History of pronghorn population monitoring, research, and management in Yellowstone National Park

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Kim A. Keating
USGS Northern Rocky Mountain Science Center
AJM Johnson Hall
Montana State University
Bozeman, Montana 59717
(406) 994-7333
kkeating@montana.edu

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INTRODUCTION

Pronghorn antelope in Yellowstone National Park (YNP) persist in a small population that historically has experienced recurrent, sometimes dramatic declines. They apparently are isolated from other pronghorns, depend partly on private lands for winter range, experience heavy predation of fawns, and concentrate during winter in a relatively small area, thereby increasing their vulnerability to factors like disease or locally extreme weather. Overall, the situation raises serious concerns about the long-term viability of this population. Although such concerns are not new, evidence of a dramatic population decline since 1991 and continued poor recruitment has created a renewed sense of urgency.

Recent efforts to revitalize pronghorn research in YNP began with fawn recruitment and habitat use studies, initiated in 1999 and 2000. With those studies drawing to a close, YNP is reviewing the status and direction of its pronghorn program. The Yellowstone Pronghorn Conservation Assessment Workshop was convened in YNP in January, 2002, to appraise the current state of knowledge about this pronghorn population and make recommendations about future management and research needs. A review of pronghorn population change, management, and research in YNP was commissioned in May, 2001, to provide historical background for workshop participants. Following is a written summary of that review.

The process of locating materials for this review was limited to 3 months. Not all relevant materials were discovered or reviewed in that time. In particular, it was not possible to find and review all original sources of information. Also, except for occasional anecdotal accounts, weather records were not reviewed, leaving a potentially serious gap in our understanding of the forces driving changes in pronghorn population counts and estimates

over time. Despite these deficiencies, considerable information was reviewed, earlier summaries of population classification and count data were updated, and previously uncited sources of information were identified that challenge important aspects of previous interpretations of the history of pronghorns and pronghorn management in YNP. Information is grouped into 4 major subject areas: distribution and habitat use, demographics and management, genetics, and disease.

DISTRIBUTION AND HABITAT USE

General Patterns

Pronghorns were once widely distributed in the upper Yellowstone drainage, likely migrating large distances to low-elevation winter ranges. In a description reminiscent of the 100- to 170-mile pronghorn migrations that occur today between Grand Teton National Park and winter ranges in southwestern Wyoming (Sawyer and Lindzey 2000), Grinnell (1918) observed that in YNP,

> "The antelope never wintered in the Park, but went down the Yellowstone River toward the lower country. T. E. Hofer has spoken of seeing their trails where Livingston now stands, where at first he thought that bands of several thousand sheep had passed along."

Hofer himself wrote that pronghorns did not winter in YNP (Hofer 1887a), but "used to go to a less snowy region to pass the winter months" (Hofer 1890). Quoting Gamekeeper Young from 1881, Skinner (1922*a*:93) wrote that "very few of the deer or antelope wintered anywhere in the park." Based on his review of the historical record, Houston (1982:24) also believed that "pronghorn wintered historically in the Paradise Valley…and further down the

Yellowstone River."

Following settlement, the situation changed dramatically. Skinner (1922*a*:93) painted an especially bleak picture when he stated that "migration now to the plains would be slaughter, for if an antelope gets out of the park, it is gone as if swallowed up." Contributing factors are reviewed below (see Demographics and Management). The net impact, however, was that the pronghorn migration north from YNP was effectively eliminated during settlement (Houston 1982:24), although the exact timing is unclear. Barmore (1981, citing Skinner 1922*a*, Nelson 1925, and Beer 1944) concluded only that extirpation occurred "sometime before 1920." An article in Forest and Stream (Anonymous 1905*b*) suggests that it may have occurred by 1905, as it quotes YNP's Acting Superintendent as stating that "[t]he valley of the Yellowstone north of the park is now completely taken up by ranchers, and their wire fences running in every direction have completely shut off the old winter range of the antelope." Whatever the timing, migrations that historically funneled "thousands of antelope" (Skinner 1922*a*:92) to spring and summer ranges in YNP ended with settlement of the Paradise Valley. Pronghorn sightings between YNP and Livingston remain sparse today (Scott and Geisser 1994), and the population is presumed to be demographically and, perhaps, genetically closed.

Within YNP, historical accounts of seasonal distributions paint a picture that broadly accords with most of what is known about pronghorn distributions today. Rangeland habitats along the Yellowstone and Lamar Rivers, and on the Blacktail Deer Plateau have long been recognized as preferred pronghorn habitat (Scott and Geisser 1994, citing Norris 1878). Hofer (1887*b*; 1889*b*; 1890; 1891*a,b*; 1905*a*) reported pronghorns wintering on Mt. Everts and along the northern boundary near Gardiner; and spring and summer sightings near

Yancey's and Junction Butte, on the hillsides between Hellroaring and Slough Creek, and on the Blacktail Deer Plateau and Specimen Ridge. Skinner (1922*a*:92) reported that "the [pronghorn] range is restricted to the great open section in the north, comprising the Gardiner Valley, Mount Everts, Blacktail Deer Valley, the slopes on both sides of Hellroaring Creek, Junction Valley, the lower slopes of Mount Washburn on the north, the lower and upper valleys of the Lamar River, and Specimen Ridge." Murie (1940:89) observed that, in summer, pronghorns were "distributed from the Game Ranch all the way to Tower Falls and to the high grassy ridges bordering Cache Creek on the east," and that "[t]hey are commonly found on top of Specimen Ridge."

Various accounts suggest that at least 3 important changes have occurred in summer distributions. First, pronghorn use of the Hayden Valley apparently has declined. Scattered reports confirm that, historically, at least small numbers of pronghorns regularly summered in the Hayden Valley (Anonymous 1885, Wilson 1885, Hofer 1887*c*). However, Skinner (1922*a*:92) stated that pronghorns no longer used the Hayden at the time of his study, while Murie (1940:89), Scott (1993*a*), and Scott and Geisser (1994) regarded sightings there as "unusual." Declining use of the Hayden Valley may have significance beyond the simple fact of a reduced pronghorn distribution. Scott and Geisser (1994:16–17) speculated that the Hayden might have been an historical "mixing site for pronghorns from the Yellowstone and Madison Valleys," with pronghorns from the Madison area migrating into the Hayden Valley via the Madison-Firehole-Nez Perce Creek route used today by bison. Sporadic sightings of pronghorns in the Lower Geyser Basin and along the Madison and Gibbon Rivers (Scott and Geisser 1994) are consistent with this hypothesis.

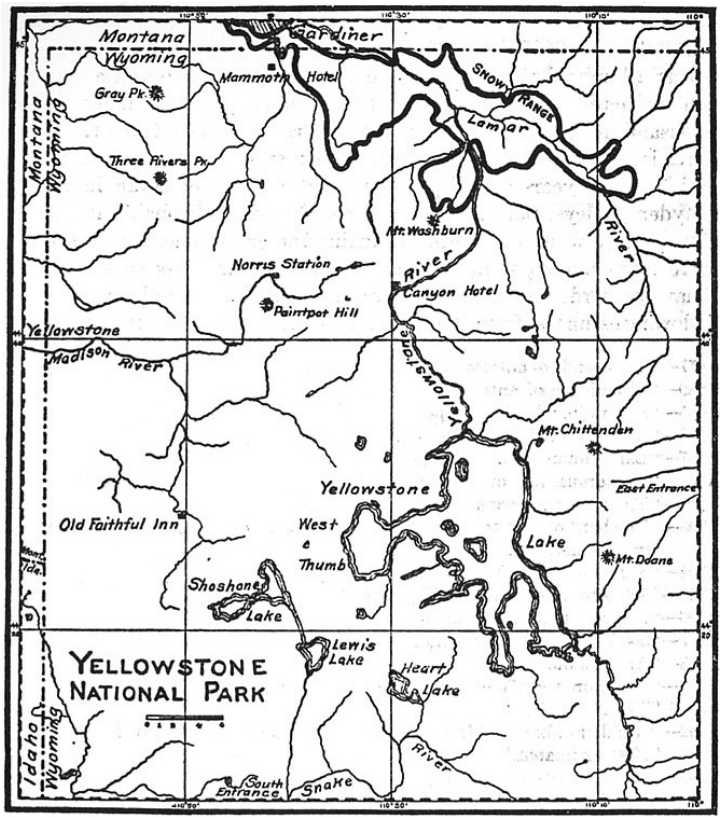

Fig. 1. Seasonal distribution of pronghorn antelope in Yellowstone National Park, as mapped by Skinner (1922). Summer range is indicated by the heavy outline, winter range by cross-hatching.

Second, there is some suggestion that pronghorn use in Gardners Hole has declined. Skinner (1922*a*:91) stated that "[f]orty years ago, limited numbers [of pronghorns] ranged the Swan Lake and Hayden Valleys, but such is no longer the case." Although pronghorns have been sighted in Gardners Hole area in recent times (J. Mack, National Park Service, pers. commun.), it is believed that use has been sporadic.

Finally, pronghorns may have been extirpated from the Antelope Creek summer range. Pronghorns undoubtedly once used this area, as Skinner (1922*a*:92) included "the lower slopes of Mount Washburn on the north" in his description of pronghorn range. Also, the Antelope Creek area is clearly contained within his mapped "Distribution of Prong-horn Antelope in Yellowstone Park" (Skinner 1922*a*:91) (Fig. 1). Greer (*c.* 1930–1931:3) similarly noted pronghorns in this area. Scott (1991:4) reported, however, that "pronghorns

stopped migrating to the Antelope Creek Valley after the Montana Department of Fish, Wildlife, and Parks and the National Park Service removed 240 of them from the Reese Creek area in January, 1947," and that "[t]his summer habitat has not been used since." Following their review of sighting records, Scott and Geisser (1994:15) reported that "[p]ronghorns were last seen in the Antelope Valley area on 8 May 1946."

Winter Distribution and Habitat Use

For over a century, quantity and quality of pronghorn winter range has been a chronic concern; one that is inextricably tied to the history of settlement and land use in the Gardiner Basin. Mining operations began at Bear Gulch in 1866 and were followed by the creation of YNP (1872), Gardiner (1880–present), Cinnabar (1883–1902), Horr (later renamed Electric, 1894–1910), Aldridge (1896–1910), and Jardine (1898–present) (Whithorn and Whithorn *c.* 1965, *c.* 1977; Anonymous 1997). Of these, Cinnabar and Electric figured most prominently in early commentaries on pronghorns. Cinnabar stood near the present-day junction with the Stephens Creek road, and was sustained by agriculture and business associated with the town's railroad terminus (Whittlesey 1995). With a combined population of 1,500, Electric and the associated community of Aldridge were built around coal mining operations near Beattie Gulch (Whithorn and Whithorn *c.* 1965). Electric occupied the flats east of the Yellowstone River (Fig. 2) and north of the present park boundary, while Aldridge was situated above Aldridge Lake, west of Cinnabar Mountain.

Settlement brought major habitat changes due primarily to agriculture, mining, and associated development. Effects of cultivation near Cinnabar and north to Reese Creek can be seen in the park today, with irrigation ditches still visible and fields dominated by exotic plant species. Areas once occupied by the town of Electric (Fig. 2) have since been

Fig. 2. Looking up the Yellowstone River toward Mt. Everts (background) from above the coal mining community of Electric, Montana (1894–1910). Electric was situated on pronghorn winter range between Spring Creek and Beattie Gulch. (Photograph courtesy of Bill and Doris Whithorn)

converted mostly to agricultural use, although recent increases in home site development in the Gardiner Basin threaten to reverse those changes. Livestock once ranged widely in this area; even within the Park, "the area between Mammoth and the north boundary of the park [was grazed] without any restrictions as to season of use, numbers or class of stock" (Houston 1982:421, citing Rush 1932). YNP's north boundary was fenced in 1903 (Acting Superintendent 1913). Afterward, Pitcher (1905) indicated that "all stock has been kept off this range during the past year [1904], or ever since the fence near Gardiner has been completed." Following addition of the boundary line area (BLA) to YNP in 1932, however, cattle continued to graze areas within the Park's northern boundary at least through 1971 (Houston 1982:338).

Using comparative photography, Houston (1982) documented vegetation changes in the BLA and north to Dome Mountain, among other areas. Changes in the amount of big sagebrush (*Artemesia tridentata*) were evident (Houston 1982:292–293 and 338–351), but generalizations about the nature and causes of the changes remain problematic. For example, Houston (1982:338) characterized areas of high sage densities in parts of the current pronghorn winter range as a disclimax induced by a combination of livestock overgrazing and fire suppression. Photos from 1871 (Houston 1982:346–351) suggest, however, that sagebrush during pre-settlement times was denser than occurs today on many parts of the pronghorn winter range within YNP. Murie (1940:88) pointed to overgrazing by native ungulates as a cause of the decline of sage within the Park, but other factors also may have been important. For example, Bauer (1938, quoted in Houston 1982:425) stated, "the drouth which persisted more or less from 1933 to 1936 had a definite adverse effect on [sagebrush]," killing off "large areas" of sage. More recent studies in the northern Rocky Mountain region also implicated drought as a major factor in the decline of sagebrush (Anderson and Inouye 2001).

Other habitat changes affected pronghorns in ways that were more calculated than those induced by settlement. Feeding of ungulates, including pronghorns, began in YNP as early as 1902 (Hofer 1902, Anonymous 1905*b*). In 1904, the Park began cultivating and irrigating alfalfa on the flats near Gardiner, providing an estimated 100–200 tons of alfalfa hay annually during winter (Pitcher 1905, Anonymous 1906*a*). This program affected the pronghorn population in at least 2 ways. First, pronghorn numbers increased dramatically (for details see Demographics and Management). Second, the presence of irrigated alfalfa apparently caused some animals to remain on the winter range year around, likely creating

the non-migratory subpopulation that exists today. Evidence that migratory habits changed is found in a series of Forest and Stream articles. Explaining the benefits of Superintendent Pitcher's new alfalfa cultivation program, one article (Anonymous 1904) stated that the flats containing the alfalfa field were "used by the antelope *only in winter*" (my italics). Within a year, that had changed (Hofer 1905*b*):

> "In the spring almost all the antelope left their winter range in front of Gardiner and the alfalfa patch; but about twenty concluded it was a favorable place to show themselves, and every evening came down from the nearby hills. They are quite tame for antelope, and thousands have seen them, where if they had returned to their old range for the summer not one tourist would have known what the animal looked like."

Hofer's (1908*b*) account suggests that mule deer summer distributions were similarly affected and that the number of pronghorns remaining on the winter range during summer continued to increase:

> "In front of town [Gardiner] every evening we can see from forty to fifty antelope and thirty to forty mule deer feeding on the alfalfa field…About twenty-five antelope used the field every evening all last summer, and there is a prospect that more will camp there this summer with the addition of the mule deer. I do not remember that any deer summered here last year."

Overall, the record suggests that YNP's alfalfa field induced unforeseen, long-term consequences for distributions and habitat use patterns of pronghorns and mule deer.

Other management activities also likely influenced pronghorn winter distributions

and habitat use. A policy of containing pronghorns within YNP began soon after the U.S. Army assumed responsibility for the Park in 1886, with "soldiers acting as herders" to drive pronghorns back into the Park (Anonymous 1887*a*). This practice continued at least through the winter of 1911–1912 (Anonymous 1911*a*,*b*; Acting Superintendent 1912). By 1900, the Superintendent was lobbying for a boundary fence, with the express purpose of protecting pronghorns and excluding livestock (Anonymous 1901, citing Superintendent's Annual Report 1900). Four miles of wire fence were completed by the U.S. Engineer Department in 1903 (Anonymous 1905*b*, quoting the Acting Superintendent; Acting Superintendent 1913). The fence apparently succeeded in limiting livestock use of winter range in the Park (Pitcher 1905) and in preventing pronghorns "to some extent from moving out of the park" (Murie 1940:88). However, repeated references to fence repair and escaping animals (e.g., Anonymous 1907; Superintendent 1910, 1911; Anonymous 1911*a*,*b*; Acting Superintendent 1913; Bailey 1930:30, as quoted by Murie 1940:101) indicate that fencing was not fully effective. Fencing also produced unintended impacts, as some pronghorns were trapped against fence lines and killed by predators (Heller 1925:466, Anonymous 1934) — a strategy still seen today (McEneaney 1997).

Although the old boundary fence was removed shortly after the BLA was added to the Park (Anonymous 1934, 1936), fences erected by private landowners are still a concern. In 1987 and 1988, for example, the Royal Teton Ranch (RTR) constructed over 2 miles of buck-and-pole fence along the park boundary near Reese Creek (Barbee 1990). Scott (1992) found that the fence inhibited trans-boundary movements by pronghorn. Subsequent increases in annual counts (see Demographics and Management, Fig. 7) and continued depredation hunts to control pronghorn numbers on the RTR suggest, however, that the fence

had little affect on the distribution or dynamics of the population.

In 1919, the National Park Service (NPS) issued the Graves Nelson Report, which "recommended the acquisition by the federal government of a great many small tracts of private land in the territory between Gardiner and Yankee Jim Canyon." (Whittlesey 1995:53). With that report, the focus of YNP's pronghorn policy expanded beyond feeding and predator control efforts to include acquisition of additional range, for by then it was believed that more winter range was needed to assure the herd's future. But how much winter range was enough? Superintendent Albright argued that "… if we could get the Hoppe Ranch, which immediately adjoins the Park on the north, we would have no more trouble with the [pronghorn] herd" (Albright 1922). Skinner (*c.* 1924:2) apparently envisioned a larger herd, for he reaffirmed that about 5,000 additional acres were needed for the herd that existed at that time, but argued for acquiring a much larger area, writing that "[i]f we had the entire valley from Gardiner to the Canyon below Electric, the continuation of our herd and the preservation of the species would be assured." Skinner's vision, apparently, was never pursued. In 1922, Thomas Cochran and George D. Pratt founded the Game Preservation Company, which eventually purchased and donated thousands of acres to YNP and the Gallatin National Forest (Whittlesey 1995:54). The Game Preservation Company purchased the Hoppe ranch in 1925 and other parcels in the BLA in the years thereafter, but the federal government could not accept title until 1931 and the 7,609-acre area was not formally appended to YNP until October 20, 1932 (Whittlesey 1995:57, 71). During the interim, the land was placed at the disposal of YNP "for the care of elk, deer and antelope in winter" (Whittlesey 1995:57). YNP operated the former Hoppe Ranch (by then known as the Game Preservation Ranch) for the feeding of native ungulates and government horses;

plowing, seeding, and irrigating large areas into hay almost as soon as it was acquired (Whittlesey 1995:57). The operation yielded 144 tons of hay the first year, and by 1931 the Park was cultivating 300 acres (Whittlesey 1995:57). Following addition of the BLA, "razing of fences and old buildings on the antelope winter range…added considerable area to the available range" (Anonymous 1936). By this time, pronghorns could move freely beyond the former boundary fence and onto the lands that had once been occupied by the town of Cinnabar.

The expanded feeding program enabled by acquisition of the BLA was short-lived. During the winter of 1931–1932, 1200 pounds of cottonseed cake and 118 tons of hay were fed at the Game Ranch (Anonymous 1933), but only 36 tons of hay were fed the following winter, and by the winter of 1933–1934 the feeding program in the BLA ended (Anonymous 1933, 1934). One year later (1934–1935) YNP's predator control program also ended (Murie 1940:16). Discontinuation of both feeding and predator control terminated a management strategy that in various guises over a 50-year period (1886–1935) had sought to preserve YNP's pronghorn herd by simultaneously increasing the food supply and limiting predation.

Within 10 years after feeding and predator control ended, management objectives were emphasizing habitat rather than herd protection. In summer 1946, a plan was approved to reduce the pronghorn herd to 400 animals (Barmore 1981:Table 105, citing Anonymous 1946). In 1950, a target population of 200 animals was recommended (Barmore 1981:Table 105, citing Anonymous 1950*a*). By 1953, the Park's management plan called for limiting the herd to 100–125 pronghorns (Hamilton 1953, Rogers 1956). The target population apparently remained in this range until the herd reduction program ended in 1967 (McLaughlin 1965). This dramatic shift in management philosophy almost certainly affected

pronghorn distributions and habitat use patterns, particularly on the winter range where feeding and predator control efforts had previously been concentrated.

Studying seasonal habitat selection by pronghorns in the area between Mammoth Hot Springs and Reese Creek, Barmore (1981) found that 79% of feeding was in xeric grasslands, the only habitat type that was preferred throughout the October–May study period. Old fields, mesic grasslands, and especially sagebrush grasslands generally were avoided, although old fields were preferred during October–December and mesic grasslands were preferred in May (Barmore 1981:236, 240, Fig. 28). Pronghorns strongly preferred level to gentle slopes throughout the study period, and also showed some preference for moderate west-facing slopes and ridge tops (Barmore 1981:241, 244, Fig. 29). No pronghorn were observed feeding in snow >15 cm deep, and most foraged in <8 cm of snow (Barmore 1981:241, 245, Fig. 30). Significant variation in habitat selection was observed within and between years, a fact that Barmore (1981:241, 246) attributed to (1) varying environmental conditions, and (2) disproportionately high mortality during 1967–1968 among pronghorns wintering west of the Gardiner River, where "essentially all the areas of old fields and considerable sagebrush grassland occurred."

More recently, pronghorn habitat use also has been monitored on areas outside YNP. During the winters of 1996–1997 through 2000–2001, pronghorn activity outside the park accounted for an estimated 13–51% of total habitat use during mid-November to mid-March (Caslick and Caslick 1997, 1998, 1999, 2000, 2001). However, such figures may underestimate the importance of these habitats for 2 reasons. First, the importance of habitats outside the park was not constant throughout the 4-month monitoring period. For every year monitored, Caslick and Caslick (1997, 1998, 1999, 2000, 2001) documented at least one 4-

week period in which estimated use of habitats outside YNP exceeded 40% of total use, and during December, 2000, exogenous habitats received an estimated 68% of total use. Second, the importance of habitats outside YNP varies among years. Major movements out of YNP in response to severe conditions were reported for pronghorns during the winters of 1897, 1908, 1910, 1911, 1917, 1939, 1968, and 1985 (Anonymous 1897, 1910; Lindsley 1897; Superintendent 1910, 1911; Murie 1940; Barmore 1970; Singer 1988). Although many of these movements took place before the park boundary was moved to include the BLA in 1932, there is little doubt that habitats outside the park remain vital in some years. Barmore (1970) indicated that all but 40 of an estimated 210 pronghorns left the park during the severe winter of 1967–1968, and that "[t]his exodus plus associated [42%] reduction in herd size emphasizes the current importance of lands outside the park to the herd's maintenance and wellbeing." Singer (1988) similarly wrote that,

> "In November–December of 1985, about 90% of the pronghorn herd migrated north of Yellowstone National Park due to heavy snows. Antelope remained out of the park for about three weeks until the snows began to melt. These migrations out of the park have occurred at periodic intervals (Scott 1987), and the movements may be critical to the herd's long-term survival (Barmore 1981; Houston 1982:168)."

Recent habitat changes outside YNP have not been thoroughly studied or documented, but may have affected pronghorn distributions and habitat use patterns. During 1981–1988, there was a net gain of 190 acres of irrigated land available to wildlife on the RTR (Francis 1987). Affected areas included Cutler Meadow (100 irrigated acres added in 1982), Beattie Gulch Meadows (45 irrigated acres added in 1985), and Electric Meadow (50

irrigated acres added in 1987 or 1988) (Francis 1987; Chris Kelley, The Church Universal and Triumphant [CUT], pers. commun.). Changes other than irrigation also occurred. For example, Singer (1988) observed that, "[i]n 1983, the [Royal Teton Ranch] plowed and reseeded two fields near Spring Creek, to which 20–25 antelope were attracted each summer." Subsequent complaints from the RTR resulted in pronghorn damage control hunts beginning in 1985 (see Demographics and Management).

Recent monitoring has included efforts to assess habitat use patterns on lands outside YNP. Of the 42% of pronghorn use-days observed outside YNP during 1996–1997, 43% were in irrigated hay or fenced pastures, 35% were in grass/shrub habitats, and 22% were in grass/forb communities (Caslick and Caslick 1997). Of the 43% of the use observed in irrigated hay or fenced pastures, most presumably was in fenced pasture, as it was later reported that observations over multiple years consistently indicated little use of cultivated or irrigated croplands, and continued use of grass/shrub and grass/forb habitats (Caslick and Caslick 1998, 1999, 2000). These findings underscore the importance of pronghorn winter habitats outside YNP, but provide no information about pronghorn use of such habitats during other seasons. Also, the various analyses by Caslick and Caslick did not consider habitat availability and, therefore, do not support inferences about habitat preference or selection.

In addition to documenting habitat use patterns, Caslick and Caslick (1997) considered effects of bison management activities on pronghorn winter distributions. They noted that during "times of high human activity, pronghorns were strikingly absent from the entire [Stephens Creek] area, for at least one-half mile around the corrals" (Caslick and Caslick 1997). Their observation is similar to earlier comments regarding effects of trapping

on pronghorn distributions. Following trapping during the fall of 1946, for example, “many of the pronghorns moved to other range sectors where they remained for several weeks,” and some “were reported to be in an area several miles north of the usual range” (Anonymous 1946). An important difference, however, is that trapping in 1946 was directed at reducing pronghorns, not bison. Caslick and Caslick (2000, 2001) further suggested that increased use of Beattie Gulch by hunters, following public acquisition of that area, might have displaced pronghorns from sage habitats west of the park boundary at Reese Creek.

Observations also suggest that pronghorn distributions on winter ranges in or near YNP may have shifted over time. Caslick and Caslick (2000) reported that, for six consecutive winters and in contrast to reported distributions during the 1960s, pronghorns were not observed on Target Flats or the northern slopes of McMinn Bench before mid-March. Barmore (1981:Table 105) confirmed that this general area was used regularly by wintering pronghorns for over a century. Caslick and Caslick (1999:6) also commented on the lack of recent pronghorn sightings north of the Yellowstone River, noting that “in the 1960s a few were seen outside Yellowstone in the vicinity of Gardiner airport and west of Bear Creek.” Murie (1940:87) similarly reported pronghorn sightings “on the bench lands outside the park north of the Yellowstone River in the vicinity of Bear Creek,” but noted that “[i]t was unusual for this species to be found here even though the range is better than within the park." It is unclear, therefore, whether pronghorn distributions in the Bear Creek area have changed appreciably.

In 1989 an advisory committee was convened to advise YNP on pronghorn research and management. The committee recommended 2 major lines of research regarding habitat use (Anonymous 1990): (1) determine the quantity and quality of food and cover needed by

pronghorns, and (2) measure the quantity and quality of food and cover available to pronghorns. Results are pending from a study of pronghorn winter habitat use begun in 2000 under the direction of Dr. R. A. Garrott, Montana State University. Other research proposed by the committee generally has not been pursued, including recommended studies of yearlong food preferences and availability, interspecific dietary overlap, interannual differences in food habits, nutritive values of major forage species, distributions of critical cover (e.g., fawning areas), yearlong habitat use and selection, habitat classification and mapping, long-term trends in vegetation cover and production, and effects of humans and other species on pronghorn habitat use patterns (Anonymous 1990).

DEMOGRAPHICS AND MANAGEMENT

Overview

Information regarding pronghorn counts, population estimates, and artificial removals during 1877–2001 is summarized in Appendix A. In developing this summary I relied heavily on Barmore's (1981:Table 105) compilation, with some corrections and additions. Dr. M. D. Scott also updated Barmore's (1981) compilation, apparently reexamining many of the original sources and locating additional information. But details of Scott's work are known only from a digital spreadsheet (Scott 1994) that contains no written summary and does not reference sources, making it difficult to judge the quality of Scott's (1994) information. Apparent population trends were broadly comparable, regardless of who compiled the data. However, differences in details affect the amount of "noise" around those trends, a fact that has important implications for viability analyses (see Population Viability, below).

Counts, estimates, and removal data are summarized in the following sections. These

should be interpreted cautiously. For example, I uncovered "counts" for 1889 and 1890, and evidence of artificial removals in 1949–1950 that were not included in the compilations of Barmore (1981) or Scott (1994), and I expect that further work would yield additional information. Also, none of the estimates or counts can be regarded as unbiased or statistically rigorous. In many cases they are not even strictly comparable, either spatially or temporally. Some counts were conducted during the fall, while many others were conducted during late-winter or early-spring; some counts included areas outside the park, while others did not; and some counts were made under poor conditions, causing them to be highly incomplete (Barmore 1981).

Despite their limitations, I believe the data presented in this section give a useful indication of long-term pronghorn trends in YNP. Following are detailed discussions of pronghorn counts and estimates in YNP, interwoven with a timeline of events deemed important in interpreting the history of this population. I have divided the discussion into 5 time periods that reflect major shifts in park management. I conclude this section with a discussion of Goodman's (1996) viability analysis, which has greatly influenced recent perceptions about the long-term risks faced by this population.

1872–1885

Congress established YNP in 1872. No counts or estimates of pronghorn numbers are available for this early period, but reports indicate that the park's population initially numbered in the thousands (Skinner 1922*a*, *c.* 1924). Unfortunately, thousands also were slaughtered. Angler (1883) wrote that "antelope of the Yellowstone Valley have been nearly exterminated" and provided figures indicating that over 12,000 pronghorn skins were shipped from Bozeman in 1874 alone. Focusing on pronghorns in YNP, Skinner (*c.* 1924:7) wrote

that "[f]rom 1872 to 1883 it is reported that antelopes were killed each year in the park 'by the thousands.'" By 1883, the slaughter of antelope had abated, "but this [was] the result more of the scarcity of the game than of any respect felt by the skin hunters" (Anonymous 1883*b*). By order of the Secretary of the Interior, hunting in the park was prohibited in 1883 (Anonymous 1883*a*), "but considerable market hunting apparently continued until an ineffective and understaffed civilian administration was replaced by the U.S. Army in the summer of 1886" (Houston 1982:11). During this same period, both hunting and poisoning impacted predator populations. "Wolves and coyotes were reported abundant in 1870, but scarce in 1880 because of poisoning activities" (Murie 1940:11).

1886–1917

Arriving in 1886, the U.S. Army provided the first real protection for wildlife in YNP. Park policy toward pronghorns during this period was clearly aimed at increasing population size. Tactics for doing so evolved over time, but focused on limiting predation and providing supplemental feed.

Efforts to limit predation on pronghorns took various forms. Initially, the Army focused on enforcing the prohibition against hunting in the park. Also, by 1887, soldiers were herding pronghorns back into the park to prevent them from being killed in areas north of the boundary (Anonymous 1887*a*,*b*). In addition to limiting predation by humans, the Army took an increasingly active role in predator control, but attitudes varied greatly among years. Murie (1940:12) reported that "Supt. Moses Harris in his annual report of 1887 was not greatly concerned over the depredations of predators." By 1889, however, "the new Superintendent, Capt. F. A. Boutelle, recommended control of predators" (Murie 1940:12). In 1896, Superintendent Anderson ordered some coyotes killed, but apparently limited the

scope of that order (Murie 1940:13). In 1899, the annual report (cited in Murie 1940:14) stated that poisoning "will be tried during the winter," but the following year (1900) Superintendent George W. Goode "appeared to be little concerned about coyote predation" (Murie 1940:14). By 1905, however, a long-term coyote control program was in place that included shooting, trapping, and poisoning (Fig. 3) (Pitcher 1905, Anonymous 1910, Lindsley 1922, Murie 1940:14–15).

Counts and population estimates from the late 1800s, together with anecdotal assessments, suggest the pronghorn population increased almost immediately after the Army began protecting park wildlife in 1886 (Fig. 3) (Appendix A). Records indicate an increase from an estimated 200 animals in 1887 to a minimum count of 323 in 1890 (Anonymous 1887*a*; Hofer 1889*a*, 1890), while Skinner (1922*a*:92) described the population as "[n]umerous, and on the increase" by 1891. Thereafter and until 1900, estimates ranged between about 500 and 1,000 animals, with peaks of 700–1,000 animals in 1891, 1896, and 1899 (Fig. 3, Appendix A).

Although Army protection undoubtedly led to increased pronghorn numbers, a detailed interpretation of pre-1900 estimates is greatly confounded by lack of population closure, as historical migration patterns probably had not been eliminated by then. Consider, for example, the 1891 estimate of ≥800 animals due to Hofer (1891*b*), who wrote:

> "There are about 250 antelope on the flat across Gardiner River from the town. Several large bands are on the hillsides between Hellroaring and Slough Creek. Others are about Junction Butte and the Blacktail country. There cannot be less than 800 antelope in the Park."

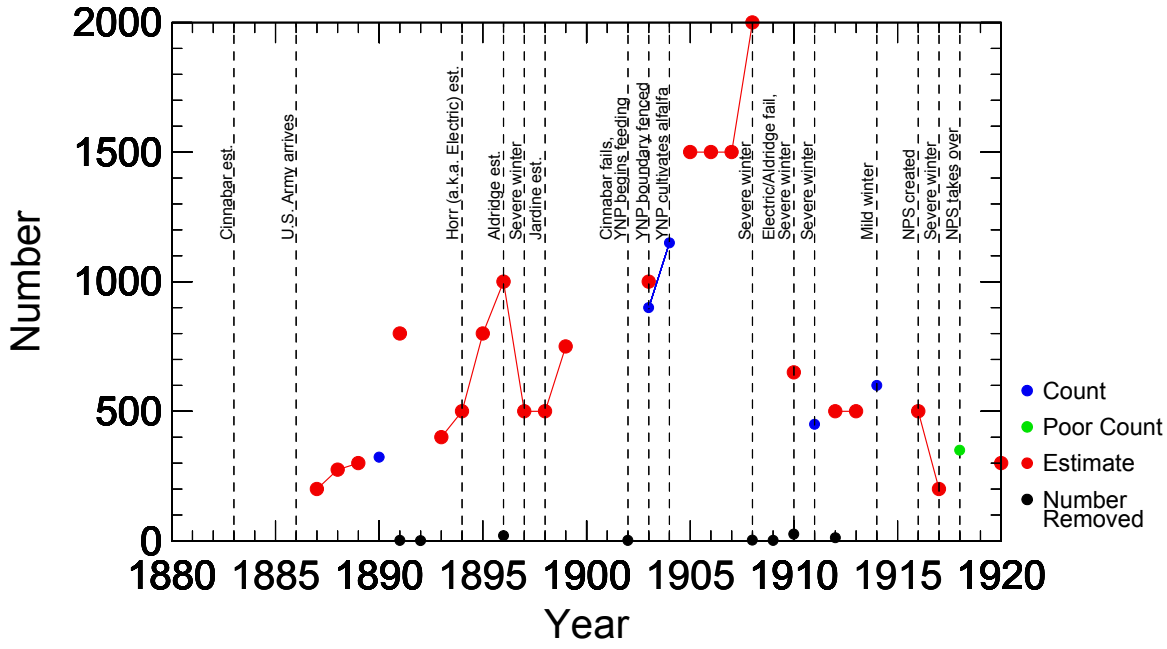

Fig. 3. Pronghorn population counts, estimates, and removals in Yellowstone National Park, 1880–1920, together with comments (see Appendix A for details). A "Poor Count" is one that was labeled as such in the historical record. Notable events that occurred before 1880 included the creation of Yellowstone National Park (1872) and establishment of the town of Gardiner (1880). At the time the park was created, it was estimated that pronghorns numbered in the thousands (Skinner 1922*a*).

Dated March 10, this account clearly is based on observations made during spring migration and, thus, may have included animals that wintered north of the park. Alternatively, the fact that pronghorns were widely distributed in the park by March 10 suggests that there was lower-than-average snowfall for that winter, combined with an early spring. Under such conditions, a greater-than-usual proportion of the herd may have wintered in the park, rather than migrating northward. Under either scenario, it is clear that large year-to-year fluctuations in population estimates could have been caused by immigration to or emigration from the park — processes that have little to do with changes in the underlying population size.

To improve pronghorn nutrition, the park began artificial feeding experiments, apparently in 1902. Before then, authors that mentioned feeding conditions (e.g.,

Anonymous 1887*a*, Hofer 1887*b*, Anonymous 1901) consistently failed to mention artificial feeding. In 1902, however, "[a]s a matter of experiment...a few bales of alfalfa hay were scattered about the parade ground" (Anonymous 1905*b*), and a Field and Stream article stated that "Major Pitcher will feed the antelope when they require it" (Hofer 1902). This program expanded quickly. In the summer of 1904, YNP planted and irrigated 50 acres of alfalfa inside the park near Gardiner, and soon was harvesting about 100 tons/year (Pitcher 1905, Anonymous 1906*a*). With the additional resources provided by the feeding program, and in combination with predator control, pronghorn population estimates doubled from 1,000 in 1903 to 2,000 in 1908 (Fig. 3). Barmore (1981:88) wrote that "[e]stimates of 1,000–2,000 [pronghorn] between 1903 and 1908 probably refer to summer rather than winter populations, which were apparently half or less as large." His interpretation is contradicted, however, by first-hand accounts clearly indicating that these were the numbers of animals that *wintered* in the park, and that access to traditional wintering areas down the Yellowstone Valley had, by this time, been largely cut off (see Anonymous 1904, 1905*a*, 1905*b*, 1906*a*, 1906*b*; Pitcher 1905).

The alfalfa-fed increase in the pronghorn population ended abruptly with a series of harsh winters (Nelson 1925). Because of ambiguities in some accounts, I found it difficult to be entirely certain of dates and recommend a detailed review of the weather record. However, severe winters appear to have occurred during 1907–1908, 1909–1910, 1910–1911, and 1916–1917 (Hofer 1908*a*; Superintendent 1910, 1911; Anonymous 1910, 1913; Murie 1940:101, quoting Bailey 1930:30; Barmore 1981:Table 105). As expected, population counts and estimates tended to decline for these years. For 1907–1908, no decline was seen. However, the estimate of 2,000 animals apparently was obtained early in the

winter and the decline occurred later when “all but 25 escaped through the park fence below Gardiner and went down to the lower valleys, where at that time they were unprotected, and many never returned" (Murie 1940:101, quoting Bailey 1930:30).

1918–1945

The National Park Service (NPS), newly created in 1916, took control of YNP in 1918 (Anonymous 1997). Pronghorn counts and population estimates remained relatively low (<400 animals) for several years thereafter. There was, however, evidence of an increase during 1922–1925, as counts steadily climbed from 253 to 417 animals (Fig. 4, Appendix A). Interpretations are confounded by the lack of count data for 1926–1928, but counts increased from 510 animals in 1929 to 668 in 1932 (Fig. 4, Appendix A), suggesting an overall increasing trend for the decade 1922–1932. Counts declined during 1934–1936, and estimates declined during 1936–1937. Counts also were notably low in 1942 and 1944, although estimates for those same years showed little change.

Interpretations of counts and estimates for this period are confounded by the many changes, both natural and man-caused, that occurred during this time. The NPS initially continued the predator control and, presumably, feeding programs begun by the Army (Murie 1940, Fig. 5). Feeding was expanded as important winter ranges were acquired from private landowners and cultivated starting in 1925 (Whittlesey 1995). These same areas were annexed to the park as the BLA in 1932 (Whittlesey 1995). In 1933, however, the park began to phase out artificial feeding, and in 1934 the program was terminated. Predator control ended in 1935 (Fig. 5). Prolonged drought during the early- to mid-1930s dramatically affected range condition (Grimm 1937, as quoted by Houston 1982:424–425) and may have contributed to a decline in big sagebrush (Bauer 1938, as quoted by Houston

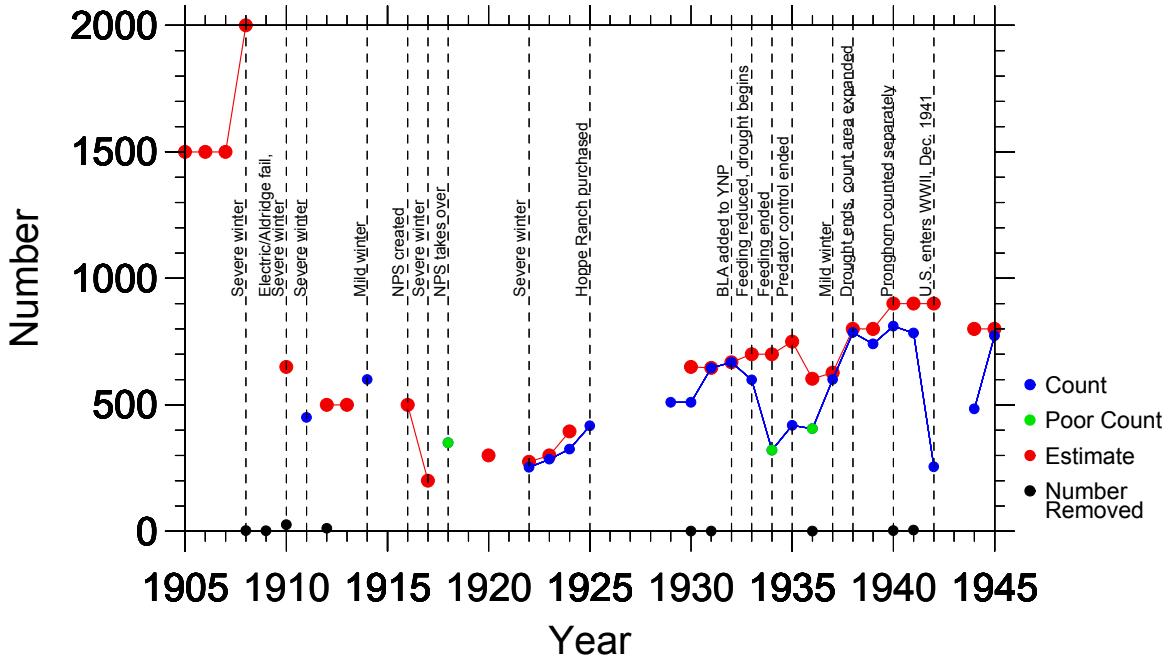

Fig. 4. Pronghorn population counts, estimates, and removals in Yellowstone National Park, 1905–1945, together with comments (see Appendix A for details). A "Poor Count" is one that was explicitly labeled as such in the historical record.

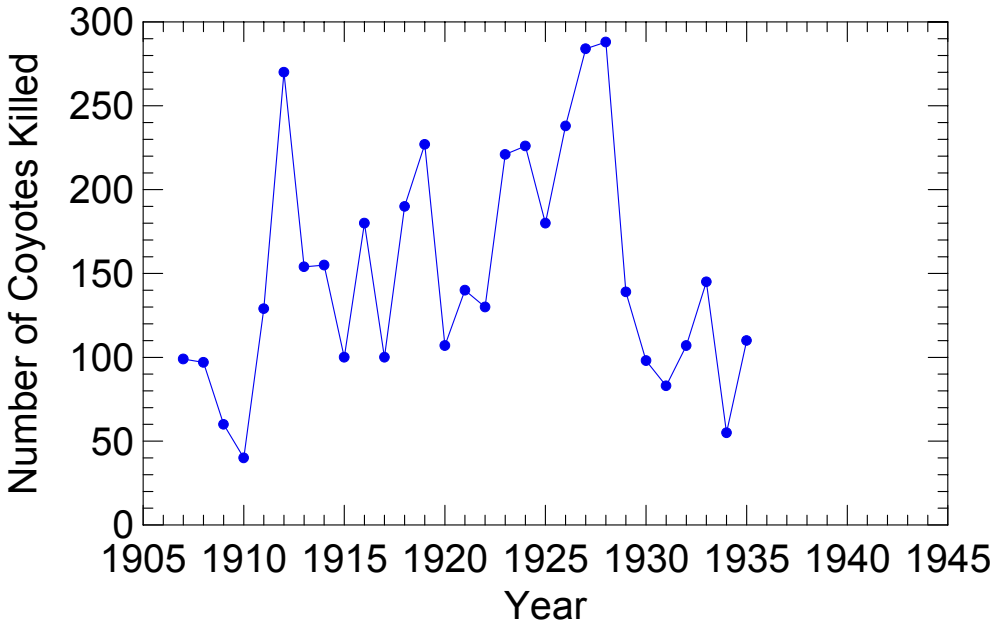

Fig. 5. Distribution of deaths for the 4,352 coyotes killed in Yellowstone National Park during 1907–1935 (from Murie 1940:15).

1982:425). Count completeness likely improved in 1937 as the count area was expanded to include areas outside the park, and again in 1940 when the park began to survey pronghorns separately (Barmore 1981). However, count completeness fell dramatically as the park experienced a personnel shortage during 1941–1945, due to U.S. involvement in World War II. Weather records (which I did not review) might also show a correlation between low counts during the early 1940s and winter severity (D. Houston, pers. commun.).

Previous interpretations of pronghorn population trends during this time have accounted for only some of these factors — sometimes in ways that do not jibe with either the count data or the chronology of events. For example, Houston (1982, citing Barmore 1981) wrote that,

> "Ground counts suggest stable winter populations of 500–700 pronghorns from 1930 to 1937. The pronghorn population increased to 600–800 from 1938 to 1947 after addition of private land to the park and removal of a boundary fence increased their winter range."

I offer a different interpretation. When the NPS assumed control of YNP, the pronghorn population had already been greatly reduced by a series of severe winters during 1908–1917. Following another harsh winter in 1921–1922 (Heller 1925), the pronghorn count was at a then-record low of 253 animals. Increased counts during 1922–1925 probably reflected normal population recovery from these events. Purchase of the Hoppe Ranch in 1925 marked the beginning of a series of important land acquisitions that culminated in annexation of the BLA in 1932, but there is no reason to believe that effects of these acquisitions on the pronghorn population were delayed until 1932, as the Game Preservation Company made the

lands available for park use immediately after purchase (Whittlesey 1995). Pronghorn carrying capacity may have increased somewhat in 1933 as fences and buildings in the BLA were razed (Anonymous 1934, 1936), but many of the benefits of annexing the BLA likely accrued during 1925–1932 as the lands were purchased. Overall, I suggest that increased pronghorn counts during 1925–1932 were fueled, at least in part, by: (1) continued population recovery from the series of harsh winters, (2) increased winter range availability, and (3) continued feeding and predator control programs. Weather records during this period should be reviewed for additional explanatory variables. Pronghorn counts and estimates dipped during 1933–1937 (Fig. 4). Although counts in 1934 and 1936 were considered poor, I note that this was a period of severe drought on the northern Yellowstone winter range (Grimm 1937, as quoted by Houston 1982:424–425). Given negative effects of drought on big sagebrush (Anderson and Inouye 2001) and the importance of sage to wintering pronghorns, it is reasonable to suggest that the drought negatively affected pronghorn numbers. Interpretations regarding the post-drought population are confounded by changes in counting protocols (Fig. 4, Appendix A), but it seems likely that, during 1938–1945, the population was relatively stable at a size equal to or, perhaps, somewhat greater than its pre-drought level. The observed decline in pronghorn counts during World War II was likely due to reduced observer effort rather than a real decline in the underlying pronghorn population, although a detailed review of the weather record might alter this interpretation somewhat.

1946–1967

Pronghorn policy shifted dramatically when, in the summer of 1946, YNP approved a plan to reduce the population to 400 animals (Barmore 1981:Table 105, citing Anonymous 1946), thereby initiating a long-term decline in pronghorn numbers (Fig. 6). By 1950, further

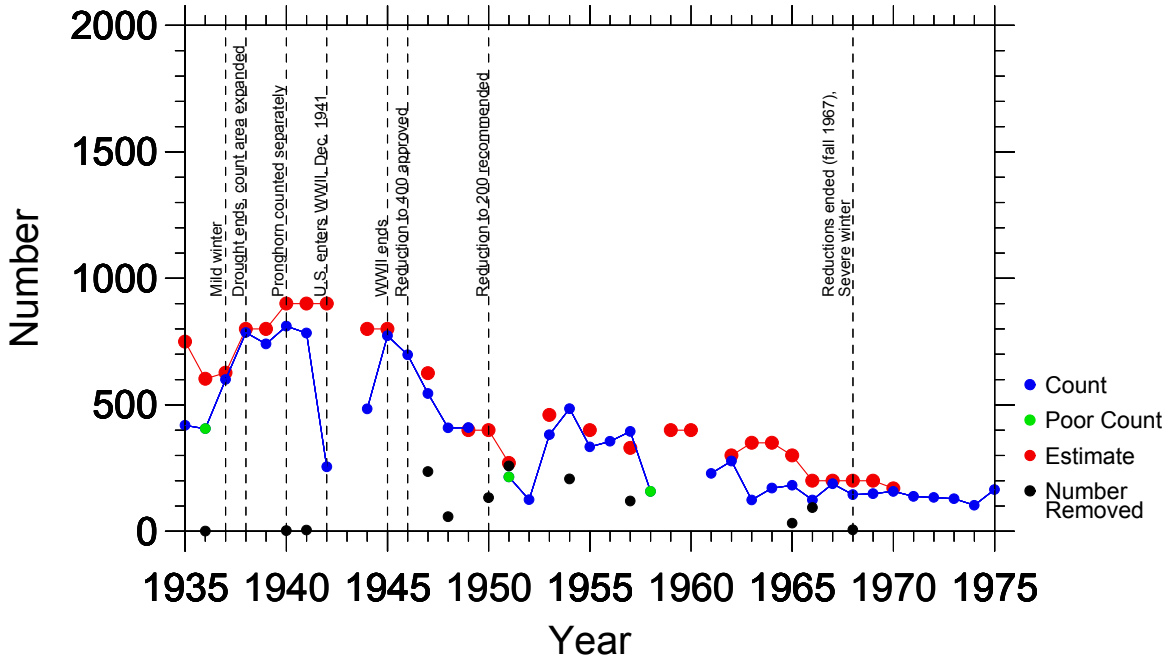

Fig. 6. Pronghorn population counts, estimates, and removals in Yellowstone National Park, 1935–1975, together with comments (see Appendix A for details). A "Poor Count" is one that was labeled as such in the historical record.

reductions were recommended, based on studies that "show[ed] that not over 200 pronghorn should be retained until seriously over-used winter range improves" (Barmore 1981:Table 105, citing Anonymous 1950*a*). By 1953, herd reduction to 100–125 animals was planned (Anonymous 1953, Hamilton 1953). The target population size apparently remained in this range until the reduction program ended in 1967 (Howe 1965*a*, McLaughlin 1965).

At least 1,144 pronghorns were removed during the 1947–1967 herd reduction program (Appendix A). Scott (1988) tallied 1,015 removals during this period, but apparently did not include 133 animals transplanted to Nevada in 1950 (Scott 1994, Anonymous n.d.). I cannot account for the remaining discrepancy of 4 animals. Also, I emphasize that 1,144 should be regarded as a minimum, as I seldom found evidence that a reduction did *not* occur during those years for which no removals are listed.

1968–2001

After the reduction program ended, pronghorn counts remained relatively stable for 15 years (1968–1982), fluctuating between 102 and 165 animals (Fig. 7, Appendix A). Concern over "precariously low numbers" led Houston (1973) to recommend that the population be augmented by a "reintroduction of 100 animals." Superintendent Jack Anderson pursued this recommendation (Freeman 1973), but apparently it was never implemented. Counts climbed to 310 animals in 1983 and peaked at 588 animals in 1991. During this period of growth the only major decline followed the post-fire winter of 1988–1989 when the count fell 17%, from 495 to 411. However, it is unclear whether the 1988–1989 count indicated a real change in population size, as it was considered a poor count, probably due to dry conditions resulting in a scattered distribution of animals. In 1992 and 1993, counts declined to 536 and 439, respectively. No count was made in 1994. The count then fell to 235 in 1995, and subsequent counts have remained relatively stable at 204–235 animals.

Causes of population trends during this period are unclear. Scott (1988) reasoned that even the decline in pronghorn numbers seen during 1946–1967 was not due to YNP's reduction program, as evidenced by density-dependent responses in 1951, 1954, and 1966, and by the fact that "the slide continued for 15 years after the removal program stopped in 1967." Instead, Scott (1988) maintained that, based on "[a]nalysis of historical management records and climatological data," 5 major interacting factors have historically determined pronghorn population trends: (1) November–March precipitation, (2) access to native winter range, (3) availability of hay and grain crops, (4) June precipitation, and (5) total annual precipitation available to food plants. Scott (1988) further concluded that:

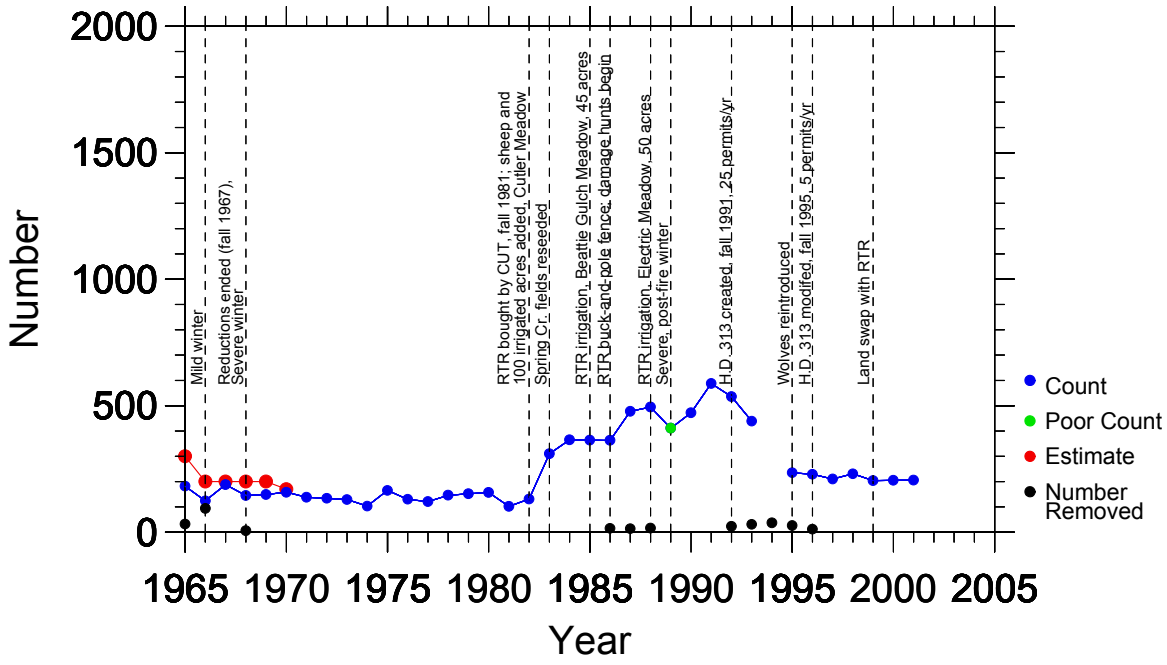

Fig. 7. Pronghorn population counts, estimates, and removals in Yellowstone National Park, 1965–2001, together with comments (see Appendix A for details). A "Poor Count" is one that was labeled as such in the historical record.

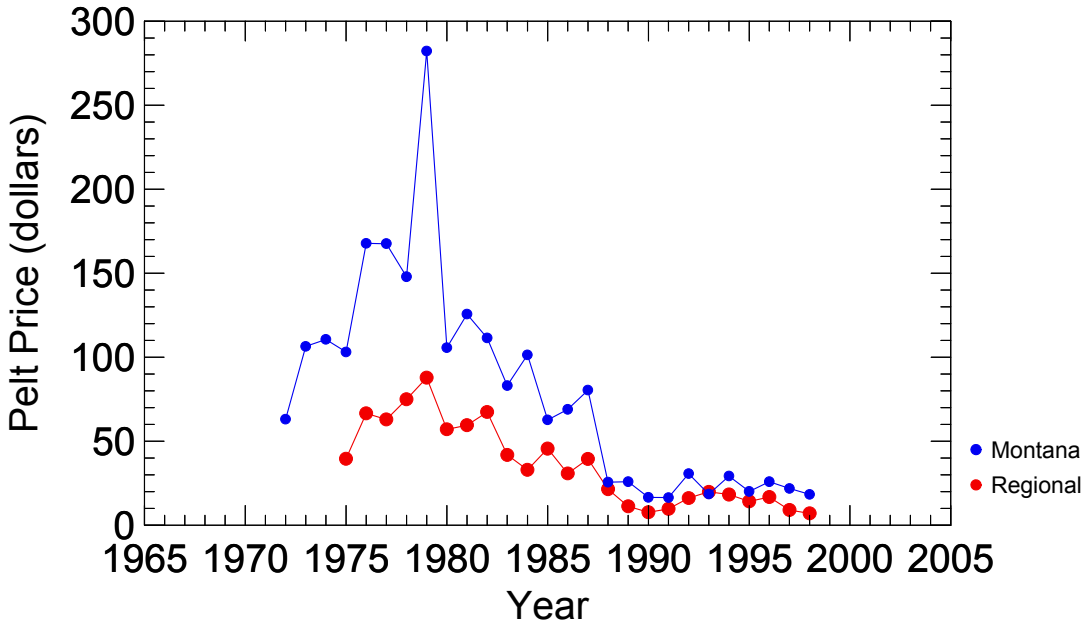

Fig. 8. Average coyotes pelt prices for Montana (Appendix B) and for the region including Montana and Wyoming (Appendix C), 1972–1998. Figures are adjusted for inflation and are given in 2000 U.S. dollars.

> "When three or more of these five factors were favorable for a number of consecutive years, the herd increased or maintained a high population level. When three or more factors were neutral or unfavorable, the herd declined or maintained a low population level. During any given time period, only one limiting factor may have been most decisive."

Unfortunately, Scott's (1988) results are known only from a 1-page abstract; thus, his data and methods, as well as details of his reasoning are beyond meaningful review. Because an analysis of weather data was beyond the scope of this review, I did not attempt to independently test Scott's conclusions, but do recommend further study of possible relationships between population trend and weather.

Another hypothesis regarding population trend is that numbers began to increase in 1983 due to increased predator control near the park boundary, prompted by high pelt prices (J. Mack, NPS, pers. commun.). According to this hypothesis, pronghorn counts should be positively correlated with coyote pelt prices, perhaps with some reasonable time lag. However, pelt prices began to climb by at least 1973 and peaked in 1979 (Fig. 7), 4–l0 years before pronghorn counts began to increase. Visual comparison of Figs. 7 and 8 suggests that, although trends in pelt prices and pronghorn counts share a similar overall shape, the chronology of pelt prices is roughly 10 years ahead of the chronology of pronghorn counts. Given the reproductive potential of both coyotes and pronghorns, it is difficult to imagine a biological explanation for such a time lag. However, it is possible that prolonged control may have been necessary before an effect was evident. Also, the RTR ran domestic sheep from 1982 until the early- to mid-1990s, and with the sheep came opportunistic control of

coyotes (C. Kelley, CUT, pers. commun.). Thus, RTR activities may have influenced coyote densities near the park boundary, independently of pelt prices.

Land-use changes during 1981–1991 may have increased pronghorn carrying capacity. The RTR borders YNP north of Reese Creek and contains areas used by a large part of the pronghorn population at various times of the year (see Distribution and Habitat Use). The RTR was purchased by CUT in 1981. By 1987, "[t]he total amount of irrigated fields on the [RTR] available for wildlife winter range use near the Park [was] increased a total of at least 190 acres" (Francis 1987). Increased irrigation included 100 acres at Cutler Meadow (added in 1982), 45 acres at Beattie Gulch Meadows (added in 1985), and 50 acres at Electric Meadow (added *c.* 1987/1988) (Francis 1987; C. Kelley, CUT, pers. commun.). In addition, fields near Spring Creek were plowed and reseeded in 1983 (Singer 1988). Complaints from the RTR resulted in damage control hunts beginning in the fall of 1985, and suggest that pronghorn use of these habitats may have been substantial. Under this hypothesis, irrigation of Cutler Meadow is the necessary explanation for increased pronghorn numbers in 1983 because irrigation had not been expanded to the other areas at that time. The explanation does not appear to be a viable one, however. Singer (1988:10) reported that "[i]n the winter of 1985–86 and 1986–87 a small group of 13–15 antelope colonized winter range on private land near Cutler Lake." However, I found no record of earlier use and it is not clear that pronghorn use of Cutler Meadow was substantial enough to account for a large increase in numbers, as anecdotal accounts have consistently placed most pronghorn use south of Cinnabar Mtn.

Other events have been suggested, implicitly or explicitly, as possible contributing factors in the post-1991 decline in pronghorn numbers. These include: (1) wolf

reintroduction, (2) fencing of the park's northern boundary, (3) disturbance associated with bison management activities, and (4) pronghorn hunting outside the park. The fact that wolves were not reintroduced to YNP until 1995 (Anonymous 1997) — after pronghorn numbers had already crashed — clearly absolves wolves of responsibility for the pronghorn decline. The RTR constructed a buck-and-pole fence along the park boundary in 1986 and Scott (1992) reported that the fence partially inhibited trans-boundary movements by pronghorns. However, population counts continued to mostly increase during the 5 years after the fence was built; thus, there is no prima facie evidence that the fence affected pronghorn numbers. Caslick and Caslick (1997) indicated that pronghorns avoided disturbances associated with bison management activities, which suggests the hypothesis that recent pronghorn trends might be tied to bison-related disturbances in the BLA. However, pronghorn numbers crashed before intensive bison management began. Also, bison management activities along the park's northern border have been minimal since the severe winter of 1996–1997, yet pronghorn counts have not increased (Fig. 7). Hunting pressure apparently increased when antelope hunting district 313 was created in the fall of 1991 and the number of permits increased from 5 to 25. Given the reproductive potential of pronghorns, this level of hunting pressure, by itself, is insufficient to have limited the population (then estimated at over 500 animals). While it might be argued that hunting-related disturbance could have excluded animals from important habitats, it seems unlikely that a fall hunt would have excluded them during a critical period.

An additional hypothesis that emerged from discussions at the Yellowstone Pronghorn Conservation Assessment Workshop is that during recent decades pronghorn trends in YNP have been driven by regional rather than local factors. Count data for Grand

Teton National Park, Wyoming, and Hart Mountain National Antelope Refuge, Oregon, were cited as support for this hypothesis. Numbers of pronghorns recorded in these areas increased during the 1980s, peaked during the early 1990s, then declined precipitously — a pattern quite similar to trends in YNP pronghorn counts (Fig. 9). Although these data provide tentative support for the hypothesis that pronghorn population trends are driven by regional factors, they should be interpreted cautiously. Observations in and near Grand Teton National Park apparently were conducted for the purpose of herd classification (McWhirter 1999). It is not clear that they provide a legitimate measure of population trend. Moreover, associated counts from Hunting Areas 86–90 in Wyoming's Sublette Management Area indicate that the general pattern observed in YNP, Grand Teton National Park, and the Hart Mountain Refuge was not universal. For example, some areas showed relatively steady increases in numbers of animals observed during 1984–1999 (Fig. 9). Overall, no definitive conclusion is possible from these data, but this hypothesis clearly merits further study.

Population Viability

Using Scott's (1994) compilation of historical counts and artificial removals, Goodman (1996) assessed population viability both qualitatively and quantitatively for the YNP pronghorn herd. Details of this work (and the database it relied upon) merit careful consideration, as this assessment has greatly influenced perceptions about the seriousness of risks facing this population.

Goodman's (1996:5) qualitative assessment of population status was that "[t]his antelope population is extremely vulnerable to wide swings in numbers, and the risk of extinction is high." Factors believed to contribute to the high risk of extinction included heavy coyote predation of young, crowding on the winter range, and concentration in one

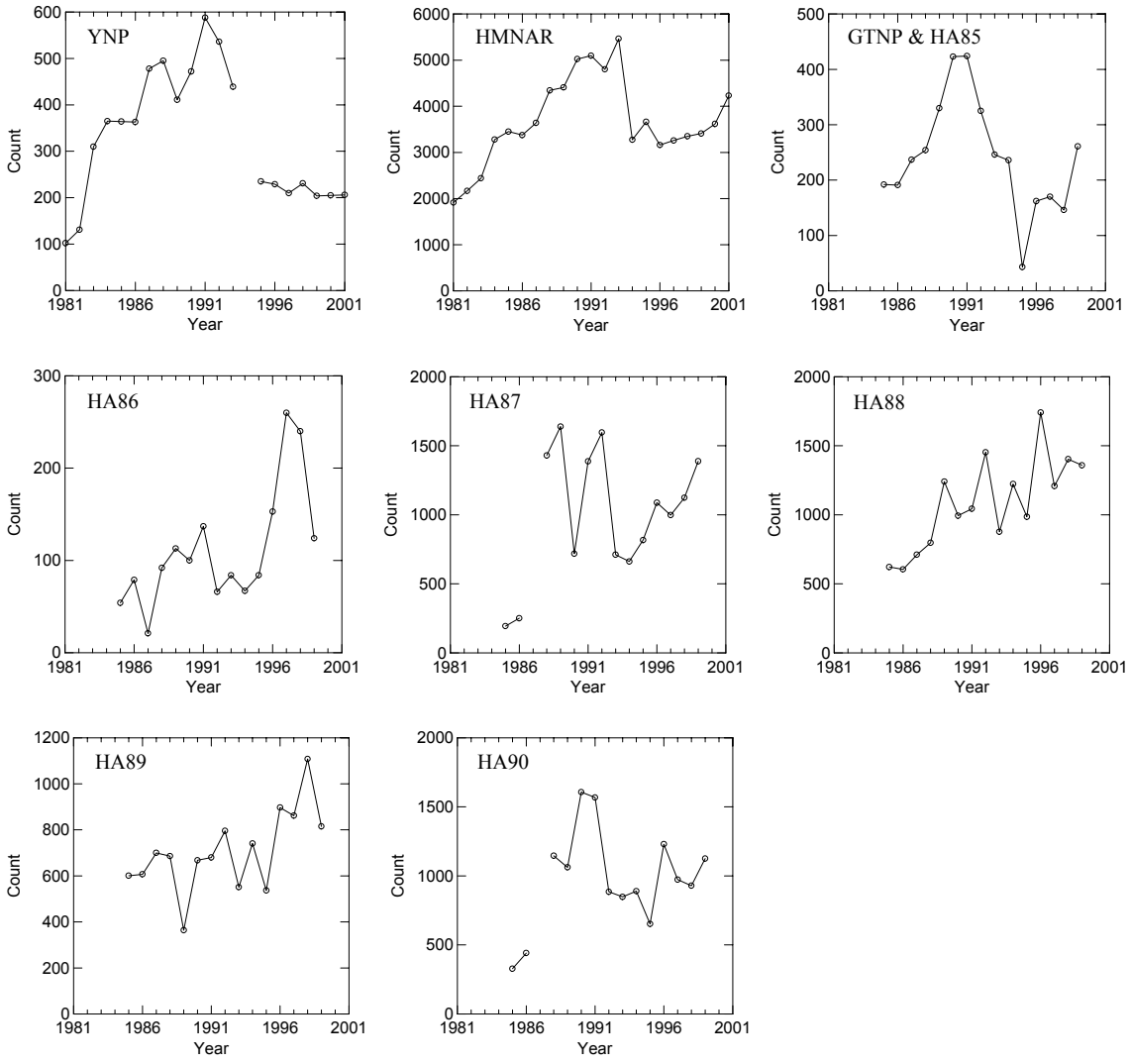

Fig. 9. Trends in numbers of pronghorns counted in Yellowstone National Park (YNP), Wyoming, and on the Hart Mountain National Antelope Refuge (HMNAR), Oregon, and surrounding areas. Also shown are numbers of animals classified during August classification counts in Grand Teton National Park (GTNP), Wyoming, and the surrounding Hunting Area 85 (HA85), as well as Hunting Areas 86–90 (HA86–HA90) in Wyoming's Sublette Management Area.

wintering area, raising "the possibility of disease or freak weather conditions" (Goodman 1996:5). Goodman (1996:5) also noted that "[t]he highest quality winter and spring habitat for this population is the agricultural land outside the park," and that the availability of these lands "is affected by hunting and other attempts to reduce the depredation of herbivores on the property…"

In his quantitative assessment of population viability (Goodman 1996:5) used a random walk process, in which annual multiplicative factors of population increase were drawn randomly and independently from a distribution formed from the observed factors of increase for 1887–1993. Observed values were corrected for recorded removals and were adjusted to achieve a geometric mean of 1.0 so that the model population would not be predisposed to either increase or decrease. Goodman's (1996) analysis yielded a mean time to extinction of 343 years, an 18% probability of extinction within 100 years, and a 41% probability of extinction within 200 years. Assumptions important to Goodman's (1996) findings include:

- No future artificial removals.
- No errors in the compiled census or removal data.
- No density dependence.
- A future distribution of dynamic variation like the historic variation corrected for effects of removals.
- A single, closed population, demographically regulated together.
- A population ceiling of 2000 animals.
- No additional demographic stochasticity at population numbers smaller than those in the historical record.

Now that the State of Montana has proposed to close antelope hunting district 313 in 2002 (MDFWP 2001), it appears that the first assumption will soon be met. However, the remaining assumptions are violated, sometimes seriously. For example:

- As detailed above, known and sometimes significant errors exist in Scott's (1994) census and removal data.

- Relative stability of the population in the face of environmental variation during 1968–1982, and failure to decline from already low numbers in response to harsh winters (e.g., the winters of 1921–1922 and 1996–1997) suggests density dependence.
- To a large degree, annual factors of increase historically were driven by management actions that are no longer operative (e.g., feeding, predator control, and acquisition of habitats in the BLA).
- Early counts and estimates may reflect inter-annual differences in pronghorn distribution rather than population size, as they were based on observations of an open population at the upper elevational limit of that population's winter range.
- The present day herd apparently is composed of migratory and non-migratory sub-populations that exhibit different dynamics (J. Mack, National Park Service, pers. commun.).
- A ceiling of 2000 animals is unrealistically high, being based on figures from 1908 when the population was either open or only recently closed, and numbers were inflated by artificial feeding, predator control, and the practice of containing migratory animals within the park via fencing and/or hazing.

Overall, I believe the assumptions of Goodman's (1996) analysis are violated in a way that exaggerates the true variance in the distribution of factors of annual increase. This would lead to underestimating population persistence time and overestimating extinction risk. It is not clear that legitimate alternative approaches to viability analysis exist using available data. To the extent that a rigorous viability analysis is required, data needs should be identified and sampling protocols implemented to gather the necessary data.

GENETICS

Genetic concerns regarding YNP pronghorns have been raised only recently. In 1989, an outside advisory committee recommended research to "determine genetic relationships between Yellowstone pronghorns and herds outside the park" (Anonymous 1990:8). This item ranked sixth among the committee's recommendations and stemmed from concerns over preserving the genetic purity of Yellowstone's pronghorns, minimizing the risk of inbreeding, and understanding the degree of genetic interchange with and relatedness to adjacent pronghorn populations (Anonymous 1990). There have been 2 attempts to address this recommendation.

Lee et al. (1994) assessed allozyme and mitochondrial DNA (mtDNA) variation among 29 North American pronghorn populations, including the YNP herd. Examining tissues from 11 YNP animals, they reported that mean heterozygosity = 0.006, mean number of alleles per locus = 1.10, and 9.1% of loci were polymorphic (Lee et al. 1994:309, Table 1). These values were less than mean values based on all 29 populations, suggesting that allozyme variation in YNP pronghorns is relatively low. In contrast, YNP animals exhibited the highest mtDNA variation of any population sampled, with 4 haplotypes reported from 7 animals (Lee et al. 1994:313, Table 4). Of those, haplotype J was found only in a single animal from YNP, leading Scott and Geisser (1994:1) to label YNP pronghorns as "genetically-unique." The claim of genetic uniqueness is contradicted, however, by Reat et al. (1999), who observed haplotype J in 16 of 389 pronghorns sampled in Arizona.

Following the study by Lee et al. (1994), Dr. Douglas Scott (YNP) initiated a project with Dr. Ernest Vyse (Montana State University) to address five questions (Scott *c.* 1993):

- Is there less heterozygosity in the Yellowstone herd as compared to the nearest herds

outside the Park?

- Are there significant genetic differences between Yellowstone pronghorns and the nearest other herds that are not descendents of Yellowstone transplants?
- Are there significant genetic differences between migratory and nonmigratory pronghorns in Yellowstone?
- Which, if any, of the herds surrounding the park is the Yellowstone herd most closely related to?
- Is there evidence that animals from outside herds have immigrated to the Yellowstone herd in recent decades?

In correspondence with Dr. Vyse, Scott (1993*b*) indicated he had acquired 132 liver samples for this work. Of these, 116 were provided earlier to Lee et al. (1994), but only 30 were used — leaving 102 samples that were never analyzed. A freezer failure at Montana State University ultimately caused the loss of all samples, and the proposed work with Dr. Vyse was never completed (P. Gogan, USGS Northern Rocky Mountain Science Center, pers. commun.). Ultimately, definitive answers to the major genetic questions posed by the 1989 advisory committee are still lacking.

DISEASE

Numerous diseases and parasites have been documented in pronghorns from YNP. Skinner (*c.* 1922*b*) emphasized concerns about actinomycosis (lumpy jaw), stomach worm, tapeworm, wood tick and scab mite. Rush (1932:105) reported that, of 13 carcasses examined, "[s]ix showed necrotic ulcers in mouth (foxtail mouth); all showed decayed teeth to a greater or lesser degree; four were infested with lung worms *Dictyocaulus sp*., two with intestinal worms *Ostertagia sp*. and *Nematodirus antilocaprae*, one with tape worms

Moniezia sp., all of them with wood ticks." Examining 48 fecal samples from pronghorns shot during YNP's herd reduction program, Todd and Hammond (1967) reported that 21% were infected with *Eimeria antelopcaprae*. Necropsy of a single male pronghorn (Cornish 2000) revealed lung nematodes ("probably *Protostrongylus* sp.") and the respiratory pathogen *Pasteurella hemolytica*, as well as bacterial kidney and spleen infections. Benson (1909) provided the only suggestion that disease may have significantly affected pronghorn population dynamics:

> "…one or two antelope die each week, from what cause is not known, though they do not die violent deaths. The outpost in that vicinity have on one or two occasions seen them stagger and fall and have immediately gone to them and found them unable to arise, dying some two or three hours later. I inspected one of these immediately after death and found a large ulcer on the side of the face, but in two other cases no sore or injury of any kind could be discovered."

In the largest analysis to date, samples from 32 YNP pronghorns were examined for a variety of health parameters. The copy of the report I examined failed to indicate the author or organization responsible for the analysis, but other correspondence leads me to believe that the Wyoming State Veterinary Laboratory might have performed the tests. Trace mineral analyses were normal and gave no evidence of exposure to significant levels of arsenic or lead. Tests revealed that 75% (n = 24 animals) had been exposed to the bacterium *Chlamydia psitacci*, 59% (n = 19) to parainfluenza virus type 3, 9% (n = 3) to bovine viral diarrhea virus, and 3% (n = 1) to bovine respiratory syncytial virus. Tests revealed no evidence of exposure to *Brucella abortus*, bluetongue virus, epizootic hemorrhagic disease,

Mycobacterium avium paratuberculosis, or *Leptospira interrogans*. Only low parasite loads were found. Overall, the report concluded that "there are no obvious health problems detectable by antemortem sampling in this pronghorn herd," but that the high incidence of *Chlamydia* exposure warrants further study.

No clear evidence of management response to pronghorn disease concerns was found in the materials I reviewed. Skinner (*c.* 1922*b*) recommended preventive measures to deal with diseases and parasites, including control of certain exotic grasses, limiting contact between pronghorns and domestic livestock, fencing and fall plowing of irrigated fields within the Park, burning infected pronghorn carcasses, predator control for all native canid species and strict control of domestic dogs, and fencing or burning areas where animals congregate, particularly feeding grounds. Many of his views were later repeated and expanded (Skinner *c.* 1924), but it is unclear as to which recommendations, if any, were actually implemented. Predator control was already underway before 1922. Domestic cattle were removed from YNP, but no indication of the timing of and reasons for removals was uncovered.

As part of an overall research strategy, the outside pronghorn advisory committee, convened by YNP in 1989, recommended limited monitoring for diseases like brucellosis and leptospirosis, as insurance against possible claims that pronghorns might transmit these diseases (Anonymous 1990). They cautioned, however, that such monitoring should not be a major research item (Anonymous 1990). Subsequent analyses generally support their recommendation, as no evidence exists of a population-level health problem and serological tests yielded no evidence of exposure to brucellosis or leptospirosis. An exception is the previously cited analysis, which makes a case for studying effects of *Chlamydia*.

ACKNOWLEDGEMENTS

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Appendix A. Summary of pronghorn maximum counts, estimates, and removals on the northern Yellowstone winter range, 1872–2001.

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1872				"From 1872 to 1883 it is reported that antelopes were killed each year in the park 'by the thousands.' "	Skinner (c. 1924:7)
1877				"Thousands of antelope."	Skinner (1922*a*)
1880				"Abundance of antelope."	Skinner (1922*a*)
1886				"Antelope are here in large numbers."	Skinner (1922*a*)
1887, winter		200		"Large numbers of antelope"	Anonymous (1887*b*), Hofer (1887*a*)
1888, Jan. 1		275			Scott (1994)[1]
1889, early winter		300			Hofer (1889*a*)
1890, Feb. 20	323				Hofer (1890)
1891, Mar. 10		≥800	2	Especially mild winter, at least thru January 9.	Hofer (1891*a*,*b*), estimate and comments; Scott (1994)[1], number removed
1892			1	"Thriving and increasing."	Scott (1994)[1], number removed; Skinner (1922*a*), quote
1893, winter		300–500		"Saw great numbers of antelope, surely 300 (probably 400 or 500)…" "One herd of four to five hundred wintered on Mt. Everts and one or two smaller herds elsewhere."	Anonymous (1893), estimate and first quote; Skinner (1922*a*) second quote
1894, winter		500		"500 wintered on Mt. Everts."	Skinner (1922*a*)
1895, winter		800			Anonymous (1895)
1896, winter		1,000	20	"…great increase of numbers."	Lindsley (1897), estimate; Scott (1994)[1], number removed; Murie (1940:13, quoting Superintendent's Annual Report 1896), quote.

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1897, winter		500		"The large herd of antelope that has always wintered on the flat near Gardiner was driven out during the first severe storm after the crust formed. They passed on down beyond Gardiner and Cinnabar, and many of them have been killed.	Lindsley (1897); Skinner (1922*a*); Murie (1940:13); Anonymous (1897) for comments
1898		500			Anonymous (1898)
1899		700–800			Skinner (1922*a*)
1900				"Increasing."	Skinner (1922*a*)
1901				"all varieties, including antelope,…are increasing…"; "…an easy open winter."	Anonymous (1901), first quote, Hofer (1901), second quote
1902			2	"I do not notice any particular increase in the number of antelope." "Number of bands of from 50 to 100 wintered on slopes of Mt. Everts."	Scott (1994)[4], number removed; Hofer (1902), first quote; Skinner (1922*a*) (see, also, Anonymous 1902), second quote.
1903, fall	900	1,000		"About 900 antelope have already been seen this fall on the northern slope of Mount Everts, and near the town of Gardiner, and I believe the number in the park to be about 1,000."	Anonymous (1903)[5]
1904, winter	1,150[6]			"About 1,150 were seen and counted…" "…the average of several counts showed 1,100 antelope…"	Pitcher (1905) for first quote, Anonymous (1905*a*) for second quote
1905, winter		1,500[7]		"…there are between 1,500 and 1,700 [pronghorns]…"; "The park herd consists of about 1,500 animals and seems to be increasing in numbers quite rapidly."	Anonymous (1905*a*), first quote; Anonymous (1905*b*), second quote.
1906		1,500			Anonymous (1906*b*)
1907, winter		1,500		Scott (1994) gives an estimate of 2,000, but does not list the source of his information	Skinner (1922*a*)
1908, winter[9]		2,000	3	"…about 2,000 were estimated in the park but during the following winter all but 25 escaped through the park fence…and many never returned."	Anonymous (1908) and Skinner (1922*a*), estimate; Scott (1994)[1], number removed; Bailey (1930:30), quote.

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1909			2	"Increasing."	Scott (1994)[1], number removed; Skinner (1922*a*), quote.
1910		600–700[10]	26	Removals included animals sent to the Witchita National Game Preserve, Oklahoma, and the National Bison Range, Montana.	Skinner (1922*a*), estimate; Scott (1994)[1], number removed; Nelson (1925), comments.
1911, Feb.	450[11]			"The snow along their range has been unusually deep, and…they insist on getting over or through the fence…"; "The antelope…are scattered more than usual and so quite difficult to count."	Superintendent (1911), estimate, first quote; Anonymous (1911*a*,*b*), second quote.
1912, ?[12]		500	12	"Estimate based on actual counts or very close observations and are pretty nearly correct."	Barmore (1981, citing Superintendent's Annual Report 1912 and Halloran and Glass 1959), estimate and quote; Scott (1994)[1], number removed.
1913		500		"Increased slightly."	Scott (1994)[1], estimate; Skinner (1922*a*), quote.
1914	600			"The winter of 1913–1914 was one of the mildest ever known in the…Park…"	Skinner (1922*a*), estimate; Anonymous (1914), estimate and quote.
1916		500			Barmore (1981:Table 105, citing Bailey 1930)
1917, spring before fawning		200		"…in 1916, 500 [antelope were estimated in the park herd]. In the spring of 1917 most of these left the park and later, when driven back, only about 200 were accounted for."	Murie (1940:101, quoting Bailey 1930:30)
1918	350			"This was the number seen in one day. '…no special pains were taken to make a complete count of the herd.'"	Barmore (1981:Table 105, citing Superintendent's Annual Report 1918)
1920		300			Barmore (1981:Table 105, citing Superintendent's Annual Report 1920)
1922, spring count	253	275			Anonymous (1931), count; Skinner (1922*c*) and Superintendent (1922), estimate

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1923, spring count	285	300			Anonymous (1931), count; Barmore (1981, citing Superintendent's Annual Report 1923), estimate
1924, Jan. count	325	395			Barmore (1981:Table 105, citing Woodring 1924)
1925, late Apr.	417				Barmore (1981:Table 105, citing Superintendent's Annual Report 1925)
1929, Mar. 29	510				Scott (1994)[1], date; Anonymous (1931), count
1930			1		Scott (1994)[1], first date; Barmore (1981:Table 105, citing Baggley n.d.), counts and estimate; Scott (1994)[1], number removed
Sept. 21, 1929	638[14]				
Feb.	510				
Spring		650			
1931			1		Anonymous (1931) and Baggley (1932), count; Barmore (1981:Table 105, citing Baggley 1931), estimate; Scott (1994)[1], number removed
Feb.	646				
Spring		646			
1932, Apr.	668	668[15]			Scott (1994)[1], date; Tell (1932)
1933, spring	599	700			Barmore (1981:Table 105, citing Anonymous 1936), Anonymous (1933)
1934, Mar. 14–16	321	700		"Incomplete count."	Barmore (1981:Table 105, citing Anonymous 1936), Anonymous (1934), Murie (1940:101)
1935, Mar.	419	750			Scott (1994)[1], date; Barmore (1981:Table 105, citing Anonymous 1936) and Murie (1940:101), count and estimate
1936				"Count by 7 men considered not fully successful."	Barmore (1981:Table 105, citing Skinner 1936), Skinner (1936), and Murie (1940:101), count and estimate; Scott (1994)[1], removal data
Sept. 16, 1935			1		
Apr. 2	406	603			
1937, Mar. 2–3	600	627		"Count by 10 men was one of the most accurate and complete ever taken. Increase over last year reflects better count rather than actual increase."	Barmore (1981:Table 105, citing Barrows 1937)

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1938, Feb. 24	786	800		"Six men, excellent weather, thorough coverage of counting units. Outside count by Forest Service. Antelope are increasing."	Barmore (1981:Table 105, citing Barrows 1938)
1939, Mar. 21–24	741	800		"Park count by 12 men, excellent weather, but animals widely scattered which might account for lower count than year before. Outside count by Forest Service."	Barmore (1981:Table 105, citing Barrows 1939)
1940, Feb. 7	811	900	3	"Pronghorn, deer, sheep counted separately for first time and may have increased count accuracy. Normal to mild winter. Includes 70 reported by Forest Service and ranches near Corwin Springs which wasn't covered." Removal in March.	Barmore (1981:Table 105, citing Skinner 1941); Scott (1994)[1], removal data
1941, Mar. 24	784	900	5	"Though weather and snow not favorable for easy and thorough count, it was considered reasonably successful. Less accurate than 1940. Count by 9 men. Herd size same as in 1940." Removals: 4, spring; 1, Aug. 23	Barmore (1981:Table 105, citing Skinner 1941); Scott (1994)[1], removal data
1942, Mar. 19	255	900			Scott (1994)[1], count; Barmore (1981:Table 105, citing Superintendent's Annual Report 1942), estimate
1943				"Some losses occurred during the winter and 58 carcasses were found during the dead animal count."	Barmore (1981:Table 105, citing Superintendent's Annual Report 1943)
1944					Scott (1994)[1], count; Barmore (1981:Table 105, citing Anonymous 1944), estimate
Mar. 19	484				
Fall		800			
1945, Feb. 21–22	773	800		"Eleven men; probably missed very few."	Barmore (1981:Table 105, citing Anonymous 1945*a*,*b*)
1946, Mar. 26	698			"Favorable counting conditions. Count by 10 men in park was reasonably accurate. Lower count that in 1945 probably due to wider distribution out of park (not covered) rather than reduced numbers. Authority to reduce herd to 400 granted in summer, 1946. Trapping in fall, 1945, caused unusual disturbance."	Barmore (1981:Table 105, citing Anonymous 1946)

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1947			236[16]	"236 trapped in Jan. 1947, 58 on Dec. 16, 1947. During Dec. 16 trapping 12" of heavy, crusted snow at the tree nursery. After January trapping, most pronghorn remained out of park as far as Carbella but returned by March 1." "Estimate is based on census of April 1947 and probable summer increase."	Barmore (1981:Table 105, citing Rogers 1948 for the count, Kittams 1947 for the estimate, and LaNoue 1948 for the reduction); Barmore 1981), first quote; Kittams (1947) second quote
April	545				
Fall		625			
1948, Jan. 6	409		58[17]	"Poor weather; favorable counting conditions; count a fair appraisal of current numbers. Aerial checks during trapping prior to ground count indicated not many more than 400."	Barmore (1981:Table 105, citing Grimm 1948)
1949, Feb. 1	410	400		"Highly successful count. Weather and other conditions unusually favorable. All known pronghorn range covered."	Barmore (1981:Table 105, citing Joffe 1949 for count, Anonymous 1949 for estimate)
1950				"Despite protection, these animals do not appear to increase in number."	Anonymous (1950*b*), estimate and first quote; Anonymous (n.d.), removals and second quote
?		400			
October?			133[18]	"A total of 133 animals were trapped. Twenty head were lost in trap accidents, and 9 others died while enroute to the release site. Fifty-one antelope were released in the southwestern edge of Ruby Valley, Elko County on October 16, 1950. On the same day, an additional 53 antelope were released in the vicinity of Potts Ranger Station in Monitor Valley, Nye County."	
1951				"Livetrapping done Jan. and Feb. Winter range almost snowfree and animals were widely scattered with many much higher than usual. Recent airplane herding partly responsible."	Barmore (1981:Table 105, citing Johnston 1951 for count, Evans 1951 for estimate), first quote; Anonymous (1951), estimate and second quote
Jan.–Feb.			258		
Feb. 21–22	215				
Fall		270		"This figure represents the estimated winter population of the district and is based on last census plus annual increase."	
1952					Scott (1994)[1,19]
Dec., 1951	125				

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1953 Feb. 12 Fall	 382 	 460	 	"Mild, little snow, pronghorn in small bands and scattered, but counters felt they saw nearly all animals and avoided duplication."	Barmore (1981:Table 105, citing Chapman 1953)
1954 Dec. 15, 1953 ~Jan.	 485 	 	 207	"All range to Corwin Springs was covered by 10 men. Count believed to be fairly accurate." "Livetrapping was early in 1954." "On January 13, 1954, a total of 131 antelope were released in Nevada. Seventy-one were released at a site 3 1/2 miles west of the J. D. Ranch in Pine Valley, Elko County. Another group of 60 animals were released on the west side of Smith Creek Valley at a site two miles north of U.S. Highway 50, in Lander County."	Barmore (1981:Table 105, citing Chapman 1953 and Anonymous 1955), estimate, removals, and first and second quotes; Anonymous (n.d.), third quote.
1955 Dec., 1954 Fall	 334 	 400	 	"Trapping tried in early 1955, but unsuccessful."	Barmore (1981:Table 105, citing Anonymous 1955)
1956, Mar. 20–26	356–431			"Helicopter census. Good conditions. Total seen was 356 with possibly 75 more on North end Mt. Everts where separation of bands was questionable."	Scott (1994)[1], dates; Barmore (1981:Table 105, citing Kittams 1956), estimate and quote
1957 Dec. 7, 1956 Feb. 14–15 ?	 395 	 330	 120 	Regarding Dec. count: "Ideal counting conditions." "In February 1957, 120 antelope were removed from the herd by trapping, reducing the previously counted number to 275."	Scott (1994)[1], date and removal data; Barmore (1981:Table 105, citing Kittams 1956), count and first quote; Kittams (1958), second quote
1958	158			"Seven men, poor counting conditions. ' I seriously question the completeness of the recent count, as antelope very probably were dispersed over more area than that…covered…' "	Barmore (1981:Table 105, citing Kittams 1958)
1959, ?		400			Barmore (1981:Table 105, citing Chapman 1960)
1960, ?		400[20]			Scott (1994)[1]
1961, Mar. 17	299			"Helicopter census specifically for pronghorn."	Barmore (1981:Table 105, citing Howe 1961)

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1962				"Helicopter census specifically for pronghorn; 35 min. flying time; coverage to about 1 mile north of park boundary."	Barmore (1981:Table 105, citing Howe 1962*a* for count, Howe 1962*b* for estimate, Management Assistant for YNP 1962 for coverage)
Apr. 4	278				
?		300			
1963					Barmore (1981:Table17), count; Barmore (1981:Table 105, citing Howe 1963), estimate
Apr.	124				
Spring		350			
1964					Barmore (1981:Table 17), count; Barmore (1981:Table 105, citing Howe 1964), estimate
Dec., 1963	171				
Spring		350			
1965				"Partial helicopter census in conjunction with livetrapping of pronghorn." "Livetrapping [of 25 animals] Dec. 16, 1964." "Livetrapping [of 7 animals] Jan. 6, 1965."	Barmore (1981:Table 105, citing Barmore 1965 for count, Howe 1965*b* for estimate)
Dec. 16, 1963			32		
Jan. 5	182–210				
Spring		300			
1966				"Reduction by shooting between summer 1965 and April 1966."	Barmore (1981:Table17), count; Barmore (1981:Table 105, citing Barmore 1966), estimate, removal data, and quote
Jan.	124				
Spring		200			
See comments			94		
1967				"Helicopter census; good to excellent condition; partial coverage outside park; probably included 95% of pronghorn on winter range inside the park."	Barmore (1981:Table 105, citing Barmore 1967*a* for count, Barmore 1967*b* for estimate)
Mar.	188				
Spring		200			
1968				"Reduction by shooting in October 1967." Regarding Mar. count: "Helicopter census specifically for pronghorn. Area outside of park covered to Carbella but not as intensively as inside park. Severe winter had caused many to leave the park; hard to get complete count."	Barmore (1981:Tables 17), Nov. count; Barmore (1981:Table 105, citing Barmore 1968*b*), Mar. count, estimate, removals and quotes
Oct., 1967			6		
Nov., 1967	145				
Mar.	85	200			
Spring					
1969				Regarding Dec. count: "Special pronghorn census from Piper Supercub." Regarding Mar. count: "Special antelope count by Piper Supercub. Partial coverage outside park, but not as intensive as inside."	Barmore (1981:Table 105, citing Barmore 1968*a*)
Dec., 1968	149				
Mar.	133				
Spring		200			

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1970				Special antelope count by Piper Supercub. Partial coverage outside park, but not as intensive as inside.	Barmore (1981:Table 105, citing Bucknall 1970 for estimate), Jan. count, estimate, and comments; Scott (1994)[1], Mar. count
Jan.	158				
Mar. 19	134				
Spring		170			
1971, Apr. 1	138				Scott (1994)[1]
1972, Jan. 28	134				Scott (1994)[1]
1973, Mar. 9	129				Scott (1994)[1]
1974, Apr. 22–23	103				Scott (1994)[1]
1975, Feb. 18	165				Scott (1994)[1]
1976, Apr. 8	130				Scott (1994)[1]
1977, Mar. 15	121				Scott (1994)[1]
1978, Mar. 21	146				Scott (1994)[1]
1979, Apr. 16	152				Singer (1988), Scott (1994)[1]
1980, Apr. 8	157				Singer (1988), Scott (1994)[1]
1981, Mar. 21	102				Singer (1988), Scott (1994)[1]
1982, Apr. 17	131				Singer (1988), Scott (1994)[1]
1983, Mar. 8	310				Singer (1988), Scott (1994)[1]
1984, Mar. 23	365				Singer (1988), Scott (1994)[1]
1985, Apr. 9	364				Singer (1988), Scott (1994)[1]
1986				Removals occurred during damage control hunt due to crop depredation complaints from the Church Universal and Triumphant. 15 permits issued. Numbers removed are (minimum?) estimates.	Singer (1988) and Scott (1994), count; Singer (1986, 1987) and Scott (1991), removal data
Fall, 1985			15[21,22]		
Feb. 28	363				

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1987 Fall, 1986 Mar. 17	478		12–15[21]	Removals occurred during damage control hunt due to crop depredation complaints from the Church Universal and Triumphant. 50 permits issued.	Singer (1988) and Scott (1994), count; Singer (1987, 1988) and Scott (1994, 1991) for removal data
1988 Fall, 1987 Apr. 14	495		16[21]	Removals occurred during damage control hunt due to crop depredation complaints from the Church Universal and Triumphant. 39 permits issued.	Singer (1988) and Scott (1994), count; Singer (1988) and Scott (1994, 1991), removal data
1989, Spring	411			"Not a good count"	Mack (1996)
1990, Mar. 20	472				Scott (1994)[1], Mack (1996)
1991, Apr. 2	588?			"Various file references refer to a total of 522, 588, 591, and 594 on this date. Caslick indicates observation forms total 588 counted."	Anonymous (1997)
1992 Fall, 1991 Mar. 24	536		23	25 licenses issued. Harvest estimated, could not reliably account for take by archers.	MDFWP (1999) and Scott (1994), removal data; Scott (1994), count
1993 Fall, 1992 Apr. 8	439		31	25 licenses issued. Harvest estimated, could not reliably account for take by archers.	MDFWP (1999), removal data; Scott (1994) count
1994 Fall, 1993			37	25 licenses issued. Harvest estimated, could not reliably account for take by archers. No count was conducted this year.	MDFWP (1999), removal data
1995 Fall, 1994 Apr. 7	235		26	25 licenses issued. Depredation hunt removed 17 does and 9 bucks. Late conditions and large decline caused Mack (1996) to assume this was merely a "Poor Count;" an assessment he later revised in light of continued low counts in subsequent years (J. Mack pers. commun., winter 2001).	MDFWP (1999) and Caslick and Caslick (1996), removal data; Mack (1996), count.
1996 Fall, 1995 Mar. 25	229		12	25 licenses issued. Harvest estimated, could not reliably account for take by archers. "…count was conducted under ideal conditions..."	MDFWP (1999), removal data; Mack (1996), count and quote

Appendix A (continued).

Date	Actual Count	Estimate	Number Removed	Comments	Sources
1997				5 licenses issued but harvest estimates are not available. "Count conditions were fair to good. 92% of the pronghorn counted were inside [YNP]…some portion of the population has already migrated eastward."	MDFWP (1999), removal data; Clark (1997*a*), count and quote
Fall, 1996			?		
Apr. 21	210				
1998				5 licenses issued. Harvest estimated, could not reliably account for take by archers. "Good Count."	MDFWP (1999), removal data; Clark (1997*b*), Nov. count; Clark (1998), Mar. count and quote; Caslick and Caslick (1999), estimate
Fall, 1997			?		
Nov. 22, 1997	252				
Mar. 31	231	284			
1999				5 licenses issued. Harvest estimated, could not reliably account for take by archers. "Good Count"	MDFWP (1999), removal data; Clark (1999), count and quote
Fall, 1998			?		
Mar. 25	204				
2000				5 licenses issued. Harvest estimated, could not reliably account for take by archers. "Good Count"	Lemke (MDFWP, pers. commun.), removal data; Mack (2000, 2001), count and quote
Fall, 1999			?		
Apr. 3	205				
2001				5 licenses issued. Harvest estimated, could not reliably account for take by archers. "Fair Count"	Lemke (MDFWP, pers. commun.), removal data; Mack (2001)
Fall, 2000			?		
Apr. 3	206				

[1]Information taken from summary data sheet compiled by Dr. M. D. Scott. Although apparently based on a review of historical records, the summary did not cite the sources of information used.
[2] Scott's (1994) estimate of "~400" animals is less than that of Anonymous (1898), the only other data source located for 1898.
[3] Scott's (1994) estimate of "~600" animals is less than Skinner's (1922*a*) estimate, the only other data source located for 1899.
[4] Scott's (1994) note of a "rapidly increasing" pronghorn herd conflicts with Hofer (1902).
[5] Skinner (1922*a*) (whom Barmore [1981] cited) estimated 1,000; Scott (1994) estimated "~900," but cited no source for his information.
[6] An estimate of 1,150 is generally cited (e.g., Barmore 1981, Scott 1994), but sources suggest this actually was a rough count. Also, Anonymous (1905*a*) lists an average count of 1,100 animals, but Pitcher's (1905) figure of 1,150 is considered to be more authoritative.
[7] Although Anonymous (1905*a*) estimates the herd at 1,500–1,700, I follow previous workers (Skinner 1922*a*, Barmore 1981, Scott 1994) and use the lower figure.
[8] Scott (1994) listed an estimate of "~2000," which may have been based on the statement (Anonymous 1906*b*) that "…about 1,500 of these animals came down to the feeding grounds…and as very few of them died or were lost from any cause, the number this year should be at least 2,000." I follow Barmore (1981) and Skinner (1922*a*) in using the lower figure of 1,500.
[9] Barmore (1981) regarded this (and, more generally, other high counts of the early 1900s) as a summer count. See text for evidence that this estimate was based on animals wintering in YNP.
[10] Scott (1994) lists "~650," apparently taking the average of Skinner's (1922*a*) range of values. The Superintendent (1910) references a herd of 700. Anonymous (1910) states that, of the animals that escaped through the park fence, soldiers at YNP "succeeded in rounding up and returning…some 800 or 900 antelope."

[11] Anonymous (1911*a*,*b*) reports "about 500" pronghorns. However, the Superintendent's (1911) report is accepted here as more authoritative source.
[12] Barmore (1981) lists this as a July count, Scott (1994) describes it as a winter count. Further work to resolve this issue is needed.
[13] Scott (1994) gives the date for this count as December, 1927. Anonymous (1931) describes this as a spring count. Barmore (1981) did not record a count for this year.
[14] Barmore (1981:Table 105) lists this count in 1929, but gives only "?" rather than the month or season. Scott (1994) gives Sept. 21 as the date of this count, which I, therefore, assigned to the 1929–1930 period.
[15] Barmore's (1981:Table 105) estimate of 646 for "Spring" is probably a typographical error, in which the estimate for 1931 was carried over to 1932. Barmore lists a count of 668 for "April" and Tell (1932) lists both the count and estimate as 668.
[16] Kittams (1947) gives a slightly different figure, stating that "[d]uring January–February 1947, 235…animals were livetrapped..."
[17] Barmore (1981:Table 105) includes these 58 animals in the reductions for 1947. Because they were trapped in Dec., 1947, they are listed here with the data for 1947–1948.
[18] This removal was not reported by Barmore (1981) or Scott (1994) and, therefore, was not accounted for in Goodman's (1996) viability analysis.
[19] Counts and estimates for 1951–1952 are particularly confused. Scott (1994) lists a count of 104 (with no season or date) as the "'best' count — usually cited in literature." However, he also lists a count of 125 for Dec. 15, 1951. Barmore (1981:Table 105) does not give a count for this period, but does list an estimate of 270 for fall of 1951. It seems likely that no concerted effort to obtain a reliable count was made during this period.
[20] Barmore (1981) gives no count or estimate for 1960.
[21] Scott (1994) listed many removals during 1985–1994, including: 11 (Nov. 1985), 14 (Nov. 1986), 16 (Oct. –Nov. 1987), 2 (Dec. 1987), 1 (Jul. 1987), 2 (Feb. 1988), 1 (Apr. 1988), 2 (Aug. 1988), 1 (Oct. 1988), 51 (Oct.–Nov. 1988), 1 (Dec., 1988), 1 (Mar. 1989), 1 (Apr. 1989), 1 (Apr. 1990), 1 (May 1990), 4 (Aug. –Sep. 1990), 1 (Jan. 1991), 1 (Jun. 1991), 4 (Aug. –Dec. 1991), 23 (Oct. 1991), 3 (Jan. –Jun. 1992), 2 (Jun. –Jul. 1992), 4 (Mar. 1992), 8 (Mar. 1993), 25? (Oct. 1993; Scott's question mark, not mine), 1 (Oct. 1993), and 1 (Jan. 1994). Scott (1994) did not list causes of removals. Only removals clearly due to depredation hunts were included in the figures in Appendix A, as it was unclear whether other losses were natural or human-caused.
[22] Scott (1994) lists only 11 removals during Nov. 1985.
[23] Scott (1994) lists the maximum count for 1988–1989 as 372 animals observed on Apr. 9, 1989.

Appendix B. Average coyote pelt prices for Montana, 1972–1998, according to the Montana State Office of the USDA APHIS Wildlife Services (Larry Handegard pers. commun.). Corrected prices were adjusted for inflation using the Consumer Price Index (CPI) and the inflation calculator found at http://stats.bls.gov/cpihome.htm, and were standardized to values for the year 2000. Prices are in US dollars.

Year	Average Price	CPI Corrected Price
1972	15.31	63.07
1973	27.44	106.42
1974	31.66	110.59
1975	32.21	103.10
1976	55.43	167.75
1977	58.97	167.57
1978	56.00	147.90
1979	119.00	282.26
1980	50.57	105.68
1981	66.33	125.65
1982	62.44	111.42
1983	48.06	83.09
1984	61.17	101.38
1985	39.17	62.69
1986	43.88	68.94
1987	53.03	80.39
1988	17.60	25.62
1989	18.62	25.86
1990	12.57	16.56
1991	13.00	16.44
1992	25.00	30.68
1993	15.50	18.47
1994	25.18	29.26
1995	17.77	20.08
1996	23.59	25.89
1997	20.35	21.83
1998	17.36	18.34

Appendix C. Average coyote pelt prices, 1974–75 to 1977–78, for the region of the United States that includes Idaho, Montana, and Wyoming. Data were compiled by the International Association of Fish & Wildlife Agencies (Brian Giddings, MDFWP, pers. commun.). Corrected prices were adjusted for inflation using the Consumer Price Index (CPI) and the inflation calculator found at http://stats.bls.gov/cpihome.htm, and were standardized to values for the year 2000. Prices are given in US dollars.

Year	Average Price	CPI Corrected Price
1974–75[1]	12.42	39.55
1975–76[1]	22.12	66.59
1976–77[1]	22.27	62.95
1977–78[1]	28.51	74.90
1978–79[1]	37.22	87.82
1979–80[1]	27.45	57.07
1980–81[1]	31.56	59.47
1981–82[1]	37.94	67.35
1982–83[1]	24.32	41.83
1983–84[1]	19.96	32.91
1984–85[1]	28.61	45.55
1985–86[1]	19.69	30.77
1986–87[1]	26.14	39.42
1987–88[1]	14.79	21.42
1988–89[1]	8.13	11.23
1989–90[1]	5.85	7.67
1990–91[1]	7.68	9.66
1991–92[1]	13.20	16.12
1992–93[2]	16.74	19.84
1993–94[2]	15.76	18.22
1994–95[2]	12.62	14.19
1995–96[1]	15.34	16.75
1996–97[1]	8.42	8.99
1997–98[1]	6.65	6.99

[1]Average price for region that included Alaska, Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Texas, Utah, Washington, and Wyoming
[2]Average price for region that included Arizona, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, South Dakota, Utah, and Wyoming