, therefore, that beavers actually did inhabit at least a part of the eastern slope of the Sierra Nevada south of Lassen County."

In referring to the nearby Walker River, Fitz-James (aka Fitz-Mac) MacCarthy (1906) wrote in the Nevada State Journal that the Mason's Valley near Yerington, Nevada was trapped by Kit Carson: "...Carson knew it to the bone...The beavers of course were all trapped long ago, and you never see an elk nowadays...".

Among geographic references to beaver, French Camp in the Central Valley became the popular name for an 1832 encampment of Michel Laframboise's fur brigade, although he called it Castoria, "castor" being the French word for beaver. The toponomastic scholar, Erwin Gudde (Gudde and Bright 1998:30), wrote that place names using the word beaver were rare in California because the mammal "had been almost exterminated by the Hudson's Bay Company...before the American occupation". However, a search of the GNIS revealed

that there are, or were historically, no less than ten place names incorporating the word "Beaver" in the Sierra Nevada. All ten occur in at least seven major river watersheds widely distributed from north to south across the mountain range, and are located at elevations (using stream mouth elevations to be conservative) two to seven times higher than the 305 meter altitudinal limit for beaver promulgated by Grinnell et al. (1937) and Tappe (1942) (Table 2, Figure 1).

TABLE 2.—US Geological Survey geographic place names in the Sierra Nevada that include the word "beaver", California, USA. Superscripts in the table refer to maps predating translocations of beavers by the California Department of Fish and Game (i.e. pre-1923).

Feature Name /		Watershed	Source	Mouth
Historic Name	County	River	Elevation (m)	Elevation (m)
Beaver Meadow (on Grouse Creek)	Alpine	Mokelumne	2743	2189
Beaver Creek ¹	Amador	Mokelumne	1829	1006
Beaver Creek ²	Calaveras	Stanislaus	2256	762
Beaver Canyon Creek	Kern	Kern	1036	625
Beaver Ponds (on North Fork Sand Creek)	Madera	San Joaquin	2091	1571
Beaver Ponds (on Indian Creek)	Plumas	Feather	2045	904
Little Beaver Creek	Tuolumne	Stanislaus	1737	1460
Crane Creek / Beaver Creek	Tuolumne	Stanislaus	2058	1547
Brandy Creek / Beaver Creek ³	Yuba	Yuba	988	738
Willow Glen Ranch / Beaver Ranch ³	Yuba	Yuba	666	666

¹ Pyramid Peak Historic Topo Map. 1896. California Historic Topographic Map Collection. Merriam Library, California State University, Chico, California, USA.

All of these geological features named with the term "beaver" occur at altitudes that support riparian vegetation such as willow or aspen and have substantial stretches of low gradient streams that appear to be ideal beaver habitat. Three of the "Beaver Creeks" were identified on nineteenth century maps, predating the twentieth century government-sponsored beaver translocations that began in 1923, as did the Beaver Ranch place name on Willow Glen Creek. Although one could conjecture that these are references to "mountain" beaver, *Aplodontia rufa*, there is little to support how the two genera and their different habitat requirements (aquatic v. terrestrial) (Kays 2009:48) would have been confused.

² General Land Office Map for Township 6N, Range 17E, M.D.M. 1877. Stanislaus National Forest, Supervisor's Office, Sonora, CA, USA.

³ Smartsville Historic Topo Map. 1895. California Historic Topographic Map Collection. Merriam Library, California State University, Chico, California, USA.

Ethnographic evidence that beaver existed above the Sierra Nevada foothills is suggested by a 500-1,000 year old Yokuts Indian pictograph of a beaver that is located above 488 m elevation on the western slope of the southern Sierra Nevada, at Painted Rock along the Tule River on the Tule Indian Reservation (Grant 1979:28). However, since the Yokuts' territory in Tulare County extended to the San Joaquin Valley, this is only suggestive that beavers were present in the higher elevations of the Sierra Nevada. Alfred Kroeber (1922:455) observed that beavers had a unique importance to the moieties of the Miwok, with differing properties ascribed to coastal, Central Valley, and Sierran aspects. Again, however, historic Miwok references to beaver could be explained because their territory stretched westward from the Sierra crest (including Yosemite Valley) and overlapped with the Central Valley.

The northern Paiute of Walker Lake, Honey Lake and Pyramid Lake were visited by Stephen Powers to collect Indian materials for the Smithsonian Institution in preparation for the Centennial Exhibition of 1876. Powers reported that the northern Paiute wrapped their hair in strips of beaver fur, made medicine from parts of beaver, and that their creation legend included beavers, which they called *su-i'-tu-ti-kut'-the* (Fowler et al. 1970). Stewart (1941) also reported that the Northern Paiute ate beaver and that the men wore beaverskin caps. However, as the Paiute moved extensively within their territory, it is possible that the beaver they utilized were from east of the Sierran flank (i.e. from the Humboldt River). Therefore, we explored ethnographic evidence of beaver among tribes with territories that did not overlap with the Central Valley, namely the Washoe, Owens Valley Paiute and the Mountain Maidu.

The Washoe people wintered on the eastern slope of the Sierra Nevada, in the Carson and Walker River watersheds, and their hunting grounds extended westward beyond Lake Tahoe and the Sierra crest, but probably not further than Calaveras County. There is a Washoe word for beaver, *c'imhélhel*, and they have no pre-European contact words for animals that were not native, lending credence to the notion that the term refers to beaver found within their territory (University of Chicago Contributors 2011). In 1926 Robert Lowie (Lowie 1939:345) interviewed Washoe elders who described a Washoe legend of "Weasel" asking "Beaver", whether he "played" in a location described as across a "high mountain near Sheridan (Sheridan, Nevada is at elevation 1,467 m and 13 km southeast of Lake Tahoe) "to the other side, to a big lake". Beaver answered, "Yes, I play here every day..." in a location that appears, from the description, to be Lake Tahoe.

The Mountain Maidu, another Sierran tribe, whose territory began high on the western flank of the Sierra Nevada around Bucks Lake and Humbug Valley (elevations 1,573 m and 1,311 m, respectively), and extended to the eastern Sierra flank on the west side of Sierra Valley and at Janesville (Middleton 2008), also have a pre-European contact word for beaver, *hi-chi-nem*, according to Farrell Cunningham (personal communication 2010), a Mountain Maidu tribal historian. Additionally, in his work on the Washoe and Owens Valley Paiute on the eastern slope of the Sierra Nevada, anthropologist William Sturtevant (Sturtevant and D'Azevedo 1986:80) included beaver in his list of common edible mammals.

Hensley (1946) summarized the virtually state-wide translocation of 338 beavers from 1923-1945, to 29 of California's 58 counties. Maps of current beaver populations show beavers thriving across the Sierra Nevada from north to south and all along its eastern slope (University of Washington Contributors 2011). In addition, Yosemite Park Naturalist Robert McIntyre (1948) reported that California Golden beaver (*C. c. subauratus*) from

near sea level in the Central Valley (Waterford and Snelling, elevations 16 m and 78 m, respectively) had been successfully translocated to Ackerman Meadow near Mather Station (elevation 1,378 m) in 1940 and had built >20 dams by 1947. McIntyre noted that these beavers had built dams and lodges at elevations of 1,372 m, although that behavior was traditionally considered atypical of Central Valley beaver, which were regarded as "bank burrowers" (Tappe 1942, McIntyre 1948). These beaver colonies have continued to expand over the intervening seventy years, and beavers now thrive on the Merced River in Yosemite National Park, providing further evidence of habitat suitability in higher elevations of the Sierra Nevada.

DISCUSSION

The paucity of museum specimens prior to 1923 is not surprising, given that beaver were nearly extinct even in their last refuge, the Central Valley's Sacramento-San Joaquin River Delta, at a time when California's museums were just initiating their mammal collections. Our expanded review of reliable observer records produced two independent reports of beaver on the Carson River (eastern Sierra Nevada), and two on the Kings River (western Sierra Nevada), and multiple single reports that placed beaver before 1923 at relatively high elevations in the northern, southern, and western Sierra Nevada, as well as on its eastern slope. Curiously, Tappe himself provided three such observations, contradicting his central thesis that beaver were not native to higher elevations, or to the eastern slope, of the Sierra Nevada. In a footnote (Tappe 1942) noted that he received the report of beaver on the Carson River, "after this manuscript was written" and then, "It seems, therefore, that beavers actually did inhabit at least a part of the eastern slope of the Sierra Nevada south of Lassen County."

The additional indirect evidence reported in this review is valuable because it is consistent with the accounts of earlier observers. For example, the newspaper account of Kit Carson trapping beavers on the Walker River, the findings of Washoe and Northern Paiute words for beaver, and the hydrological connectivity of the Humboldt Sink with the Carson sink, all support the dual reports of beaver by trappers on the nearby Carson River. Similarly, the presence of "Beaver Creek" and "Beaver Ponds" place names in the Kern and San Joaquin watersheds above 1,000m and 2,000 m, respectively, supports historical observer accounts of beavers at elevations up to seven times higher than the limits posited by Grinnell et al. (1937) and Tappe (1942). In addition, the "Beaver Ponds" place name at the headwaters of Indian Creek is consistent with the radiocarbon dating evidence of historical beaver dams on Red Clover Creek, whose waters flow to Indian Creek via Last Chance Creek, in Plumas County.

The discovery of two separate historic beaver dams in the East Branch North Fork Feather River watershed (James and Lanman 2012), which were constructed or reconstructed, from wood samples with radiocarbon dates spanning more than a millennium and extending through the early nineteenth century represents, to the best of our knowledge, the first direct physical evidence of beaver at higher elevations of the Sierra Nevada. Since that discovery, additional well-preserved wood from remnant beaver dams has been found while conducting extensive restoration of incised channels in Feather River watershed montane meadows, as well as high meadows in the Mokelumne and Carson river watersheds. Samples from additional ancient beaver dam sites should be analyzed with radiocarbon dating to confirm those results, and dendrochronological analysis could provide alternative

methodological confirmation, if larger conifer branch samples suitable for dendrochronology can be located. Additional buried beaver dams could also be located using ground penetrating radar, as has been recently demonstrated in Colorado (Kramer et al. 2012).

Although a great deal of historical information is presently digitized and searchable and our review of that material was exhaustive, further historical records of beavers in the Sierra Nevada may remain to be located in California and Nevada state archives, college or university special collections, as well as Hudson Bay Company archives in Canada. Similarly, as more historic maps are digitized, a more exhaustive search of pre-1900 maps might identify more "beaver" place names than we listed (Table 2). Lastly, naturalists and collectors from various European countries visited California in the nineteenth and early twentieth centuries, but foreign museum collections were not searched (Beidleman 2006). Further research is needed to extend our findings by establishing how uniformly beavers were formerly distributed throughout the Sierra Nevada and its eastern slope.

Museum specimens in the NMNH from the Pit River and its Hat Creek tributary from 1892-1893 should also be carefully considered. There is no biogeographical barrier separating the Shasta beaver (*C. c. shastensis*) in the Pit River from the Sierra Nevada, and Hat Creek originates within the northern boundary of the Sierra Nevada (defined roughly as a line from Fredonyer Pass to the Susan River). In fact, in southeastern Shasta County, the East Fork of the Pit River's Hat Creek runs only 0.5 km away and over gradual terrain from the Summit Creek headwaters of the North Fork of the Feather River (Figure 1). Similarly, the Robbers Creek tributary of the North Fork of the Feather River begins within 0.5 km of the Susan River. Traversing these distances of less than 1 km between the Pit River, Susan River, and Feather River upper watersheds should not be difficult for beavers, since two- to three-year-old beavers can naturally disperse over 30 km by land or 50 km by stream (Müller-Schwarze and Sun 2003).

Establishing the historical range of beavers in the Sierra Nevada is an important consideration for their management as a native species. The beneficial effects of beavers in the Sierra Nevada have been documented and include increased trout abundance and diversity (Gard 1961), reduced nutrient and sediment loads (Muskopf 2007), and expansion of aspen woods in riparian zones in the Tahoe Basin (Ayers 1997). It is tempting to speculate that the extirpation of beaver, when combined with the overgrazing by introduced domestic cattle or sheep on Red Clover Creek, precipitated the channel incision in the surrounding montane meadow. In fact, Wilcox (2007) reported that "prior to 1880, Red Clover Creek, was reported as a low gradient, narrow channel with a well-developed riparian zone comprising hardwoods, sedges, and willow...and had a reputation as a good trout fishery. By 1985, the actively eroding channel was 50 to 60 feet wide and had vertical cut banks up to 10 feet high...The lowered water table in the meadows adjacent to the stream bank converted the once-productive wet meadows to a dry sagebrush-dominated basin." His observations strengthen that of Hughes (1934), who also indicated that Red Clover Creek was a low gradient stream historically connected to riparian meadowlands until heavy sheep and cattle grazing removed riparian vegetation, thereby causing the channel to erode.

The degradation of Red Clover Creek post-extirpation of beaver may be a microcosm for stream channel incision in montane environments throughout the Sierra Nevada. Studies conducted and reviewed by Pollock et al. (2003) and Pollock et al. (2007) in semi-arid Western habitats similar to the Sierra Nevada, have found that re-introduction of beaver can rapidly aggrade stream sediments, elevating incised channels and reconnecting them to their floodplains, ultimately converting formerly incised xeric valleys into gently

sloping ones with abundant riparian vegetation. Therefore, wildlife policies that currently lead to the removal of beaver from fragile montane environments in the Sierra Nevada should be reconfigured to promote beaver populations. As a case in point, recent beaver depredation on Lake Tahoe's streams by government agencies likely has an adverse impact on sediment and pollution discharges into the lake.

Additional evidence in the form of genetic analyses has the potential to yield new information on the historical distribution of beavers in California. Although contemporary beaver populations in the Sierra Nevada are considered to have resulted from early twentieth century translocations, Tappe (1942) himself speculated whether there were still native beaver in the Sierra Nevada. In addition, current Sierra Nevada beaver populations were translocated not only from the Delta's Golden beaver stock, but also from Oregon, Idaho and Shasta beaver stock. Whether the latter are genetically different from native Sierra beaver is germane to current wildlife management policy. In the absence of genetic investigations of this question, we opine that the historical taxonomic distinctions between Shasta beaver, which inhabit the same Sacramento River watershed (Pit and McCloud rivers) as the Delta's Golden beaver (C. c. subauratus), should be questioned. In Eurasia, the Eurasian beaver (Castor fiber) was historically divided into eight subspecies on morphological grounds, yet recent genetic studies (Durka et al. 2005, Halley 2010) reported that only two evolutionarily significant units (an eastern and a western ESU) exist based on mitochondrial DNA evidence. Studies using DNA and other biological evidence may help resolve whether current beaver populations in the Sierra Nevada are genetically distinct from other native California beaver.

Surprisingly few contemporary studies have been conducted with the primary goal of determining the historical geographic range of a particular species (Schwartz et al. 2007). Using modern data acquisition and investigative techniques, we have extracted and synthesized multiple lines of evidence (physical, ethnographic, historical, as well as habitat suitability) indicating that beaver historically occurred throughout some, if not most, of the Sierra Nevada and on its eastern slope. Although more physical evidence is needed to define how broadly beaver were distributed and particularly to very high elevations, the direct evidence presented, in conjunction with the abundant indirect evidence, supports our conclusion. Moreover, the one hypothesis that posited why beaver did not colonize the Sierra (that steep western slope canyons presented a barrier) is not supported by current knowledge of beaver dispersal patterns, or by the proximities of watersheds to the north and east of the Sierra Nevada; both would have enabled relatively easy colonization. Further, the continuing expansion of twentieth century beaver translocations in the Sierra suggests that suitable hydrogeomorphic habitat conditions existed in the past. Our findings contradict earlier assertions that beaver were not native to higher elevations in the Sierra Nevada. Reassessment of the historical distribution of beaver (and other native fauna) are recommended in other regions of California, especially when current wildlife management policy is based largely on dated investigations that were conducted in the absence of modern research tools such as radiocarbon dating, extensively digitized historical records, and genetic analyses.

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