The historical distribution of bighorn sheep in the Sierra Nevada, California

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Bighorn sheep in the Sierra Nevada disappeared from most of their historic range, surviving in only 3 populations west of the town of Independence in the Owens Valley. As a primary basis for restoration of these sheep, we compiled historical sightings and skull remains for Sierra Nevada bighorn sheep by twelve geographic regions, along with early estimates of population sizes where they existed. Historic sightings suggest that at least 10 populations survived to the twentieth century of which 2 persisted to the middle of that century before disappearing; but the sighting record does not distinguish viable populations from those that may have been declining to extinction. While it is possible for some populations to assign a decade when they disappeared, those populations may have lost viability earlier. Our data base probably represents the historical north-south distribution of these sheep and provides distributional details for some populations. However, it is remarkably sparse for some regions, suggesting that it may not have captured the full historical distribution of this animal, particularly west of the Sierra crest, where the earliest population losses may have occurred. Restoration efforts need to recognize this potential shortcoming.

Key words: bighorn sheep, endangered species, historical distribution, *Ovis canadensis sierrae*, Sierra Nevada

Information on historical distribution is an important foundation for wildlife restoration programs. Bighorn sheep in the Sierra Nevada (*Ovis canadensis sierrae*; SNBS) disappeared from the majority of their native ranges following the appearance of Europeans and their domestic animals in the mid 19th century. By the 1970s SNBS persisted in only three populations in a region from George Creek to Taboose Creek west of the town of Independence in the Owens Valley, Inyo County, California (Wehausen 1979, 1980). Translocations were used to begin restoring extirpated populations during 1979–88 (Bleich

et al. 1990). While those restoration efforts succeeded in re-establishing populations in three regions, subsequent reductions in all populations of SNBS led to the listing of these sheep as endangered under state and federal laws in 1999. Those actions ultimately placed a stronger emphasis on further restoration of extirpated populations as one criterion for removal of these sheep from endangered species status (U.S. Fish and Wildlife Service 2007).

Two fundamental adaptations substantially dictate the nature of suitable habitat for bighorn sheep: keen eyesight and agility on steep rocky slopes. The first is how these sheep detect predators and the second is how they evade them. Preferred habitat is visually open (low vegetation) and on or close to steep, rocky slopes. The extensive alpine habitat along the crest of the Sierra Nevada provides a large expanse of relatively continuous suitable habitat that is steep, rocky, and visually open. The pattern of uplifting of the Sierra Nevada fault block has resulted in a considerably steeper eastern slope compared with the western side of the range (Hill 1975), with the former providing a considerable amount of steep and rocky terrain needed by bighorn sheep.

Additionally, because of the prevailing direction of winter storms and the strong rain shadow effect of this high mountain range, the eastern slope of the Sierra Nevada is much drier than the western side. This climatic pattern also has enhanced bighorn sheep habitat on the eastern side of the range by limiting the height and density of many plant communities, resulting in patches of low stature vegetation below timberline. This is particularly evident along the eastern base of the escarpment where the rain shadow is strongest and the plant community consists of Great Basin desert scrub types below and in conjunction with the lowest trees in the mid-elevation forest belt. In contrast to the extensive forested habitat found at mid elevations on the western side of the Sierra Nevada, forested habitat on the drier eastern slope of this range is more fragmented and often with low tree density on steep rocky slopes, thereby providing habitat used by SNBS. The result is a network of suitable habitat along the eastern side of the range at these mid elevations.

In the southern Sierra Nevada the Kern River drainage is a deep north-south canyon sandwiched between the main crest of the range and the Great Western Divide, a separate high alpine crest parallel to the main crest to the west with its own rain shadow. There is historical evidence that resident populations of SNBS also occupied a portion of the Great Western Divide.

While alpine habitat in the southern and central Sierra Nevada is relatively continuous, this does not imply that the native bighorn sheep were one continuous population. Bighorn sheep in general show a great deal of population substructuring defined by separate female home range patterns, and these female home range patterns are the fundamental building blocks of metapopulations for the species (Bleich et al. 1996). In contrast to the extensive alpine habitat, suitable low elevation winter range habitat on the eastern slope of the Sierra Nevada is quite discontinuous and limited in area, consisting of patches of varying size. The low elevation patches used by SNBS in winter and early spring naturally divide them into separate demographic units typically known as herds, and some existing historical data are specific to such herds. There are also larger natural distribution gaps, such as the Kern River drainage, that separates the two southern alpine crests. Those larger gaps were recognized in the recovery plan for SNBS where they were used to define four larger distributional units termed recovery units (U.S. Fish and Wildlife Service 2007).

In general, male bighorn sheep range considerably further than females. The much larger horns and supporting skull structure of male bighorn sheep allow skull remains to

persist much longer than those of females, resulting in a very male-biased historical data base of documented remains. While skull data provide important historical information, there is a need to recognize this bias in interpreting these data relative to the distribution of native herds of reproducing females.

SNBS are a unique and clearly distinguishable subspecies of bighorn sheep (Wehausen and Ramey 2000, Wehausen et al. 2005), and can be viewed as alpine specialists relative to habitat use patterns and life history, which distinguishes them from most desert bighorn sheep. Consequently, the native distribution of SNBS can be defined in part relative to alpine habitat, limiting the southern distribution to Olancha Peak and the Great Western Divide, while historical evidence puts the northern end of the native distribution in the Sonora Pass region. The details of historical distribution within that region are the subject of this paper; specifically, we attempt to synthesize all historical evidence of bighorn sheep within that geographic area. In so doing we address the temporal pattern of herd losses to the extent possible, and provide information on habitat attributes and historic herd sizes where available.

DATA SOURCES

A variety of authors addressed questions about SNBS beginning in the late 19th century (Muir 1894, 1898; Ober 1911, 1914, 1931; Grinnell and Storer 1924; Bailey 1932; Grinnell 1935; Dixon 1936), but the first attempt to catalogue historical information was that of Jones (1949), particularly the appendix, which is lacking in the subsequent publication (Jones 1950a). Wehausen (1979, 1980) added to that compilation, and further evidence in the form of skull remains has emerged since then.

We critically examined potential evidence and mapped only data that clearly documented the presence of bighorn sheep either as location-specific sightings or skull remains in our maps of historical evidence (Figure 1, Figure 2). Clyde (1971) noted that male mule deer (*Odocoileus hemionus*) can utilize high alpine habitats. They leave tracks that cannot be reliably distinguished from bighorn sheep, and the same can be said of visual identification of their feces. In recent years the first author has genetically analyzed numerous fecal samples from alpine habitat outside of the known range of SNBS where the collectors believed the samples were from SNBS. Most have proven to be from mule deer. Consequently, in this data synthesis we excluded all reported sign of bighorn sheep, recognizing that in some cases this meant ignoring what could have been good information. In addition to skulls and sightings, there were also historical, subjective estimates and even counts for some populations. These were not plotted; instead, this information was brought into regional narratives along with other pertinent information.

Some focused data collection on surviving native herds began in the 1960s (Riegelhuth 1965, McCullough and Schneegas 1966, Dunaway 1970). Since our purpose was largely to describe the distribution of extirpated populations, we did not consider that information to be historical and pertinent to this study and did not include it. However, we included earlier sighting data for surviving native herds that were entered into a class called historic sightings, defined as pre-1960 sightings. This allowed comparisons of numbers of recorded sightings between regions, such as surviving versus extirpated herds. For extinct herds that survived into the second half of the 20th century it was also important to acknowledge and utilize more recent data, so we included a second category of recent









sighting data for 1960–1979. Skull remains were treated as a third class in our data base and on maps, and all skull data were included for extirpated herds regardless of when found.

We divided the historic range of SNBS into twelve geographic regions numbered 1-12 from south to north. Those regional boundaries were defined in a way that would not place any extant or historic population in multiple regions, but some regions include the ranges of multiple populations, while others represent the range of a single population.

Early field observers lacked the tools needed to identify seasonal migration patterns that are typically used to define separate populations (herds), and they consequently sometimes made false assumptions regarding population definitions that have been corrected in recent decades. We point these out where appropriate.

Our regional boundaries are included on the maps that summarize our data base and below we discuss the historic information by region. We discuss this evidence of historic presence of SNBS beginning with the Great Western Divide.

Great Western Divide (1).—Bighorn sheep occupied a region of the Great Western Divide at least from the Kaweah Peaks to Mineral King and further south to Maggie Mountain (Figure 1). Early cattlemen operating in this region noted that SNBS could be found most commonly at the head of Big Arroyo (an alpine basin west of the Kaweah Peaks), and on Red Spur, a prominent point along the Kern River at the eastern end of the Kaweah Peaks (Jones 1950a). The Mineral King area had an estimated 125 SNBS in the 1870s distributed as 75 in the Farewell Gap area and 50 around Sawtooth Peak according to Guy Hopping, an early superintendent of National Park Service lands in that region (Jones 1950a).

Guy Hopping told the second author of a die-off of bighorn sheep in the Kaweah Peaks in the 1870s which was attributed to scabies, presumably contracted from domestic sheep. This is the only documented die-off of SNBS, but it apparently did not eliminate that population, as sightings of SNBS continued to be made in this region of the Great Western Divide to about 1918 (Table 1).

		Historic	Recent	Earliest	Latest	
Region	History	Sightings	Sightings	Year	Year	Skulls
1. Great Western Divide	Е	8	0	1905	1918	8
2. Round Mt. to Muah Mt.	Е	16	2	1906	1966	6
3. Cottonwood Cyn. to Lone Pine Cr.	Е	17	8	1909	1976	14
4. Mt. Whitney to University Peak	Ν	33	-	1875	-	4
5. Kearsarge Pass to Taboose Pass	Ν	53	-	1912	-	4
6. Taboose Pass to Coyote Ridge	Е	4	0	1935	1957	11
7. Bishop Creek to Pine Creek Pass	Е	5	6	1873	1936	11
8. Pine Creek to Rock Creek	Е	2	1	1944	1962	1
9. Mono Pass to Mammoth Pass	Е	15	3	1913	1975	7
10. Mammoth Mt. to Mt. Dana	Е	7	7	1870	1976	33
11. Tioga Pass to Green Creek	Е	4	1	1939	1960	9
12. North of Green Creek	Е	4	13	1877	1975	14
TOTALS		168	41			122

TABLE 1. Summary of historic data compiled for Sierra Nevada bighorn sheep. Historic sightings are pre-1960. Recent sightings are for 1960–1979. E = extirpated; N = native.

In recent decades SNBS living along the main crest of the Sierra Nevada in a variety of locations have demonstrated the ability to live year round at high elevations. Critical to that behavioral pattern are networks of predictably windswept habitat on and just east of the Sierra crest that are substantially free of snow in most winters. The Great Western Divide differs from the main crest of the Sierra Nevada in essentially lacking such high elevation snow-free habitat. The very limited historical information on the bighorn sheep that once occupied the Great Western Divide lacks data on where they wintered. While the east-facing slope of the Kern River Canyon and south-facing habitat near the mouths of Big Arroyo, Rattlesnake Canyon, and Laurel Canyon are likely candidates, there may have been winter range patches used on the western side of the Great Western Divide. This is suggested by multiple historic sightings in the Maggie Mountain area that lies about 14 km southwest of the extensive high alpine summer range near Mineral King. Not far from Maggie Mountain to the north is Sheep Mountain, which may have been named because of regular use by bighorn sheep. The recovery plan for SNBS postulated that two populations inhabited this region historically (U.S. Fish and Wildlife Service 2007), and restoration of SNBS to this region via translocations began in 2014.

Round Mountain to Muah Mountain (2).—This region once supported the Olancha Peak herd. Olancha Peak lies near the southern end of this region and contains the southernmost alpine habitat in the Sierra Nevada; but it is a small somewhat isolated patch of alpine habitat that is connected to the extensive alpine of the main crest of the Sierra Nevada north of the Kern Plateau only via the steep eastern escarpment west of Owens Lake. The historical information on SNBS in this region (Table 1, Figure 1) clearly indicates that SNBS occupied Olancha Peak and the habitat east of the Kern Plateau between Olancha Peak and the Mount Langley region to the north and perhaps some areas of the Kern Plateau. There are multiple patches of good, low-elevation winter range at the base of the escarpment in this region. Because Olancha Peak is otherwise a small isolated patch of habitat, gene flow across the habitat above Owens Lake with the Mount Langley herd would have been critical for the persistence of this population.

The largest sighting in this region was 19 sheep of all sizes in 1916, after which no sighting exceeded 4. Jones (1949, 1950a) treated the Olancha Peak herd as part of the Mount Langley herd, but given the natural population structure of bighorn sheep there is a high likelihood that it contained an independent population of females. When this population disappeared is not clear. Of 15 scattered sightings after 1920, 7 are specified to be males, and many others may have been the same. These may have been primarily rams from the Mount Langley herd. It is possible that the Olancha Peak herd was no longer a viable reproducing population by the early 1920s. SNBS were restored to Olancha Peak via translocations in 2013 and 2014.

Cottonwood Canyon to Mount Hitchcock and South of Lone Pine Creek (3).—The native Mount Langley herd was probably the last population to go extinct, with many reported sightings in this region (Figure 1) in the first half of the twentieth century and continuing into the second half of that century, even to the 1970s (Table 1). Of note is some evidence in the form of skull remains that historically SNBS (at least males) may have used the suitable habitat patch around Boreal Plateau and Rocky Basin Lakes. This may reflect what once was an important stepping stone in a migration route connecting the Mount Langley herd with sheep on the Great Western Divide. A steep rocky canyon connects the Boreal Plateau area to the Kern River in the region of historic SNBS range on the Great Western Divide.

SNBS were successfully restored to Mount Langley beginning in 1980 (Bleich et al. 1990) and have grown to a population slightly larger than 100 (Few et al. 2012). While this population currently utilizes much of the potentially suitable habitat in this region, it is not clear that it yet utilizes habitat as fully as the native herd did. One historic sighting is of 15 bighorn sheep at low elevation in Cottonwood Canyon in 1946, and suggests that this excellent patch of low elevation habitat may once have been a winter range for the Mount Langley herd. In recent years this habitat patch has been utilized only occasionally by small numbers of males.

Mount Whitney to University Peak (4).—This region supports one of the persisting native herds, the Mount Williamson herd. Mount Williamson itself represents the distribution center of this herd, where females reside year round. In the past four decades males have utilized habitat as far north as Pinyon Creek, as far south as Vacation Pass, and west along the Kings-Kern Divide, especially Diamond Mesa, but also further west (Figure 1). Two reported ram skulls in the Milestone Basin at the northern end of the Great Western Divide might have been from this herd, but also could have been from the extirpated population in the Kaweah Peaks. There is also historical evidence from sightings that females utilized habitat at the eastern end of the Kings-Kern Divide from Junction Pass to Forrester Pass.

To the south of Mount Williamson there is historical evidence that females used the high plateau between Mount Barnard and Trojan Peak, and areas south of Mount Barnard probably to Vacation Pass, but evidence of SNBS further south suggests only ram use of Mount Russell and Mount Carillon. Evidence of SNBS in the Mount Whitney area is sparse, but not entirely lacking. Clyde (1971) noted that in about 50 ascents of Mount Whitney from all directions, he had never seen any evidence of bighorn sheep, but there are a few historical data points (Figure 1), including the carcass of a female in 1933 at Whitney Portal that was probably from the Mount Langley herd.

Kearsarge Pass to Taboose Pass (5).—This section of the range continues to support native populations. The persistence of SNBS in this region is evidenced by numerous references through time (Ober 1911, 1914, 1915, 1916, 1931; Clyde 1936; Dixon 1936; Blake 1941, 1949) and many recorded sightings (Table 1, Figure 1). Its persistence allowed Joseph Grinnell to obtain permission to collect 5 sheep for the Museum of Vertebrate Zoology at the University of California, Berkeley in 1911 (Grinnell 1912).

When focused attention began to be given to surviving bighorn sheep in the Sierra Nevada in the 1960s and 1970s the SNBS in this entire region between Kearsarge Pass and Taboose Pass were all referred to as the Mount Baxter herd. Since the early 1980s this region has been divided into the Mount Baxter and Sawmill Canyon herds because of distinct home range patterns of females, with Sawmill Creek the dividing line east of the crest. Home range fidelity over a series of years by naturally marked sheep observed by the first author was one of the bases for recognizing separate populations, which subsequent radio telemetry data have corroborated. Previously, Ober (1911) used Sawmill Canyon as the division between herds, thereby correctly defining a separate herd in the range of what is currently known as the Mount Baxter herd. North of Sawmill Creek, however, he combined the Sawmill Canyon and Taboose Creek herds into a single demographic unit. So did the 1921 and 1923 Invo National Forest Fish and Game Reports. In discussing winter observations of those sheep, Ober (1911) noted that they could be found along the snow line as far north as Red Mountain Creek; and the 1921 Inyo National Forest Fish and Game Report noted, "A considerable number ranging from Goodale Mountain to Birch Mountain, and wintering along the foothills in the Black Rock region during heavy snow."

For the past 35 years SNBS from the Sawmill Canyon herd have been known to winter as far north as the north side Goodale Creek, including the front slopes as far as the south-facing slope of Shingle Mill Bench, and to utilize higher elevations on Goodale Mountain extensively in all seasons, but not north of Taboose Creek in winter. This early herd definition therefore appears to have combined the north end of the range of the Sawmill Canyon herd with the Taboose Creek herd to its north.

Ober (1914) stated that only three SNBS herds persisted at that time, of which one appears to have coincided with the current Mount Baxter herd. In 1911 he reported reliable summer sightings of a group of 20 and another of upwards of 40 SNBS observed for this herd, and he proposed that its size was at least 40–50 (Ober 1911). Three years later he recorded having counted 65 different sheep at one time and estimated the population at 85–90 (Ober 1914); but the following year he noted having encountered more than 200 in a two-week period in spring, and intimated that the population was much larger than his earlier estimate (Ober 1915). The 1927 Inyo National Forest Fish and Game report included an estimate of 30 sheep for a Thibaut Creek herd, but for 40 years Thibaut Creek has been just the southern end of the primary winter range of the Mount Baxter herd.

Ober's (1911) description of the combined Sawmill-Taboose Creek herd put its size at about 22, and three years later he increased that estimate to about 30, but gave a geographic description that appeared to be only north of Taboose Creek (Ober 1914). The 1921 and 1923 Inyo National Forest Fish and Game reports, respectively, provided estimates of 40 and 70 sheep for a Goodale-Birch Mountain "band", which also would have been a mixture of sheep from the northern end of the Sawmill Canyon herd winter range and the Taboose Creek herd winter range. These estimates and herd designations illustrate the lack of understanding of what constituted a population in that time period; nevertheless, they clearly documented the continued presence of SNBS in the regions discussed.

This region from Kearsarge Pass to Taboose Pass appears to have the best habitat for SNBS in the entire central and southern Sierra Nevada. While it contains extensive summer range at high elevations with a rich mixture of patches of different alpine and subalpine plant communities, what is notably different is low elevation winter range where SNBS can exploit an early forage growing season and greatly increase annual nutrient intake (Wehausen 1992). In the middle of this region the eastern base of the escarpment extends further east and to lower elevations than any other SNBS winter range, allowing SNBS to feed in winter and early spring as low as 1,460m on either side of Sawmill Creek. These lower elevations translate to warmer winter temperatures and more rapid progression of forage growth once it is initiated (Wehausen 1992), providing greater nutrient availability compared with other, higher winter ranges. This difference is coupled with higher plant species diversity than other winter ranges. Additionally, lower elevations also result in much larger areas of visually open habitat lacking taller vegetation. This is particularly evident in the Mount Baxter winter range immediately south of Sawmill Creek that in recent decades has supported the largest population (150 in 1978) of SNBS recorded to date (30% higher than the next largest population). The high habitat quality in this region may have played an important role in the persistence of native SNBS in this region. This region was the source of SNBS translocated in the 1979-1988 restoration efforts (Bleich et al. 1990).

Taboose Pass to Coyote Ridge (6).—As noted above, one of Ober's (1914) three SNBS populations used habitat north of Taboose Creek that is now referred to as the Taboose Creek herd unit. The 1921 and 1923 Inyo National Forest Annual Fish and Game

reports also made reference to this population with estimates as high as 70 sheep. These population definitions apparently combined sheep from the northern winter range of the Sawmill Canyon herd with the Taboose Creek herd; however, in noting SNBS wintering north of Taboose Creek, these sources effectively documented the existence of a Taboose Creek herd that was presumably distinct from what is now known as the Sawmill Canyon herd. The Taboose Creek herd apparently used lower elevation winter range from Taboose Creek to Red Mountain Creek.

Compared with other herds of SNBS in the southern Owens Valley, the Taboose Creek herd is conspicuous by the sparsity of specific sightings that would support its existence (Table 1, Figure 1). Despite Ober's earlier discussions of this herd (Ober 1911, 1914), Ober (1931) made no mention of it, suggesting that it may have disappeared during the intervening 15 years. Such an early extirpation could explain the lack of sightings. Specific evidence of the Taboose Creek herd consists only of some weathered ram skulls and occasional sightings of live rams, all of which could have reflected rams wandering north from the Sawmill Canyon herd. The evidence supporting the past existence of a Taboose Creek herd as a potentially reproducing population consequently consists only of the discussions of SNBS wintering in the region from Taboose Creek to Red Mountain Creek in the 1921 and 1923 Inyo National Forest Fish and Game Reports and Ober (1911, 1914). While there is the possibility that only rams used winter ranges north of Taboose Creek, there is extensive summer range in that area that would appear suitable to support a reproducing population, and it has been recognized as an extirpated population (U.S. Fish and Wildlife Service 2007).

In summer one might expect the distribution of this herd to extend further north, but Ober (1914) indicated that these sheep did not go further than the south fork of Big Pine Creek. Yet further north the Sierra crest branches, with the eastern branch terminating at Coyote Ridge. While there are patches of habitat suitable for bighorn sheep on this spur, including some potential winter range along its eastern base, and some scattered historical evidence of SNBS (Figure 1), there is a lack of any historical evidence suggesting that this region once supported a reproducing population. This is the reason why it was not listed as a herd unit requiring occupancy as part of recovery goals for SNBS (U.S. Fish and Wildlife Service 2007).

Bishop Pass to Pine Creek Pass (7).—Ober (1914) identified a Mount Tom herd as the last, and second largest, of the three SNBS herds he knew to exist at that time, and he later reaffirmed its existence (Ober 1931). He estimated its size at 40–50 in 1914 and 35 in 1931 (Ober 1914, 1931). Ober described this herd as wintering and summering on Mount Tom. Additional evidence indicates that this herd ranged further south along the crest and west of the crest in summer. There were sightings west of Piute Pass in 1934 (Jones 1949) and on Mount Emerson in 1936 (1936 Inyo National Forest Fish and Game Report). Fred Ross (pers. comm. 19 January 1979) reported having occasionally seen bighorn sheep west of the Humphreys Basin in the area of Mount Senger, Turret Peak, and Mount Gemini in the 1930s, and that he knew of several skulls having been found in that area, as well as on the Glacier Divide. John Muir described in his journal an encounter with members of this population on 27 September 1873 west of the Sierra crest that occurred one day prior to his reaching the crest from the west (Wolfe 1938). Sightings from this area in the mid 1930s appear to be the last evidence of this herd, which apparently died out during that decade.

Pine Creek to Rock Creek (8).-The 1921 and 1923 Invo National Forest Annual Fish and Game Reports both mentioned a herd referred to as the Pine Creek - Rock Creek band, which wintered at the base of Wheeler Ridge, and Jones (1949) interviewed locals who knew of the presence of SNBS in this region as early as 1910. The Inyo National Forest Fish and Game Reports from 1921 and 1923 estimated this herd at 25 and 30 sheep, respectively. However, Ober (1911, 1914, 1931) never mentioned this herd, and we have found no reference to it after 1923. Additionally, we found only a single reference to skull material from this area (a ewe horn) and the only other specific sighting data are each lone males that might have wandered in from herds to the north or south: one observed in Pine Creek in 1944 (Sequoia and Kings Canyon National Parks files), and one killed by boys in Pine Creek in 1948 (Jones 1949). The sparsity of historic data for this herd (Table 1, Figure 2) is difficult to explain for habitat that has recently supported a population a little in excess of 100 sheep (Stephenson et al. 2011) resulting from restoration efforts beginning in 1979 (Bleich et al. 1990). This was the first location chosen for the restoration of SNBS because of its extensive winter range and apparent overall habitat potential for supporting a viable bighorn sheep population.

Mono Pass to Mammoth Pass (9).—SNBS in this region have been referred to as the Convict Creek herd since Jones (1949, 1950a) defined it. While Jones (1949) did not have time to investigate this region on the ground, there were numerous reliable reports of SNBS persisting in this region (Table 1, Figure 2). As such, it was one of two populations (along with the Mount Langley herd) that did not disappear until the second half of the twentieth century. The Convict Creek herd apparently disappeared early in the second half of the twentieth century, given that there is only a single recorded sightings of live sheep after Jones (1949) compiled evidence of the existence of this herd in 1948. By the 1960s reports were only of skulls. The 1936 Inyo National Forest Deer Census and Game Survey reported 30 bighorn sheep between Laurel Creek and Convict Creek. In 1955 Joe Smith of Laws stated that just after 1900 there were about 40 bighorn sheep between Rock Creek and Convict Creek (California Department of Fish and Game files). Together these two figures speak to the approximate numbers of SNBS that might have once occupied this herd unit. This herd unit now supports a small population of SNBS as a result of a recent range expansion of the Wheeler Ridge herd.

Mammoth Mountain to Mount Dana (10).—This region apparently lost its populations of SNBS early. Grinnell and Storer (1924) concluded that SNBS in the Yosemite region had essentially disappeared by the early 1880s, which appears to be supported by Muir's (1898:624) statement just prior to the twentieth century that "Few wild sheep, I fear, are left hereabouts". One result of this early extirpation is the limited opportunity for historical evidence in the form of sightings of live sheep, leaving evidence of the former presence of SNBS in this region largely in the form of numerous skull remains.

Muir (1894) reported 3 SNBS in Bloody Canyon in winter prior to 1874 that were so snowbound that mountaineers crossing the range in that season were able to kill them with an axe. This may be the only recorded sighting of live bighorn sheep in the northern part of this region. At the southern end of this area a deer hunter killed a bighorn ram on San Joaquin Mountain in 1954 (Yosemite National Park files). In that same year U. S. Forest Service employees reported several bighorn sheep near Glass Creek on the eastern side of San Joaquin Ridge and another observer reported seeing single and small groups of bighorn sheep on San Joaquin Ridge from the air during 1955–1957. From a metapopulation standpoint

San Joaquin Ridge is geographically a critical habitat corridor for bighorn sheep in this region, which would have allowed migration between populations to its south and north. San Joaquin Ridge itself, however, does not appear to have habitat that would have supported a resident population of bighorn sheep. The reports from the 1950s are consequently difficult to interpret, but they may have in some way reflected the persistence of SNBS in the Convict Creek herd to the immediate south into the second half of the 20th century.

There were multiple recent sightings of bighorn sheep in this region (Table 1, Figure 2) that are unexpected and not easily explained given many prior decades without any evidence of live individuals. Intensive investigations in summers and winters of 1977 and 1978 failed to find any evidence of bighorn sheep in this region (Wehausen 1979), and further evidence has not surfaced.

This region has a large number of documented skull remains (Table 1, Figure 2), including a mummified ram found emerging from under the Mount Lyell glacier in 1933 (Sharsmith 1938, Wasmund 1938). While there is the expected scattering of such data along the crest from Mount Dana and the Dana Plateau southward, there is also a noteworthy concentration further west along a considerable length of the Cathedral Range from Mount Ritter to Parsons Peak (Figure 1). Because those specimens are all male, they may simply reflect a separate summer range utilized only by males, as documented for the native Mount Baxter herd (Wehausen 1980). The divide that Donahue Pass crosses would provide a continuous high-elevation habitat corridor to this region of the Cathedral Range. However, there also may have been a separate population in that region that had its own winter range somewhere west of the Sierra crest. This high concentration of skulls may simply reflect the early creation of Yosemite National Park and the long-standing attention of the National Park Service to recording and preserving historical information.

SNBS were restored to this area unintentionally in 1986 when three of the females translocated to Lee Vining Canyon earlier that year (Bleich et al. 1990) migrated south with two lambs born in Lee Vining Canyon to found a separate herd (Chow et al. 1993).

Tioga Pass to Green Creek (11).—Grinnell and Storer's (1924) suggestion that bighorn sheep in the Yosemite region largely were gone by the early 1880s also applies to this region. The proximity to the large mining community at Bodie may have played a role in early extirpation of SNBS in this northern region. A surviving restaurant menu from Bodie included mountain sheep meat. This population also suffers from a lack of early records of bighorn sheep sightings (Table 1, Figure 2). The few that exist all stem from more than half a century after the early 1880s beginning with eight rams at Burro Lake in 1939. About the same time (1954–1955) that bighorn sheep were recorded on San Joaquin Ridge (see above), there were also three sightings near Lee Vining. The remaining observation for this region was in 1960 near Mount Conness and included both a ewe and a ram. Like the sightings on San Joaquin Ridge and more recent ones south of Tioga Pass, these scattered sightings are difficult to interpret. This region also was part of the investigation in the late 1970s which found no evidence of an extant population (Wehausen 1979).

We found nine records of old skull remains in this region, all scattered south of the ridge that separates the Lundy Canyon and Virginia Lakes drainages (Table 1, Figure 2). Two Native American hunting blinds at high elevations apparently situated for hunting wild sheep provide further evidence that this region once supported a population of SNBS. One of these is at the northeastern corner of Mount Warren next to the Deer Creek drainage. In recent years the bighorn sheep restored to this area created a trail immediately adjacent to

that blind. The other hunting blind is on Dunderberg Peak (C. Millar, U.S. Forest Service, pers. comm.). SNBS were restored to this region via translocations in 1986 and 1988 (Keay et al. 1987; Bleich et al. 1990, 1991).

North of Green Creek (12).—This region encompasses the remaining historic range of SNBS and extends northward to the Sonora Pass region. Here SNBS also apparently suffered early extirpation, leaving little opportunity for recorded sightings. The notable exception was about a dozen bighorn sheep observed on the east side of Sonora Pass in three successive summers (1876–1978; Grinnell and Storer 1924). Grinnell and Storer (1924) and Jones (1950b) both cited anecdotal information that suggested that some bighorn sheep may have persisted past 1900 in this northern region.

Similar to the other areas north of Mammoth Lakes, this region includes a number of sightings from long after the apparent extirpation of SNBS. Unlike those other two regions, however, this region has more recent sightings than any other region (Table 1) and they include a set of nine sightings that cluster both geographically (Matterhorn Peak to Grouse Mountain) and temporally (1968–1975), and are detailed enough to specify observations of females in four cases. Some of these sightings were a prime focus of investigations in 1977–1978 that failed to find any evidence of bighorn sheep in that region (Wehausen 1979), and no additional sightings have surfaced since that time. We found references to 14 skull remains in this region (Table 1, Figure 2).

DISCUSSION

In addition to adding information that has emerged since the compilation by Jones (1949), we categorized and discussed data by regions defined geographically relative to known populations, and we mapped the historical information by three categories (Figure 1, Figure 2). The historic distribution of SNBS includes about a 290 km linear distance of the Sierra Nevada between northern and southern extremes. Our historical database included 168 sightings prior to 1960, 41 more recent sightings for 1960–1979, and 122 skull remains (Table 1). Given the large area involved, this is a rather meager data set. A number of factors are probably involved. One is the early decimation, if not loss, of many populations, and the resulting lack of opportunity for sightings. Another is that SNBS occupy habitat that most people do not venture into because it is steep, rocky, and lacks trails, and there were considerably fewer people in California and the Sierra Nevada in the late 19th and early 20th centuries. However, our limited data probably largely reflect the fact that only a small percentage of information of this sort is ever recorded. Even today, most of the public has little understanding of why the reporting of such information might be useful, and in earlier periods this may have been even more the case. Our database includes only five sightings from the 1800s!

The lack of any coordinated interest in these sheep in early years appears well illustrated by the lack of consistency among different sources relative to where populations persisted, and the fact that multiple populations that persisted well into the 20th century were unknown to state or federal employees that filed reports on these sheep. Our research suggests that at least nine SNBS populations in the eastern Sierra persisted to the second and third decades of the twentieth century: Olancha Peak; Mount Langley; Mount Williamson; Mount Baxter; Sawmill Canyon; Taboose Creek; Mount Tom; Wheeler Ridge; and Convict Creek. During his tenure as a game warden in the Owens Valley in that time period, Ober

(1911, 1914, 1915, 1916, 1931) failed to recognize the existence of five of these populations (Olancha Peak, Mount Langley, Mount Williamson, Wheeler Ridge, and Convict Creek), despite his numerous written contributions and an apparent keen interest in bighorn sheep. Our finding that fish and game reports from the local National Forest recognized two populations never mentioned by Ober (Wheeler Ridge and Convict Creek) suggests both a lack of coordination and a lack of communication among personnel representing different agencies, but both of those sources failed to report three surviving populations in the southern Sierra Nevada from Mount Williamson to Olancha Peak. These discrepancies and shortcomings suggest that development of data on these sheep was incidental to other priorities, which is consistent with the overall low amount of historic data on these sheep. The differential knowledge of extant populations by individuals from different governmental agencies may simply reflect the locations where these government personnel were stationed and the travel difficulties of that era. Ed Ober was stationed in Big Pine, while the National Forest headquarters were further north in Wells Meadow at the base of the Wheeler Ridge herd winter range — a population documented by that agency, but not by Ed Ober. The low density of our historical data begs a number of questions, which follow.

Does this data base include some representation from all habitat patches occupied by SNBS in 1850? Probably not! We found remarkably little historical evidence for the Wheeler Ridge herd (Region 8 in Table 1 and Figure 2); yet, it is excellent habitat that now supports about 100 animals resulting from restoration efforts beginning in 1979. That some historic ranges of SNBS may not be represented in our data base is further supported by the apparent natural colonization of habitat on the north side of Bubbs Creek in the second half of the 1990s. That population was discovered through a reported sighting in 2001 and has persisted in habitat entirely west of the Sierra crest since then. There is, however, no historical evidence of bighorn sheep in that region prior to 2001. This situation begs the question of what other locations west of the Sierra crest might once have been occupied by SNBS, but lack any historical evidence because of early extirpation.

Major die-offs from diseases contracted from domestic sheep were most likely the primary cause of population losses of SNBS (Wehausen et al. 2011). Domestic livestock grazing in the Sierra Nevada began in the 1860s during severe droughts that precluded the previous patterns of year-round cattle grazing in the Central Valley (Vankat 1970). Mountain grazing of domestic sheep followed quickly because that species could be herded much further into the mountains than could cattle. Since this began on the western side of the range, SNBS populations that might have existed in suitable west-side habitat patches may have been the first to disappear, and could have done so without any record of their existence.

What our data base appears to provide is adequate documentation of the overall north-south range of SNBS and probably most of the areas along the eastern side of the range that they occupied. While there is some historic evidence of early domestic sheep grazing in the Owens Valley region, more intensive grazing on the eastern side of the Sierra Nevada apparently began later than the western side as a response to implementation of grazing restrictions on the western slope in the 1890s following the creation of Yosemite National Park and Sequoia National Park and the forest reserves that later became national forests (Wehausen 1988). It took some years for enforcement of grazing regulations to be implemented, but one result was an annual grazing circuit that began in winter in the Central Valley, crossed the southern Sierra Nevada to the western Mojave Desert for spring grazing, then moved north through the Owens Valley to summer grazing areas in higher mountains, with a reverse pattern in fall (Austin 1906).

To what extent can our data base be used to track the temporal pattern of herd losses? Are the numbers of sightings for different herds inversely related to how long they persisted? If this inverse relationship is strong, the extant native populations should have the most recorded historical sightings. This expectation is met to the extent that the two regions of native SNBS (4 and 5) clearly have the most sightings in the historic period before 1960 (Table 1). However, when those data are parsed further, this relationship weakens substantially. Region 4 represents just one population (Mount Williamson herd), but region 5 includes two: the Mount Baxter herd south of Sawmill Creek and the Sawmill Canyon herd further north. The Mount Baxter herd accounts for 42 (79%) of the sightings for its region, while there are only 11 for the Sawmill Canyon herd. Thus, there is high variation among the three native herds in the numbers of recorded sightings prior to 1960 (11, 33, and 42), and three extirpated herds exceed the lowest of these values (Table 1), indicating at best a weak relationship between the number of recorded sightings and persistence time. Factors in addition to persistence time have probably greatly influenced the sighting record. One of those factors may be biases in locations to which backcountry users, especially peak climbers, have been attracted.

Relative to the timing of extirpations, the historic information we compiled clearly documented that the Mount Langley and Convict Creek herds survived through the first half of the twentieth century, and that the Mount Tom herd persisted into the fourth decade of that century. Despite the lack of recorded sightings, the Wheeler Ridge herd apparently survived to the early 1920s, while the Taboose Creek and Olancha Peak herds also apparently survived into the beginning of the third decade of the 20th century, but appear to have disappeared in the early 1920s.

Extirpated populations may have declined to where recovery was unlikely (loss of viability) following one or more major disease die-offs, yet produced long temporal tails of sightings as the few remaining sheep declined to extinction. Following the initial major die-off of bighorn sheep of all ages from introduced respiratory disease, the disease organisms can persist in some surviving adults and cause most lambs to die for numerous years, resulting in a steady population decline (Cassirer et al. 2013). Such potential time lags make it difficult to assign meaningful dates of extirpations from a sparse record of sightings. The apparent persistence of SNBS on the Great Western Divide into the twentieth century may be an example of such a lag between loss of viability and the end of sightings.

The historical data we discuss provide considerable information useful for the restoration of SNBS, much of which served as an important basis for the recovery plan for SNBS through input from the first author (U.S. Fish and Wildlife Service 2007). However, it is important that restoration efforts recognize the limitations of these data; they do not necessarily include all habitat patches occupied by SNBS in 1850, and in many regions lack sufficient information to infer seasonal patterns of habitat use. In recent decades a great deal of detailed information on habitat use has been obtained as a result of various types of telemetry collars installed on translocated SNBS as part of restoration efforts during 1979–1988, and more recently on resident and translocated SNBS. This information has steadily expanded the understanding of the variety of habitats SNBS can use successfully. Once regions known to have been occupied historically have been restocked or naturally colonized, restoration efforts might use the growing data base on habitat use to identify additional habitat patches potentially suitable for these sheep, and consider efforts to restock those.

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Big Arrovo: Tulare	Mount Emerson: Invo		
Birch Mountain [•] Invo	Mount Gemini: Fresno		
Bloody Canyon: Mono	Mount Hitchcock: Tulare		
Bodie ⁻ Mono	Mount Langley. Invo Tulare		
Bubbs Creek: Fresno	Mount Lyell: Mono Madera Tuolumne		
Burro Lake: Mono	Mount Ritter: Madera		
Cathedral Range: Mono, Madera, Mariposa.	Mount Russell: Invo. Tulare		
Tuolumne	Mount Senger: Fresno		
Convict Creek: Mono	Mount Tom: Invo		
Cottonwood Canvon: Invo	Mount Warren: Mono		
Covote Ridge: Invo	Mount Whitney: Invo. Tulare		
Deer Creek: Mono	Mount Williamson: Invo		
Diamond Mesa: Tulare	Muah Mountain : Inyo		
Donahue Pass: Mono, Tuolumne	Olancha Peak: Invo. Tulare		
Dunderberg Peak: Mono	Owens Lake: Invo		
Farewell Gap: Tulare	Parsons Peak: Madera, Mariposa, Tuolumne		
George Creek: Inyo	Pine Creek: Inyo		
Glass Creek: Mono	Pinyon Creek: Inyo		
Goodale Creek and Mountain: Inyo	Piute Pass: Inyo, Fresno		
Great Western Divide: Tulare	Rattlesnake Canyon: Tulare		
Grouse Mountain: Mono	Red Mountain Creek: Inyo		
Humphreys Basin: Fresno	Red Spur: Tulare		
Independence: Inyo	Rock Creek: Mono		
Kaweah Peaks: Tulare	Round Mountain: Inyo, Tulare		
Kearsarge Pass: Inyo, Fresno	San Joaquin Ridge/Mountain: Mono,		
Kern Plateau: Tulare	Madera		
Kern River: Tulare	Sawmill Creek and Canyon: Inyo		
Kings-Kern Divide: Tulare	Sawtooth Peak: Tulare		
Laurel Canyon: Tulare	Sheep Mountain: Tulare		
Laurel Creek: Mono	Shingle Mill Bench: Inyo		
Lee Vining: Mono	Sonora Pass: Mono, Tuolumne		
Lundy Canyon: Mono	Taboose Creek: Inyo		
Maggie Mountain: Tulare	Taboose Creek: Inyo		
Mammoth Pass: Mono, Madera	Taboose Pass: Inyo, Fresno		
Matterhorn Peak: Mono, Tuolumne	Thibaut Creek: Inyo		
Milestone Basin: Tulare	Tioga Pass: Mono, Tuolumne		
Mineral King: Tulare	Trojan Peak: Inyo, Tulare		
Mono Pass: Inyo, Fresno	Turret Peak: Fresno		
Mount Barnard: Inyo, Tulare	University Peak: Inyo, Tulare, Fresno		
Mount Baxter: Inyo, Fresno	Vacation Pass: Inyo, Tulare		
Mount Carillon: Inyo, Tulare	Virginia Lakes: Mono		
Mount Conness: Mono, Tuolumne	Wheeler Ridge: Mono		
Mount Dana: Mono, Tuolumne			

APPENDIX I: COUNTIES OF GEOGRAPHIC LOCATIONS IN THE SIERRA NEVADA AND REFERENCED IN THIS PAPER