Sagebrush and ungulate relationships on Yellowstone's northern range

Carl L. Wambolt

Abstract Sagebrush (*Artemisia* spp.) ecology and forage relationships with ungulates are related to the Northern Yellowstone Winter Range (NYWR). The NYWR in northern Yellowstone National Park (YNP) and adjacent Montana is an important area for ungulates. I synthesized research published in peer-refereed and peer-edited literature related to the historical and present associations between ungulates and sagebrush on the NYWR. The NYWR habitats preferred by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) were dominated by sagebrush, and these ungulates preferently foraged on 4 sagebrush taxa. There were significant differences in development between protected and browsed sagebrush at 19 locations across the NYWR. Elk foraging on sagebrush significantly increased utilization and held sagebrush populations below their potential in the absence of other browsing ungulates. Sagebrush had not recovered from burning 10–19 years earlier. Knowledge of sagebrush taxa should provide resource managers important information for management of the extensive NYWR habitats.

Key words *Artemisia tridentata*, big sagebrush, *Cervus elaphus*, elk, mule deer, *Odocoileus hemionus*, winter range, Yellowstone

Big sagebrush (*Artemisia tridentata*) taxa are dominant on the largest vegetation type of the Northern Yellowstone Winter Range (NYWR; Houston 1982). These taxa are particularly important in portions of the NYWR that are relatively free of snow and thereby accessible for ungulate foraging throughout winter. Twentieth-century naturalists (Rush 1932; Wright and Thompson 1935; Cahalane 1943; W. H. Kittams. Sagebrush on the lower Yellowstone range as an indicator of wildlife stocking, Yellowstone Natl. Park files, unpubl. rep., Wyo., 1950) have commented on the conspicuous use of sagebrush for forage and cover by ungulates, primarily elk (*Cervus elaphus*), on the NYWR and expressed concern over what they considered excessive use of sagebrush in the winter diets of ungulates at Yellowstone National Park (YNP).

The effects of Yellowstone's large populations of ungulates on sagebrush taxa on the NYWR have been debated for ≥70 years (Rush 1932, Wright and Thompson 1935). Debate has also centered on other species of woody plants like aspen (*Populus tremuloides*) and willows (*Salix* spp.). However, the National Park Service (NPS) was concerned enough about sagebrush and other browse on the NYWR that they constructed 10 2-ha exclosures on the NYWR in 1957 and 1962 to investigate the relationships between ungulate foraging and plant communities. Eight of the exclosures still exist; 4 contain only sagebrush habitats, and 4 contain large areas within sagebrush habitats.

The NPS (YNP 1997) stated that big sagebrush is holding its own or increasing on 97% of the NYWR, and the decline in sagebrush on the other 3% is a departure from prehistoric conditions or an artifact of past human activities, such as livestock grazing. However, published research, absent before 1987, has confirmed that concerns of early naturalists about sagebrush habitat were well based. Those investigations determined the mechanisms that influence sagebrush-herbivore interactions on the NYWR and their effects. I synthesized the peer-refereed and peer-edited literature on the NYWR that has investigated aspects of sagebrush ecology and forage rela-

Author's address: Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717, USA

tionships with ungulates. This information should be useful in understanding effects of different management strategies on the NYWR and similar areas.

The Northern Yellowstone Winter Range

The NYWR occupies approximately 100,000 ha over an 80-km stretch along the lower elevations in northern YNP and extends northward into Montana along the Yellowstone River drainage (Fig. 1; Houston 1982). The Lamar and Gardiner rivers also drain portions of YNP lowlands that are relatively free of snow, thereby providing a reliable winter location for foraging ungulates (Houston 1982). Singer (1991) reported that 80% of the ungulates in YNP during winter were found on the NYWR. In addition, ≥2,544 Rocky Mountain mule deer (*Odocoileus hemionus*) and 8,626 Rocky Mountain elk have wintered on the portion of the NYWR north of the YNP boundary in Montana during the last decade (T. Lemke, Mont. Fish, Wildl. and Parks, unpubl. data).

The generally favorable climate for ungulate winter foraging varies across the NYWR. P. E. Farnes (SCS, Mean annual precipitation for Yellowstone National Park, unpubl. map, Bozeman, Mont., 1975) reported approximately 280 mm of annual precipitation at Gardiner, Montana (1,616 m), 400 mm at Mammoth (1,899 m), and 410 mm at Tower Falls (1,912 m). Fifty percent of the precipitation is received as snow, although peak moisture occurs in spring and early summer (Farnes 1991). Soils on the sagebrush habitats have been described by Lane (1990) as typic calciboralls, aridic haploborolls, and aridic calciborolls. The Boundary Line Area (BLA) near Gardiner, Montana (Fig. 1) is located on ancient mudflows that are higher in clay and lower in fertility than the rest of the area.

The area surrounding Gardiner, Montana known as the Gardiner Basin, which includes the BLA, has less snow than the majority of the NYWR that lies to the east in YNP. The Gardiner Basin is particularly important for pronghorn (*Antilocapra americana*) in the BLA portion and mule deer throughout. Elk are able to negotiate the deeper snow at higher elevations in the remaining portions of the NYWR. The natural winter range provided by the Gardiner Basin is created by the orographic effects on precipitation of mountain peaks ≤3,353 m. Ideal winter range on extensive south- or west-facing aspects in the Gardiner Basin have been influenced by glacial scouring, morainal deposition, and outwash sediments.

Elk are the only browsing ungulate found in large numbers during winter on the remaining portions of the NYWR within YNP (Singer and Renkin 1995). Bison (*Bison bison*) are an important herbivore over the NYWR, but no evidence exists that bison have had a direct impact on the shrubs of sagebrush habitats.

Big sagebrush is the largest vegetation type on the NYWR. Big sagebrush taxa are dominant over 22% of the NYWR (Houston 1982). More important, sagebrush is the dominant vegetation form on the portions of the NYWR that are most valuable as winter range for ungulates (DeSpain 1990). Additionally, sagebrush communities often furnish security and thermal cover for ungulates and other animals (Wambolt and McNeal 1987). The sagebrush habitats found within the NYWR include the Wyoming big sagebrush (*Artemisia tridentata wyomingensis*)-bluebunch wheatgrass (*Agropyron spicatum*) type that is found primarily at lower elevations in the Gardiner Basin. Over the rest of the NYWR the mountain big sagebrush (*A. t. vaseyana*)-Idaho fescue (*Festuca idahoensis*) habitat type dominates (Wambolt and Sherwood 1999). Other sagebrush are the basin big sagebrush (*A. t. tridentata*) and black sagebrush (*A. nova*). Important plants include the sprouting shrubs usually associated with sagebrush habitats, specifically rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidi-*

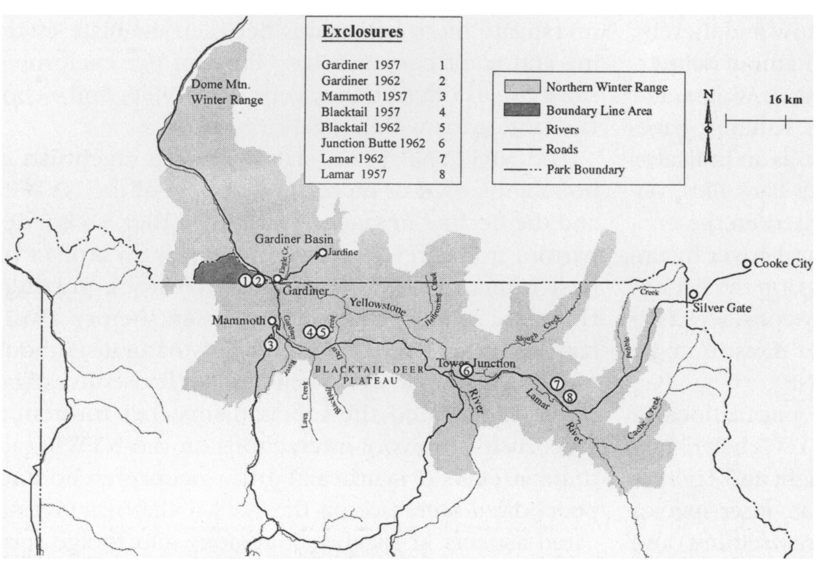

Fig. 1. The Northern Yellowstone Winter Range, Montana and Wyoming. The circled numbers represent locations of the exclosures constructed in 1957 and 1962 that still exist. National Park Service map.

Table 1. Crude protein (%) of bluebunch wheatgrass dry matter by cattle-grazing treatment and season, averaged over a 3-year study (Wambolt et al. 1997).

	Crude protein (%)			
Grazing treatment	Spring	Summer	Fall	Winter
Spring	11.4A[a]	6.8A	4.6A	3.2A
1-year rest	10.0B	5.9B	3.8B	2.9A
Long-term rest	9.6B	5.5B	3.3C	2.9A

[a] Means differ ($P \leq 0.05$) among grazing treatments within each season when followed by a different letter.

florus), and gray horsebrush (*Tetradymia canescens*) found throughout the NYWR. Other important grasses are prairie junegrass (*Koeleria macrantha*) and Sandberg bluegrass (*Poa secunda*).

Sagebrush forage relationships on the NYWR

Sagebrush taxa are highly nutritious and preferred forage for ungulates (Welch and McArthur 1979). They have been bred and selected to improve the forage values of rangelands (Welch and Wagstaff 1992). Sagebrush is particularly high in protein. Welch and McArthur (1979) found the mid-winter crude protein content of 21 big sagebrush accessions averaged 12.4% (range = 10–16%). Grasses incur a large drop in protein and other nutrients during winter. Wambolt et al. (1997) found that during fall and winter in southwestern Montana, bluebunch wheatgrass, the dominant grass of relatively snow-free portions of the NYWR, does not meet the minimum protein levels required for elk (Nelson and Leege 1982). Bluebunch wheatgrass did not meet protein gestation requirements for elk during the gestation period (Table 1). Even in summer, when protein content was highest, bluebunch wheatgrass did not meet elk lactation requirements by August. Wambolt et al. (1997) discussed why elk would be physically unable to consume enough bluebunch wheatgrass to meet protein-maintenance requirements during winter, which are significantly less than requirements for production. The winter nutritional deficiencies of grasses, contrasted to sagebrush, explain why sagebrush is an important forage on the NYWR (Welch and McArthur 1979). The concerns of Nagy (1979) regarding inhibitory effects of sagebrush volatile oils on ruminant digestion have been proven unimportant under natural circumstances. When sagebrush is browsed, the highly volatile compounds are lost with minimal influence on digestion (Cluff et al. 1982, White et al. 1982).

The effects of secondary compounds from the NYWR sagebrush taxa have been studied in detail. The influence of crude terpenoid content on in vitro organic matter digestibility (IVOMD; Striby et al. 1987) and preference (Personius et al. 1987, Bray et al. 1991) by mule deer was determined for 4 sagebrush taxa in the Gardiner Basin. The order of increasing digestibility among taxa was black sagebrush, mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, respectively (Table 2; Striby et al. 1987). Sagebrush IVOMD generally increased from January to April as crude terpenoids decreased. Although extraction of crude terpenoids from sagebrush foliage did increase IVOMD, it resulted in few differences in IVOMD among taxa and collection dates during the winter (Striby et al. 1987). Striby et al. (1987) found no significant differences in sagebrush digestion among wild NYWR mule deer or domestic sheep and steers. Therefore, it appears that no significant differences would exist in mule deer, elk, and pronghorn found on the NYWR.

From 31 compounds isolated from sagebrush, Personius et al. (1987) selected 7 by discriminant analysis as preference indicators among the 4 taxa. Seven other compounds were useful for separating individual plants within a taxon into browse form classes. Bray et al. (1991) used the compounds selected by discriminant analysis to differentiate preference among taxa in conducting a mule deer feeding trial to determine if deer would discriminate against forage

Table 2. In vitro organic matter digestibility (IVOMD; %) of 4 sagebrush taxa at 3 dates on the NYWR using wild mule deer, sheep, and steer inoculum (Striby et al. 1987).

	IVOMD		
Taxon	1 Jan	15 Feb	1 Apr
Mule deer			
Black sagebrush	37.6AE[a]	45.3AF	46.2AF
Mountain big sagebrush	45.8BE	47.9AE	53.5BF
Wyoming big sagebrush	46.0BE	49.5AE	57.4BCF
Basin big sagebrush	47.2BE	63.4BF	62.4CF
Sheep			
Black sagebrush	41.5AE	44.7AF	50.4AG
Mountain big sagebrush	45.4BE	48.5BF	52.7AG
Wyoming big sagebrush	50.3CE	52.5CF	58.1BG
Basin big sagebrush	54.0DE	55.3DE	59.6BF
Steer			
Black sagebrush	42.4AE	42.8AE	47.0AF
Mountain big sagebrush	48.3BE	52.0BF	53.0BF
Wyoming big sagebrush	50.5CE	53.7BF	57.8CG
Basin big sagebrush	55.8DE	56.6CE	58.4CE

[a] Means among taxa differ ($P \leq 0.05$) within date and inoculum source when followed by a different letter (A, B, C, D). Means among dates differ ($P \leq 0.05$) within taxon and inoculum source when followed by a different letter (E, F, G).

treated with these compounds individually. Mule deer selected significantly higher quantities of untreated forage with each compound tested. Personius et al. (1987) and Bray et al. (1991) found that volatility of compounds had little influence on preference at the concentrations found in nature. Volatile compounds and nonvolatile sesquiterpene lactones were responsible for deterring foraging. This research (Personius et al. 1987, Bray et al. 1991) has explained the major role that plant chemistry plays in determining sagebrush palatibility and,thus, preference by herbivores.

Wambolt and McNeal (1987) determined site characteristics for elk and mule deer foraging on the NYWR. Elk were physically capable of using most regions of the Gardiner Basin including timbered areas. Yet their most intensive feeding activity was in mountain big sagebrush habitats with relatively abundant grass, at least partially due to a decline in sagebrush from long-term heavy browsing (Rush 1932, Wright and Thompson 1935, Wambolt 1996, Wambolt and Sherwood 1999). Mule deer preferred areas with Wyoming big sagebrush cover adjacent to steep and dry topography at lower elevations. Such areas furnished security and thermal cover while meeting forage requirements. The distribution and concentrations of elk on the NYWR vary with wind, snow, temperature, and crusting that expose or conceal forage (Greer et al. 1970, Houston 1982). North of the YNP boundary, hunting affects animal distribution on the NYWR (Houston 1982, Wambolt 1996). On the lower portions of the Gardiner Basin, elk are not present as consistently as mule deer because elk hunting occurs from autumn through late winter. This is especially true during open winters when elk can forage within the security of YNP (Houston 1982, Farnes 1991). When elk are forced by forage limitations to leave the security of YNP, the number of elk harvested during Montana's special late hunting season (mid-Dec through Feb) in the area is a good index of winter severity. This elk harvest is positively correlated to use of sagebrush leaders by taxon (Wambolt 1996). Foraging on sagebrush increases when more elk are forced from higher elevations during severe winters (Greer et al. 1970, Wambolt 1996). Under these conditions the selectivity of browsers for certain subspecies of sagebrush is minimized (Wambolt 1996).

Wambolt (1996) established preferences by mule deer and elk for the 4 sagebrush taxa discussed previously over 10 winters of varying severity in the Gardiner Basin. The purpose of the 10-year length of the study was to avoid conclusions from anomolies that can occur for shorter periods. Each year approximately 2,500 leaders were tagged on 244 plants to later determine if winter browsing had occurred. Mule deer and elk browsed very substantial amounts of the 4 sagebrush taxa. Mule deer diets averaged 52% big sagebrush over the 10-year study as determined by microhistological techniques (Sparks and Malechek 1968) on composite samples of feces collected early each spring. During the study, no 1 year was significantly above average in severity of temperature or snow depth compared to the long-term average (Farnes 1991). Mule deer and elk displayed distinct preferences among the 4 taxa. The percentage of total tagged sagebrush leaders used during a given winter reached 91% for mountain big sagebrush, the preferred taxon that averaged 56% utilization at the study sites over the 10-year study. Wyoming big sagebrush was narrowly preferred (39%) over basin big sagebrush (30%). Black sagebrush was least preferred (17%). These long-term preferences supported the findings of Personius et al. (1987) and Bray et al. (1991) regarding sagebrush terpenoid content and its affect on herbivory.

Wambolt et al. (1994) developed regression models that avoid colinearity problems of earlier models and accurately predict production of winter forage for the 3 big sagebrush subspecies on the NYWR. Previous modeling of forage production from big sagebrush had not considered possible subspecies differences or different browsing histories that affect shrub morphology. The consideration of taxon and form class resulted in an average increase of 10% in R_a^2 values to 0.90 (Wambolt et al. 1994). The models facilitate determination of carrying capacity, detecting trends in forage production, and measuring plant response to management. They also emphasized the importance of taxon recognition and the role of past browsing history on present forage production.

Big sagebrush status on the NYWR

Hoffman and Wambolt (1996) tested the hypothesis that Wyoming big sagebrush plants protected from browsing for 35 years would exhibit growth characters similar to browsed plants. They made paired comparisons in and out of a 2-ha NPS exclosure erected in 1957 (Fig. 1; Gardiner 1957). Because of heavy browsing, plants outside the exclosure had no terminal leader growth. The plants inside the exclosure were dominated by terminal growth, and axial long shoots were rare. Thus, for further investigation, it was necessary to compare the terminal leaders of protected plants inside the exclosure to axial long shoots on browsed plants. Unbrowsed plants

Fig. 2. A Wyoming big sagebrush killed by browsing in the Gardiner Basin, 19 June 1998. The sizable trunk, but small plant size, indicates this plant experienced heavy use for years before dying.

had consistently higher production than browsed plants. The average production per plant was 10 g with browsing and 45 g with protection. No measurements of dead crown were taken, but plants under protection appeared vigorous, whereas plants outside the exclosure had large amounts of dead crown (Fig. 2).

The greatest difference between browsed and unbrowsed plants was in seedhead production. Seedheads averaged 0.08 per browsed plant, and 60.3 per unbrowsed plant (range = 0–3). Related studies confirm that stress, such as herbivory, may delay or prevent flowering for several years (McConnell and Smith 1977, Bazzaz et al. 1987, Maschinski and Whitham 1989). The lower overall production of browsed sagebrush plants (Hoffman and Wambolt 1996) indicates that foliage loss results in reduced reproductive potential. Bilborough and Richards (1991) found that buds for flowering stems on mountain big sagebrush were located on short shoots at the distal end of the terminal leader. Because almost all terminal leaders were removed on browsed plants (Hoffman and Wambolt 1996), flowering stems would have to be initiated from elsewhere. The loss in seedhead production from browsing on the NYWR has undoubtedly resulted in declines in reproduction for sagebrush as the taxon lacks any asexual means of reproduction.

The addition of average seedhead weight improved the capability of models to predict production of winter forage from the 3 NYWR big sagebrush subspecies (Wambolt et al. 1994). Improved models were used when the 3 taxa exhibited light use (browse form class). Heavily used plants produced few inflorescenses; therefore, the addition of average seedhead weight to the model was most useful for predicting forage production from low-use plants. The segregation of browse form classes and inclusion of average seedhead weight in the models acknowledge the impact browsing has had on the annual production and reproduction of NYWR sagebrush and compliment Hoffman and Wambolt (1996).

Although snow cover is relatively light on the NYWR, some snow falls each winter and may protect small sagebrush plants for several years before ungulates find them available for foraging. Nearly half (47%) of the mountain big sagebrush plants that were established between 1978 and 1992 germinated in 1988, when Yellowstone had numerous fires. That year offered relatively good seed production due to plentiful spring moisture, followed by a winter with considerably more snow than typical through the 15-year period. The snow protected the seedlings from herbivory. Those conditions coincided with a 35–40% reduction in elk, due to the most severe winter (1988–1989) of the period, that allowed the seedlings to establish during the next several years of reduced numbers of elk (T. Lemke, Mont. Fish, Wildl. and Parks, unpubl. data).

Big sagebrush taxa are not tolerant of fire. Fire on NYWR sagebrush habitats has been an additive injury, along with intense herbivory, to sagebrush. Mehus (1995) studied a wildfire in the Gardiner Basin to determine how much reestablishment of sagebrush and rabbitbrush taxa had occurred under continuous browsing. Nineteen years after the fire, recovery in canopy cover was at levels between 1 and 20% of that of the 3 big sagebrush subspecies in adjacent, unburned sagebrush stands, which were already in decline from historically heavy browsing (Houston 1982, Wambolt 1996, Wambolt and Sherwood 1999). Wyoming big sagebrush recovered to a lesser extent than mountain or basin big sagebrushes. Similar relationships were found for big sagebrush density and production.

Hoffman (1996) studied 7 prescribed burns conducted 10–14 years earlier by the U.S. Forest Service on mountain big sagebrush sites in the Gardiner Basin. These burns were compared with 33 unburned sites to determine recovery following burning. Sagebrush canopy coverage and densities on unburned sites averaged 12 and 15 times, respectively, greater than on burned sites. Mehus (1995) and Hoffman (1996) confirmed that burning accelerates the browsing-induced decline (Houston 1982, Wambolt 1996, Wambolt and Sherwood 1999) of NYWR sagebrush. In addition to directly eliminating sagebrush, fire concentrates browsing on surviving or reestablishing shrubs.

Thirty-five percent of mountain big sagebrush plants were killed by heavy browsing (Fig. 2) between 1982 and 1992 (Wambolt 1996). Many surviving plants developed a heavy-use browse form class with a high percentage of dead crown. The dead crown in the 3 big sagebrush subspecies increased in proportion to the overall amount of browsing received by each taxon. The percentage of dead crown in live plants for mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, was 58.7, 45.4, and 30.1%, respectively (Wambolt 1996).

The 10-year average browsing level of 56.1% on mountain big sagebrush north of YNP may be above the level that can be sustained (Wambolt 1996). Bilbrough and Richards (1993) confirmed that this level of use could inflict heavy damage on sagebrush when they reported that sagebrush was not efficient in compensitory growth following heavy winter browsing. In general, plants with evergreen leaves depend more on those leaves for storage than do plants with deciduous leaves (Bryant et al. 1983). Sagebrush carries 50% of its nitrogen (N) and total nonstructural carbon (TNC) pool in its leaves (Bilbrough 1990); each time a leaf is removed, the N and TNC it contains is lost to the plant.

Wambolt and Sherwood (1999) considered the effect of herbivory on sagebrush across the NYWR. They compared parameters between shrubs that were browsed by ungulates or protected since NPS exclosures were constructed in 1957 and 1962. Their measurements were taken in (protected) and near (browsed) the 6 NYWR exclosures (Fig. 1) that were not burned during the Yellowstone fires of 1988. Because the 2-ha exclosures contained considerable environmental variation, the sagebrush habitat within each exclosure was stratified (Hurlbert 1984) by separating topographic, soil, and microclimatic variation into 19 paired sites. With random sampling using paired sites, (in and out of the exclosures) it is unlikely that comparable distributions of topo-edaphic positions would have been obtained, regardless of sample size (Coughenour 1991). Predictably, Wambolt and Sherwood (1999) obtained different results than did Singer and Renkin (1995) sampling at the same locations. Singer and Renkin (1995) used randomly placed plots as warned against by Hurlbert (1984) and obtained smaller samples of <8% of the transect area the first 5 years and 23% the last 2 years of that sampled by Wambolt and Sherwood (1999).

Wambolt and Sherwood (1999) found a significant difference between the development of protected and browsed big sagebrush communities (Table 3). Wambolt and Sherwood (1999, In press) stated, "Since the period of exclosure construction in 1957 and 1962, there has been a significant difference in the development of protected and browsed big sagebrush communities. Average big sagebrush canopy cover on protected sites was 202% greater ($P \leq 0.0027$) than on browsed sites over the 19 paired sites. The average big sagebrush cover for all 19 sites was 19.7% inside and 6.5% outside the exclosures. This relationship was universal on sites with Wyoming big sagebrush or mountain big sagebrush, flat to very steep topographies, and all aspects and precipitation levels."

Table 3. Percent canopy cover of big sagebrush at 19 environmentally paired sites either browsed or protected. The paired sites are associated with the exclosures established either in 1957 or 1962 (Wambolt and Sherwood 1999).

Site	Canopy cover (%)		
	Protected	Browsed	Probability > t[a]
Mammoth–57	49.5	28.7	0.0004
Junction Butte–62A	31.9	11.6	0.0000
Junction Butte–62B	32.1	11.5	0.0001
Lamar–57A	3.2	0.1	0.0291
Lamar–57B	2.9	0.1	0.0002
Lamar–57C	44.3	19.8	0.0004
Lamar–57D	25.4	16.9	0.0015
Lamar–62A	9.3	1.3	0.0005
Lamar–62B	29.6	8.2	0.0001
Lamar–62C	41.7	9.3	0.0004
Lamar–62D	42.1	9.7	0.0000
Gardiner–57A	3.9	0.0	0.0001
Gardiner–57B	3.6	0.1	0.0004
Gardiner–57C	4.5	1.1	0.0001
Gardiner–57D	1.4	0.4	0.0073
Gardiner–62A	21.8	0.4	0.0001
Gardiner–62B	17.6	4.3	0.0000
Gardiner–62C	2.4	0.2	0.0012
Gardiner–62D	6.8	0.0	0.0001

[a] The comparative P value for similar inferences is 0.0027.

The Wyoming big sagebrush sites under protection averaged almost 10 times more sagebrush cover than where browsing had continued following exclosure construction (Fig. 3). Mountain big sagebrush cover was almost 3 times as great where protected (Fig. 4). Ungulate browsing also affected numbers of big sagebrush plants. Across the NYWR big sagebrush plants were twice as numerous with protection as with browsing. There was an average density of 30.5 plants/60 m^2 inside and 15.3/60 m^2 outside the exclosures. Individual mountain big sagebrush plants produced 88% more winter forage where protected across the NYWR (Wambolt and Sherwood 1999). The production differential for Wyoming big sagebrush was even greater, but because browsed plants were so reduced in size, their growth parameters were not suitable for production models (Wambolt et

Fig. 3. At the Gardiner (constructed in 1957) exclosure, near Gardiner, Montana, 19 June 1998. The foreground without sagebrush is outside the exclosure while a thriving stand of Wyoming big sagebrush inside the exclosure shows the recovery that has occurred since the long period of overuse before exclosure construction. The recovery illustrates the site's potential.

al. 1994). The response of the sprouting shrubs (green rabbitbrush, rubber rabbitbrush, and gray horsebrush), as measured by canopy cover and density, was similar to that of big sagebrush across the NYWR.

Singer and Renkin (1995) and Wambolt and Sherwood (1999) found a large impact from browsing on the Wyoming big sagebrush in the Gardiner Basin (Fig. 3). Wambolt and Sherwood (1999, In press) considered the difference in impact between Wyoming big sagebrush and mountain big sagebrush (Fig. 4) with this statement: "Pronghorn and mule deer often forage heavily on big sagebrush taxa (Welch and McArthur 1979). Mule deer diets averaged 52% big sagebrush over a 10-year period (Wambolt 1996) only a couple of kilometers away from the 8 Wyoming big sagebrush paired sites. A high degree of utilization is reflected in the great impact on Wyoming big sagebrush populations at these 8 sites where elk may also be present with pronghorn and mule deer (Singer and Renkin 1995). However, as Singer and Renkin (1995) point out, elk are the only significant browsers at the other 11 paired sites due to excessive snow depths. Therefore, with our findings, it becomes obvious that elk numbers were large enough on the NYWR for a sufficient number of years before exclosure construction started in 1957 to greatly reduce big sagebrush populations."

Wambolt (1996) concluded that any of the 4 NYWR sagebrush taxa would be heavily browsed if severe winter conditions precluded ungulates from exercising their preferences. However, mountain big sagebrush was clearly the preferred taxon by mule deer and elk. The fact that Singer and Renkin (1995) and Wambolt and Sherwood (1999) found Wyoming big sagebrush to be more impacted than mountain big sagebrush was a function of snow depth limiting pronghorn and mule deer foraging over the larger distribution of mountain big sagebrush.

Conclusion

Big sagebrush is the native dominant on the large portion of the NYWR considered most important for ungulates (Houston 1982, DeSpain 1990). Although NYWR sagebrush ecology and forage relationships with ungulates has been a concern since the 1920s, no peer-reviewed research on the topic had been published prior to 1987. The historical evidence and recent studies (Patten 1993, Hoffman and Wambolt 1996, Wambolt 1996, Wambolt and Sherwood 1999) indicate a significant decline of NYWR sagebrush. This potentially impacts ungulates that rely on sagebrush habitat for meeting their nutritional needs and other requirements. Species, such as mule deer, with well-documented reliance on sagebrush, have already been impacted. Singer and Renkin (1995) related a 66% decline in mule deer using the lower elevations of the NYWR over the 2 decades previous to their study to be likely due to a decline in Wyoming big sagebrush. I agree with this assumption because, despite decades of both sagebrush and mule deer declines in the Gardiner Basin (outside YNP), mule deer diets averaged 52% big sagebrush over a climatically mild 10-year period during which sagebrush continued to decline (Wambolt 1996). However, elk are the only significant browser on 97% of the sagebrush habitats on the NYWR (YNP 1997). Therefore, elk browsing is responsible for sagebrush declines over

Fig. 4. At the Lamar (constructed in 1957) exclosure, near the confluence of Soda Butte Creek and the Lamar River, 19 June 1998. The foreground without sagebrush is outside the exclosure and the heavy growth of mountain big sagebrush beyond the fence is inside the exclosure. The Lamar River is seen downslope in the distance.

most of the NYWR (Wambolt and Sherwood 1999). As noted in 1 report, "Because elk are so much more abundant than pronghorn on the northern range, even very low consumption rates of sagebrush by individual elk could result in a large cumulative amount of sagebrush consumed" (YNP 1997). Elk are impacted as the loss of their highest winter protein source (sagebrush) continues (Welch and McArthur 1979). This loss will manifest itself in a decreasing ability of elk to meet their nutritional needs and requirements for reproduction. But, whatever the long-term consequences to the elk herds that have been unmanaged inside YNP since the adoption of the Natural Regulation policy by YNP in 1968 (Houston 1982), the implications for other organisms are clear. In concert with the decline of the native vegetation (sagebrush and dependent species), it is reasonable to expect that numerous animals (Welch 1997), in addition to mule deer, relying on sagebrush habitats will also be impacted. The information available on NYWR sagebrush should provide an understanding of important relationships and management opportunities in YNP and elsewhere.

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Carl Wambolt received his Ph.D. and M.S. in range science from the University of Wyoming, and his B.S. with majors in wildlife management and range management from the University of Idaho. He has been a professor of range science at Montana State University since 1970.

Associate Editor: Krausman