Sagebrush-Ungulate Relationships on the Northern Yellowstone Winter Range

Carl L. Wambolt

Abstract—Sagebrush (*Artemisia*) taxa have historically been the landscape dominants over much of the Northern Yellowstone Winter Range (NYWR). Their importance to the unnaturally large ungulate populations on the NYWR throughout the twentieth century has been recognized since the 1920s. Sagebrush-herbivore ecology has been the focus of research on the NYWR for 2 decades. Specific research topics include general ungulate use of the NYWR, forage relationships involving sagebrush taxa, the effects of browsing and sagebrush taxa on forage production, the results of long-term rest from severe browsing on the NYWR, sagebrush plant and community characteristics related to herbivory, and the relationships of sagebrush taxa to fire on the NYWR. Sagebrush taxa have been very important on the NYWR but are generally in a state of decline.

The Northern Yellowstone Winter Range (NYWR) is dominated by big sagebrush (*Artemisia tridentata*) taxa. Big sagebrush occupies relatively snow-free portions of the NYWR, making it accessible to ungulates throughout the winter. Heavy foraging use of sagebrush by the large ungulate populations of the region has been discussed by naturalists for almost a century (Wright and Thompson 1935) (fig. 1). My research has confirmed that early naturalists were right to be concerned about sagebrush habitat on the NYWR. Those investigations have determined the mechanisms that influence sagebrush-herbivore interactions on the NYWR and their effects.

Area Description

The NYWR is an extensive area covering about 100,000 ha along the lower elevations in Northern Yellowstone National Park (YNP), and extends northward into Montana along the Yellowstone River drainage (fig. 2). The Lamar and Gardiner River drainages, important lowland areas within YNP, are relatively free of snow and provide reliable winter foraging for ungulates. During the winter, 80 percent of all ungulates are found on the NYWR within YNP. In addition, there have been as many as 2,544 Rocky Mountain mule deer and 8,626 Rocky Mountain elk wintering on the portion of the NYWR north of the YNP boundary in Montana during the last decade.

Carl L. Wambolt is Professor of Range Science, Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717 U.S.A., FAX: (406) 994-5589, e-mail: cwambolt@montana.edu

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The climate is favorable in this area for ungulate foraging during winter. The mean annual precipitation is approximately 280 mm (1,616 m) at Gardiner, MT, 400 mm (1,899 m)

Figure 1—Photo from Wright and Thompson (1935). The original caption read: "End of the range. The right side of the picture shows elk winter range within Yellowstone National Park. The fence is the boundary. The left side of the picture shows the rank growth of sagebrush just outside the park. Here we can compare the original and the present state of the range. There can be no doubt of what has happened. (Photograph taken June 1, 1932, near Gardiner, Wildlife Division No. 2501.)"

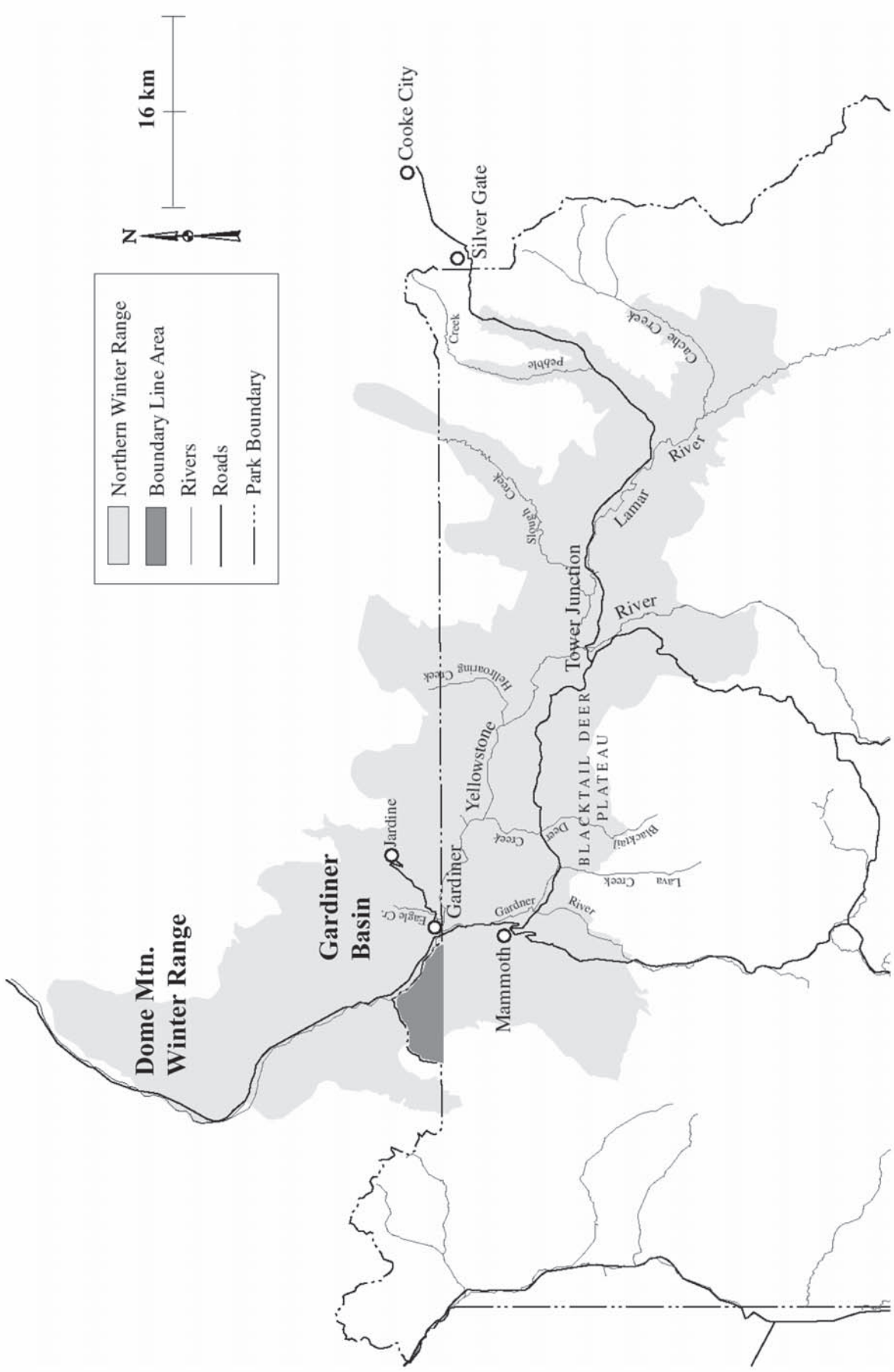

Figure 2—The Northern Yellowstone Winter Range, Montana and Wyoming (National Park Service Map).

at Mammoth, and 410 mm (1,912 m) at Tower Falls. About half of the moisture each year is received as snow, the peak occuring in spring and early summer.

The Gardiner Basin, an area near the town of Gardiner, MT, includes the boundary line area (BLA), and has less snow than the majority of the NWYR that lies to the east in YNP. Therefore, the Gardiner Basin is especially important for pronghorn and mule deer. Elk are usually able to negotiate deeper snow at higher elevations. Elk and bison tend to dominate the foraging over the remaining portions of the NYWR, but there is no strong evidence that bison have had an impact on the shrubs of sagebrush habitats. Therefore, elk are the only browsing ungulate found in significant numbers during winter on the portions of the NYWR outside the Gardiner Basin.

Not only is big sagebrush the largest vegetation type on the NYWR, but perhaps more importantly, sagebrush taxa are the dominant vegetative form on the portions of the NYWR that are most valuable as winter range for ungulates (DeSpain 1990). Sagebrush communities also furnish important security and thermal cover for ungulates and other animals (Wambolt and McNeal 1987).

The variety of sagebrush habitats within NYWR includes the Wyoming big sagebrush- (*Artemisia tridentata wyomingensis*) bluebunch wheatgrass (*Agropyron spicatum*) type that is found primarily at lower elevations in the Gardiner Basin. Mountain big sagebrush- (*A. t. vaseyana*) Idaho fescue (*Festuca idahoensis*) habitat type dominates the majority of the NYWR (Wambolt and Sherwood 1999). Other important sagebrush are basin big sagebrush (*A. t. tridentata*) and black sagebrush (*A. nova*). Important subdominant plants are the sprouting shrubs often found in sagebrush habitats including rubber rabbitbrush (*Chrysothamnus nauseosus*), green rabbitbrush (*C. viscidiflorus*), and gray horsebrush (*Tetradymia canescens*). These shrubs are found throughout the NYWR in various sagebrush habitat types.

Results and Discussion

Sagebrush Forage Relationships

The relationships of secondary compounds found in the foliage of sagebrush taxa to foraging by NYWR ungulates was studied. The relationships between crude terpenoid content of sagebrush and *in vitro* organic matter digestibility (IVOMD) as well as preference by mule deer was considered for the four dominant sagebrush taxa found on the NYWR. Basin big sagebrush was the most easily digested by mule deer followed in order of decreasing digestibility by Wyoming big sagebrush, mountain big sagebrush, and black sagebrush. The IVOMD for all four taxa generally increased from January to April as crude terpenoids decreased in the foliage. When the crude terpenoids were removed from the sagebrush foliage the IVOMD increased. However, terpenoid removal resulted in few differences in IVOMD among the taxa and collection dates during the winter (Striby and others 1987). Wild mule deer from the NYWR were compared to domestic sheep and steers for their ability to digest sagebrush. There were no significant differences found among the three species of animals; therefore, it appears that there should be no significant differences between the wild ungulates (mule deer, elk, and pronghorn) found on the NYWR.

Personius and others (1987) isolated 31 compounds from sagebrush foliage and found that seven of them were particularly important for preference indicators among the four sagebrush taxa. In order to separate the individual plants within a taxon into browse-form classes (use classes), seven other compounds were helpful. The compounds above were used by Bray and others (1991) to differentiate mule deer preference among sagebrush taxa during feeding trials. This study determined if the deer discriminated against forage treated with the individual compounds. During this feeding trial, mule deer selected significantly higher quantities of untreated forage compared to the same forage treated with the suspect compounds (table 1). These studies found that volatility of compounds had little influence on preference at the concentrations found in nature. Both volatile and nonvolatile compounds were found to be responsible for deterring foraging on the four taxa. The combination of nonvolatile sesquiterpene lactones with certain volatiles explained why one sagebrush taxon is often preferred over another.

Site characteristics that might be responsible for elk and mule deer foraging on the NYWR were studied (Wambolt and McNeal 1987). Most portions of the Gardiner Basin — even the timbered areas—were used by elk. However, elk fed mostly in mountain big sagebrush habitat types. The mule deer in the same area preferred to forage in the Wyoming big sagebrush type when it was found adjacent to steep and dry topography at lower elevations. These areas tended to furnish good security and thermal cover while also meeting foraging needs. Elk distribution and concentration on the NYWR vary with wind, snow depth, temperature, and snow crusting that might expose or conceal forage. In addition, hunting north of YNP affects animal distribution on the winter range.

Mule deer and elk preferences for the four sagebrush taxa were studied over 10 winters of varying severity in the Gardiner Basin (Wambolt 1996). This study was purposely long term in order to avoid anomalies over shorter periods that might lead to erroneous conclusions. Approximately 2,500 leaders were tagged on 244 plants each winter over the 10-year period to determine if browsing had occurred.

Table 1—Mule deer preference for seven compounds found in four sagebrush taxa. All seven significantly influence intake and are listed in decreasing order as a foraging deterant.

Compound
1,8-cineole [a]
Black sage NVCTF [b]
Wyoming big sage NVCTF
p-cymene [a]
Basin big sage NVCTF
Methacrolein [a]
Mountain big sage NVCTF

[a] Volatile.
[b] Nonvolatile crude terpenoid fraction.

Overall, the two ungulates browsed large amounts of the four sagebrush taxa, particularly considering that the 10-year period was below average for winter severity. In addition, mule deer diets averaged 52 percent big sagebrush over the 10-year study. The diets were determined by microhistological techniques on composite samples of feces collected early each spring. Both ungulates displayed a distinct preference among the four taxa. The amount of sagebrush use varied with winter and taxon, as expected. Use reached 91 percent for the preferred taxon, mountain big sagebrush, which averaged 56 percent over the 10-year study (fig. 3). Average use of Wyoming big sagebrush was 39 percent and basin big sagebrush was 30 percent. The least preferred taxon was black sagebrush at 17 percent. The results of our study of actual use by wild ungulates supported the findings of Personius and others (1987) and Bray and others (1991) that sagebrush terpenoids affect herbivory.

Regression models were developed to determine the production of winter forage for the three big sagebrush subspecies on the NYWR (Wambolt and others 1994). Models available in previous literature did not consider the variation among sagebrush subspecies nor use classes (developmental differences from past browsing) that might be present. During this study (Wambolt and others 1994), the consideration of taxon and form class increased the R_a^2 an average of 10 percent with values to 0.90. These models help with the determination of carrying capacity, detecting trends in forage production, and measuring plant responses to different management options. In addition, they clearly show the importance of taxon recognition and the role of past browsing history on present forage production of sagebrush taxa (table 2).

Ecology of Big Sagebrush on the NYWR

The question of whether Wyoming big sagebrush plants that had been protected from browsing for 35 years would exhibit similar growth characteristics to browsed plants was considered (Hoffman and Wambolt 1996). To test this hypothesis, paired comparisons in and out of a 2-ha National Park Service (NPS) exclosure constructed in 1957 were made. Because heavy browsing had occurred outside the exclosure for many years, plants there had no terminal leader growth. Plants inside the exclosure were dominated by terminal growth, and axial long shoots were rare. Therefore, to further investigate differences between protected and unprotected plants it was necessary to compare terminal

Table 2—Variables selected to model big sagebrush winter forage production (g).

Variables
Average seedhead weight (g)
Height (cm)
Average cover (cm)
Crown depth (cm)
Circular area (cm^2)
Major axis (cm)
Minor axis (cm)

Figure 3—Elk browsing mountain big sagebrush on the Northern Yellowstone winter range.

leaders of protected plants inside the exclosure to axial long shoots on browsed plants. The unbrowsed plants had a consistently higher production level than browsed plants (table 3). The average production per plant was 10 g with browsing and 45 g with protection. The browsed plants had large amounts of dead crown as well, although no measurements were taken of this parameter. Production of seedheads by big sagebrush plants was the parameter with the greatest difference between browsed and unbrowsed plants. The browsed plants averaged 0.08 seedheads per plant, where the unbrowsed plants averaged 60.3 per plant. Almost all terminal leaders on browsed plants were removed so flowering stems would have to be initiated from elsewhere (Hoffman and Wambolt 1996). This loss of seedhead production from browsing has undoubtedly resulted in reproductive declines for NYWR sagebrush, as these taxa do not reproduce asexually.

The importance of average seedhead production as expressed by their weight was discovered to be important for the construction of regression models to predict sagebrush production of winter forage from the three big sagebrush subspecies found on the NYWR (Wambolt and others 1994). Models improved for all three taxa when average seedhead weight was included for the lightly used (browse form class) plants. Because heavily used plants did not produce many inflorescences, the addition of average seedhead weight to the model for those plants was not beneficial. Separation of browse-form classes and inclusion of average seedhead weight in the models both recognized the impact browsing has had on the annual production and reproduction of NYWR sagebrush.

Snow cover is naturally light on the NYWR, but some snow falls each winter and may protect small sagebrush plants for several years before ungulates find them available for foraging. Among the mountain big sagebrush plants that established between the years 1978—1992, nearly half (47 percent) germinated in 1988. That was the year of the Yellowstone fires. That was also a year that offered relatively good seed production due to good spring moisture followed by a winter with considerably more snow than other winters during the 15-year period. The snow protected the seedlings from herbivores and provided an insulated environment for their welfare during this usually precarious establishment period. These conditions also coincided with a 35 to 40 percent reduction in elk that occurred during that most severe winter (1988—1989) of the 15-year period. This also benefited the seedlings that were allowed to establish during the next several years of reduced elk numbers.

Table 3—Average differences between browsed and unbrowsed Wyoming big sagebrush plants.

	Browsed	Unbrowsed
Production (g/plant)	10.0[a]	44.7[b]
Seedheads per plant	0.08[a]	60.3[b]
Leader length (mm)	22.9[a]	22.3[a]
Leader dry weight (g)	0.02[a]	0.02[a]

Values followed by different letters are significantly different ($P<0.01$).

Fire Relationships

The NYWR sagebrush taxa have no mechanisms to cope well with fire. Therefore, when fire has occurred on NYWR sagebrush habitats, they have been an additive injury, along with intense herbivory, to sagebrush plants. A wildfire in the Gardiner Basin was studied (Wambolt and others 1999) to determine, among other things, the rate of reestablishment of sagebrush and rabbitbrush taxa under continuous browsing following fire. Nineteen years after the fire, recovery of the three subspecies of big sagebrush was at levels between 1 and 20 percent (canopy coverage) of that in adjacent unburned sagebrush stands. This was found despite the fact that the adjacent stands were already in decline from historically heavy browsing (Wambolt 1996; Wambolt and Sherwood 1999). The recovery of Wyoming big sagebrush was less than that of mountain or basin big sagebrush in this burn. Similar relationships were also found for big sagebrush density and production when comparing burned areas to unburned portions.

Wambolt and others (1999) also studied seven prescribed burns conducted by the USDA Forest Service on mountain big sagebrush sites within the Gardiner Basin. These burns had been conducted 10 to 14 years before they were studied. The burns were compared with 33 unburned sites in the Basin to determine recovery following burning. The canopy coverage and densities of the sagebrush on the unburned sites averaged 12 and 15 times greater than on burned sites. This confirms that burning accelerated the browsing-induced decline (Wambolt 1996; Wambolt and Sherwood 1999) of NYWR sagebrush. Sagebrush not directly eliminated by fire were also subjected to unusually heavy browsing on surviving or reestablishing shrubs due to the loss of normally available forage from the fires.

Rens (2001), when studying the effects of fire on the NYWR, considered the effect of elk browsing on the recovery from fires on the Black-tailed Deer Plateau. This investigation also found significant differences in the development of protected and browsed shrubs. One decade after burning mountain big sagebrush, canopy cover averaged 20 percent with protection from elk browsing and 9.7 percent where browsed. Similar differences were found in density and production of protected and browsed mountain big sagebrush following fire on the Black-tailed Deer Plateau.

Browsing Impacts

Wambolt (1996) found that 35 percent of the heavily browsed mountain big sagebrush plants died between 1982 and 1992. Most of the plants that survived the decade of heavy browsing developed a form that clearly showed the effects of their past heavy use, and contained a high percentage of dead crown. The amount of dead crown found in the three big sagebrush subspecies was in direct proportion to the amount of browsing received by each taxon. Among the plants that survived the heavy browsing, the percentage of dead crown from mountain big sagebrush, Wyoming big sagebrush, and basin big sagebrush, was 58.7, 45.4, and 30.1 percent, respectively (Wambolt 1996).

The impact of herbivory on sagebrush across the NYWR was studied by Wambolt and Sherwood (1999) using NPS

exclosures that were constructed in 1957 and 1962. The exclosures were originally constructed to learn what would happen under protection from the heavy herbivory that was occurring throughout the northern part of Yellowstone Park. Wambolt and Sherwood (1999) compared shrub parameters between browsed and unbrowsed plants with the aid of these exclosures. They discovered a significant difference between the development of protected and browsed big sagebrush communities across the NYWR.

> 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 (Wambolt and Sherwood 1999).

Wambolt and Sherwood (1999) found that Wyoming big sagebrush sites that were protected by the exclosures averaged almost 10 times more sagebrush cover than where browsing had continued unabated (fig. 4). Where mountain big sagebrush was the dominant cover type, the same figure was almost three times as much sagebrush cover where protected.

The density of big sagebrush plants was affected in a similar manner by ungulate browsing. Across the NYWR, big sagebrush plants were twice as numerous where they had not been browsed in exclosures as where browsing had occurred throughout the interval since exclosure construction. This amounted to an average density of 30.5 plants per 60 m^2 inside and 15.3 per 60 m^2 outside the exclosures. In addition, individual mountain big sagebrush plants produced 88 percent more winter forage where protected. A similar production figure was not practical to obtain from Wyoming big sagebrush plants even though the differential between protected and browsed plants was even greater than it was for mountain big sagebrush. The Wyoming big sagebrush plants could not be quantified for this character because browsed plants were so reduced in size that their parameters were not suitable for inclusion in the models.

Summary

Both the historical evidence and our recent studies clearly show a significant decline of sagebrush on the NYWR. This decline has already impacted ungulates that rely on sagebrush habitats for nutritional and other requirements (fig. 5). Among the ungulates, it is likely that elk will be the least impacted from the decline in the sagebrush habitat types

Figure 4—National Park Service exclosure near Gardiner, MT, erected in 1957 after Wyoming big sagebrush was nearly eliminated by browsing. Shrubs inside show some recovery (photo taken September 2001).

Figure 5—Even large ungulates use sagebrush for cover. This is one of a dozen elk standing in a patch of basin big sagebrush on the NYWR. Only a portion of the elk's head is visible in the center of photo.

because of their abilities to use other types when available. However, it is clear that elk browsing has been responsible for declines of sagebrush over the majority of the NYWR (Wambolt and Sherwood 1999). It is logical to assume that numerous fauna will be affected by the decline of any native vegetative type. This is especially true with one as extensive as the sagebrush type in the region of the NYWR. The decline of an important habitat type should be given serious consideration when land management opportunities present themselves.

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