FINAL REPORT

The Effect of Elk Grazing Intensity on the Vegetation Structure and Breeding Birds in the Shrubsteppe of Grand Teton National Park, Wyoming

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ABSTRACT

Elk (*Cervus elaphus*) graze more intensely in certain areas of the shrubsteppe in Grand Teton National Park, Wyoming. This allowed examination of whether elk grazing intensity may lead to changes in shrubsteppe vegetation structure, including the presence of invasive weed species, and whether higher order effects were evident. Higher order effects were assessed by measuring the community structure of breeding bird species in relation to elk habitat use and vegetation structure. High elk use areas were characterized by lower shrub cover (density) and height, with lower forb and grass cover and increased bare ground. Only one species of noxious weed (musk thistle, *Carduus nutans*) was detected during the study and at only 2 of 60 study sites that both experience relatively low ungulate use but that had localized anthropogenic soil disturbance. Total breeding bird abundance, avian species richness, and abundance of 5 of 6 individual bird species (Brewer's sparrow, *Spizella breweri*, Green-tailed towhee, *Pipilo chlorurus,* Sage thrasher, *Oreoscoptes montanus*, Western Meadowlark, *Sturnella neglecta*, and Brewer's Blackbird, *Euphagus cyanocephalus*) were inversely correlated to elk grazing intensity. By contrast, the abundance of Vesper Sparrows (*Pooecetes gramineus*) increased with higher elk use. Avian abundance and species richness were positively correlated to shrub cover, shrub height and % forb cover. High elk use may thus impact breeding shrubsteppe bird communities by initiating changes to the shrub and forb layer, although direct causative links cannot be inferred from these data. An alternative explanation is that elk select areas with low shrub and forb cover. Regardless, in order to facilitate healthy populations of shrubsteppe birds, managers should focus on ways to maintain areas with high shrub density and structural complexity, and a dense forb layer.

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INTRODUCTION

Background

Shrubsteppe habitats throughout the Great Basin have become extensively altered due to human land use practices such as livestock grazing, clearing for agriculture, the introduction of non-native species, development, altered fire regimes, and recreational activities. Several native species associated with this ecosystem type, namely many neotropical migrant landbirds, are exhibiting concomitant population declines (Saab et al. 1995). Avian species exhibit sensitivity to habitat structure and alteration at a variety of spatial scales (Cody 1981, Martin 1988, Donovan et al. 1997, Saab 1999, Sallabanks et al. 2000). Birds, moreover, have been viewed as important indicators of environmental integrity, especially because they are top predators, have relatively low birthrates, and long lifespans (Maurer 1992, Bradford et al. 1998). In order to identify factors underlying species declines in shrubsteppe ecosystems, studies are needed that improve our understanding of the habitat requirements of these species. Such work is especially appropriate on public lands such as those run by the National Park Service whose mandate is to "preserve and protect" our natural resources. Nonsustainable uses of natural resources can ultimately lead to ecosystem degradation, and it is important to identify which activities may do so.

Intensive large herbivore grazing regimes on many western rangelands has led to significant changes in the structure and composition of vegetative communities (Olson 1999*b*). At intermediate levels of grazing intensity plant diversity may actually be augmented through the reduction of dominant and competitive plants which allows other less competitive plants to persist (Rambo and

Faeth 1999). Plant aboveground productivity may also be enhanced (Frank and McNaughton 1993). Conversely, heavy and/or long term grazing in many systems has led to "biosimplification", that is, increased uniformity in species composition, physical structure and organization (Sampson 1992, Olff and Ritchie 1998, DiTomaso 2000) and considerable aboveground herbaceous biomass reduction (Rumble and Anderson 1993).

In some areas, intensive large herbivore grazing regimes leading to disturbed soil substrates have also facilitated the invasion of non-native plant species, many of which are known to be noxious, or unpalatable, to both domestic and wild ungulate species (Tyser and Key 1988; Olson 1999*b*). Most North American herbivores avoid weeds while grazing on other, native plants. Severe grazing reduces a plant's ability to fix carbon and stops root growth which can put a grazed plant at a great disadvantage when competing with an ungrazed weed for soil and nutrients (Olson 1999*b*).

Many species of noxious weeds are spreading rapidly throughout the U.S. intermountain west (Sheley and Petroff 1999). Most originated in Europe and Asia where they were seldom a problem because they evolved with natural controls such as insect predators, plant pathogens, and other competing plant species. New weeds are constantly being introduced to the U.S. and once established are spread by vectors such as vehicles, recreationists, waterways, wind and domestic and wild animals. Ungulate grazers transport weed seeds by picking up seeds in their coat and between the pads of their feet. Once a weed infestation is established, (which for species such as musk thistle, *Carduus nutans*, only takes one seed) weeds can rapidly exploit available soil nutrients and outcompete many native species of plants (Olson 1999*a*). Spotted knapweed (*Centaurea maculosa*), for example, has reduced plant species diversity in Glacier National Park (Tyser and Key 1988). Noxious weeds, therefore, have the potential to further alter the structure and composition of plant communities via differential grazing by herbivores on non-weed species and competitive dominance over some native species.

With changes in plant communities undoubtedly come changes in local animal assemblages. The establishment of weed patches, for example, can act to reduce local biodiversity by displacing the fauna that depend on native plants for sustenance and refugia. Changes occurring at the vegetation level are bound to exert pressures that ripple up through ecological systems. Forbes (1887) who was seminal in developing the concept of an ecosystem recognized this potential when he commented that "...of such an organic complex, expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage".

Insect diversity, which is usually positively related to plant biomass (Lawton 1983), plant structural diversity (Lawton 1983), and plant species diversity (Siemann et al. 1998) is one characteristic that may change with intense grazing regimes and noxious weed invasion. Most insect herbivores are specialized to feed on only one or a few plant species (e.g., Strong et al. 1984) and a large percentage of North American insects are phytophagous (herbivorous)(Lawton and Strong 1981). Consequently, species such as birds that feed on shrubsteppe insects in heavily grazed/weed-infested areas are potentially forced to alter their foraging habits, subsist on diets lower in protein, enlarge their territories, or move out of those areas. Any of these possibilities could have substantial energy costs.

Although factors on overwintering grounds undoubtedly exert strong pressures on neotropical migrant survivorship, factors on breeding grounds are thought to be as important if not more important in maintaining viable populations of birds (Sherry and Holmes 1995). Demographic parameters such as nesting success (Martin 1988) and extent of nest parasitism by the Brown-headed Cowbird (Brittingham and Temple 1983) are widely known to have tremendous impacts on avian populations and are affected by habitat structure at both the local and landscape scale (Donovan et al. 1997). Nest site concealment, for example, increases nesting success and is usually more attainable in areas with higher vegetative complexity (Li and Martin 1991). Birds that experience low levels of reproductive success in certain habitat contexts may not return to those areas in the future, thus affecting local biodiversity.

Intensive large herbivore grazing may thus impact shrubsteppe songbirds by altering the vegetation structure and composition which may in turn affect local nesting conditions and food availability.

Justification for Research

Neotropical migrant landbirds can be useful bioassays of environmental health. Declines in many shrubsteppe bird species suggest that shrubsteppe habitats throughout the intermountain west may be becoming or are ecologically degraded, especially because of intensive grazing practices. Saab et al. (1995) reviewed studies examining the response of avian species that breed in western shrubsteppe habitats to grazing. Included were several species known to breed within Grand Teton National Park, Wyoming: Northern Harrier (*Circus cyaneus*), American Kestrel (*Falco sparverius*), Prairie Falcon (*Falco mexicanus*), Long-billed Curlew (*Numenius americanus*), Short-eared Owl (*Asio flammeus*), Sage Thrasher (*Oreoscoptes montanus*), Green-tailed Towhee (*Pipilo chlorurus*), Vesper Sparrow (*Pooecetes gramineus*), Brewer's sparrow (*Spizella breweri*), and Brown-headed Cowbird (*Molothrus ater*). All of these species were shown to significantly decline in abundance in response to moderate to heavy grazing in at least one study, except for Brown-headed Cowbirds which responded positively to increased grazing in two studies.

Most grazing studies have explored the effect of grazing by domestic livestock, whereas few have examined the potential impacts of heavy or concentrated grazing by native ungulates. In Grand Teton National Park (GTNP), Wyoming, there exists a unique opportunity to study such effects. Within the park resides a large, native elk *(Cervus elaphus*) population that forages partly within sagebrush habitats during the summer months and winters south on the U.S. Fish and Wildlife Service's National Elk Refuge. Concentrations of wild grazing elk are some of the highest in the country (Singer and Harter 1996). Fortunately, there exist areas of similar physiognomy within the park that experience very little grazing pressure with which we can make comparisons to more heavily grazed areas.

Study Goals

In this study, we took a two-pronged approach to assessing the impacts of elk grazing on other native shrubsteppe biota. First, we examined the relationship between elk habitat use and vegetation structure, including documenting the presence of non-native, noxious plant species. Secondly, to assess higher order effects, we tested for associations between elk habitat use and bird abundance/species richness, and vegetation structure and bird abundance/species richness, with a focus on nesting Neotropical migrant songbirds. Based on the available evidence regarding the observed impacts of livestock grazing on native vegetation, noxious weed infestation, insect populations, and nesting birds, several predictions were made regarding the possible effects of heavy elk grazing in parts of the shrubsteppe of GTNP: 1) vegetation structure would be more simplified in heavily grazed areas, 2) the relative abundance of noxious weed species would increase with higher elk use, and 3) avian abundance and species richness would be diminished in high elk use areas.

METHODS

Study Area

The study area consisted of shrubsteppe habitat within GTNP (43° 39' N latitude, 110° 40' W longitude) (Fig. 1). The elevation ranged from approximately 1982 m at the south end of the study area (near the Jackson Hole Airport) to approximately 2134 m near the north end (near Lost Creek Ranch), a difference of 152 m. The area typically experiences short summers and long winters. Average annual precipitation is 54 cm, and occurs mostly as snow. Dominant shrub species included Big Sagebrush (*Artemisia tridentata*), Low Sagebrush (*A. arbuscula*), and Antelope Bitterbrush (*Purshia tridentata*). Associated understory grasses included those of the genera *Stipa*, *Bromus*, and *Poa*. Common forbs included Lupine

(*Lupinus caudatus*), Arrowleaf balsamroot (*Balsamorhiza sagittata*), and Western yarrow (*Achillea millefolium*).

Site Selection/Elk Use

Maps of the study area generated using the GIS program ArcView were used to select sites using objective criteria. In order to control for potentially confounding variables, shrubsteppe areas were initially designated that 1) were of a similar soil and range type (gravelly loam and loamy, respectively), 2) were not currently or recently grazed by cattle, 3) were minimally or not used by grazing bison (*Bison bison*), 4) had not experienced fire since 1930 and 5) were of a similar slope and aspect. Radio telemetry data of collared elk generated by the U. S. Fish and Wildlife Service and National Park Service were then used to identify areas with high versus low elk use (Fig. 2). Thirty sites were established in relatively high elk use areas, whereas another 30 sites were established in low use areas, acknowledging that in reality these sites would represent a gradient of elk use. A final criteria was for sites to be ≤2 km from the nearest access road. The exact location of site centers was determined by randomly selecting UTM coordinates. Sites were separated by at least 400 m.

To better quantify elk habitat use, an index of elk density was also subsequently obtained at all sites by counting elk pellet groups. From each site center, 4 2 x 100-m transects were established, one in each of the cardinal directions within which pellet groups were counted. These counts were converted to pellet groups/ha to serve as a proxy for elk grazing intensity.

Avian Surveys

Birds were surveyed at each site using the variable circular-plot method (VCPM) (Reynolds et al. 1980). Each site was surveyed 3 times for 10 minutes between June 4 and July 6, 2001 with a separation of at least 5 days in between visits. Surveys were conducted between 0600 and 1000 when songbirds are most active. All birds observed visually or aurally were recorded, as well as the estimated distance and bearing of each bird from site center. Mean detections per survey visit (for all species combined and for each species individually) were calculated for each site. Total species richness was tallied by counting all species recorded at each site across the three survey visits. Only bird species that nest within the shrubsteppe were included in analyses.

Vegetation Measurements

Vegetation structure was quantified using a line-intercept method modified from Noon (1981). At each site, two 100-m transects were established from the site center. The bearing of the first transect was randomly selected prior to field work. The second transect was located directly opposite (180^o) the first. Transects were divided into 10-m sections. Shrub cover was estimated along every third section by measuring the beginning and ending distance of each shrub overlapping the vertical plane of the transect line. The intersection distances were then totaled for each site and divided by the total distance of the transects (70 m) to obtain a percent shrub cover estimate. The total distance sampled was considered adequate because within each site shrub density was relatively homogeneous. Shrub cover estimates were calculated for all shrub species combined and for each shrub species individually. Mean shrub height/site was estimated by measuring the height at the tallest point of each shrub overlapping the entire transect line, adding all of the height measurements, and dividing by the total number of plants measured.

In the understory, percent ground cover estimates were obtained using a 0.5 x 0.5-m frequency frame placed at 25-m intervals from plot center along the two transects (total of 9 locations at each site). The side of the transect on which to place the frame was chosen randomly and the frame was placed directly next to the transect line. Aerial ground cover was assessed by visually estimating the percent of ground within the frame covered by grass (bunch and sod-forming), forbs, cryptogamic soil, litter, rock, and bare ground. Basal ground cover was estimated by recording the ground cover type (vegetation, litter, bare ground or rock) touching the points of 4 tines extending from the frequency frame. The aerial and basal percent estimates were averaged from the 9 samples to obtain a mean percent per site.

Noxious weeds were surveyed at each site using two methods. First, we visually inspected a 10-m strip centered along the two 100-m transects and recorded the presence and species of any weeds observed. Secondly, we conducted an intuitive controlled survey in which we inspected any micro-sites within the site that appeared to have areas with disturbed soil substrates (old road beds, trails et cetera) for weeds.

Analytical Procedures

Analyses were performed using SPSS statistical software. Relationships between elk habitat use and vegetation variables, elk habitat use and avian variables, and avian variables and vegetation variables (Table 1) were initially explored using Pearson correlation matrices with 2-tailed tests. Variables not normally distributed were transformed using either log(x) or square root transformations. Because many of the vegetation variables were correlated, Principle Components Analysis (PCA) was used to reduce the number of variables. Multiple linear regression was used to present the best model for each comparison. Regression models were chosen using stepwise linear regression to maintain only those variables explaining the greatest amount of variation in the response variables.

RESULTS

Elk Use and Vegetation Structure

High elk use areas were characterized by relatively low total shrub cover, low *A. tridentata* cover, and low *P. tridentata* cover (Table 2; Fig. 3). No relationship was apparent between elk use and *A. arbuscula* cover. There were highly significant negative correlations between elk use and shrub height (total and *A. tridentata*). Percent bunch grass and total grass cover in the understory decreased significantly with increasing elk use (Fig. 4) whereas sod-forming grass cover was independent of elk use. Forb cover and total aboveground herbaceous cover (forbs + grass) was inversely related to elk use. Percent cryptogamic soil, bare ground and rock increased with higher elk use. Basal understory measurements were determined to be highly correlated with the associated aerial cover parameters (Fig. 5). Basal measurements were thus not strong explanatory variables and were omitted from further analysis. Based on stepwise multiple linear regression, the strongest model ($r^2 = 0.63$, $P = 0.000$) describing elk habitat use in terms of vegetation included the following variables: TOTSHCOV ($t = -4.16$, $P = 0.000$), BARE ($t = 1.835$, $P = 0.072$), and FOGR ($t = -$

5.718, $P = 0.000$).

Noxious weed presence was documented at only two sites, that both experience relatively low ungulate use. At one site, a musk thistle plant was located in the middle of an old road bed that ran through the site. At the second site, there was no sign of soil disturbance in the immediate vicinity, but there was a fairly well traveled private dirt road nearby (approximately 300 m) along which several musk thistle plants were located.

Elk Use and Avian Community Structure

A total of eight species of birds that nest within the shrubsteppe of GTNP were detected during the study (Fig. 6). These species included, in order of abundance, Brewer's Sparrow, Vesper Sparrow, Green-tailed Towhee, Sage Thrasher, Western Meadowlark (*Sturnella neglecta*), Brewer's Blackbird (*Euphagus cyanocephalus*), Horned Lark (*Eremophila alpestris*) and Sage Grouse (*Centrocercus urophasianus*). Individual abundance analyses were possible for all species except for Brewer's Blackbirds, Horned Larks and Sage Grouse which were not detected in high enough frequencies. Other bird species observed foraging within the shrubsteppe during the avian surveys included White-crowned Sparrows (*Zonotrichia leucophrys*, 16 observations), American Robins (*Turdus migratorius*, 14 observations), Northern Flickers (*Colaptes auratus*, 8 observations) Chipping Sparrows (*Spizella passerina*, 4 observations), and Mountain Bluebirds (*Sialia currucoides*, 4 observations). Common Ravens (*Corvus corax*), a notorious nest predator, were commonly observed flying in the study area, but only once was a bird seen perched in sagebrush. Brown-headed Cowbirds, a songbird brood parasite, were observed very rarely (2 observations) although cowbirds were commonly heard calling from nearby forest patches.

Total bird abundance (TOTABUND), avian species richness (RICHNESS) and the abundance of all species individually except for Vesper Sparrows were highly negatively correlated to elk use (TOTSCAT) (Table 3; Fig. 7).

Avian Community Structure and Vegetation

Birds appeared to be responding to vegetation structure attributes of both the overstory and understory of the shrubsteppe (compare Figs 8 and 9). Total breeding bird abundance was significantly positively related to total shrub cover, *A. tridentata* cover, *P. tridentata* cover, overall shrub height, *A. tridentata* height, forb cover, and total herbaceous ground cover (Table 4; Fig. 10). Bird abundance was significantly negatively related to amount of cryptogamic soil. Based on stepwise multiple linear regression, the strongest model ($r^2 = 0.47$, $P = 0.000$) explaining total bird abundance (TOTABUND) included the following variables: TOTSCAT ($t = -.1694$, $P = 0.096$), TOTSHCOV ($t = 2.942$, $P = 0.005$) and FORBS ($t = 2.656$, $P = 0.010$).

Avian species richness was significantly positively correlated to total shrub cover, *A. tridentata* cover, *P. tridentata* cover, overall shrub height, *A. tridentata* height, forb cover and total herbaceous ground cover (Table 5; Fig. 11). Richness was significantly negatively correlated to *A. arbuscula* cover, and amount of cryptogamic soil, rock and bare ground. Based on stepwise multiple linear regression, the strongest model explaining RICHNESS ($r^2 = 0.423$, $P = 0.000$) included only two variables: TOTSCAT ($t = -3.537$, $P = 0.001$) and TOTHT ($t = 2.753$, $P = 0.008$).

Brewer's Sparrow abundance was significantly positively correlated to overall shrub cover, *A. tridentata* cover, overall shrub height, *A. tridentata* height, and forb cover (Table 6; Fig. 12). Abundance of Brewer's Sparrows was inversely related to the amount of cryptogamic soil. Based on stepwise multiple linear regression, the strongest model describing BRSP ($r^2 = 0.52$, $P = 0.000$) included the following variables: TOTSHCOV ($t = 5.010$, $P = 0.000$), FORBS ($t = 4.744$, $P = 0.000$) and ATHT ($t = -2.352$, $P = 0.022$).

Vesper Sparrow abundance was significantly positively correlated to *A. arbuscula* cover, and amount of rock and bare ground (Table 7; Fig. 13). Abundance of Vesper Sparrows was negatively related to overall shrub cover, *P. tridentata* cover, overall shrub height, *A. tridentata* height, and amount of bunchgrass, total grass, and litter in the understory. Based on stepwise multiple linear regression, the strongest model describing VESP ($r^2 = 0.58$, $P = 0.000$) included only two variables: PTSHCOV ($t = -6.901$, $P = 0.000$), and ROCK ($t = 3.959$, $P = 0.000$).

Green-tailed Towhee abundance was positively related to total shrub cover, *A. tridentata* cover, *P. tridentata* cover, overall shrub height, *A. tridentata* height and amount of litter (Table 8; Fig. 14). Abundance of towhees was negatively related to *A. arbuscula* cover, and amount of cryptogamic soil, rock, and bare ground. Based on stepwise multiple linear regression, the strongest model describing GTTO ($r^2 = 0.63$, $P = 0.000$) included only two variables: PTSHCOV ($t = 6.421$, $P = 0.000$), and TOTHT ($t = 4.950$, $P = 0.000$).

Sage Thrasher abundance was positively related to overall shrub cover, *A. tridentata* cover, overall shrub height, and total herbaceous ground cover (Table 9). Abundance of Sage Thrashers was negatively related to *A. arbuscula* cover, and the amount of crytogamic soil, rock and bare ground. Based on stepwise multiple linear regression, the strongest model describing SATH ($r^2 = 0.32$, $P = 0.000$) included only two variables: TOTSCAT ($t = -5.130$,

$P = 0.000$) and ATHT ($t = -2.054$, $P = 0.045$).

Western Meadowlark abundance was significantly positively related to overall shrub cover, *P. tridentata* cover, overall shrub height, and the amount of grass and litter in the understory (Table 10; Fig. 16). Abundance of Western Meadowlarks was negatively related to the amount of cryptogamic soil, rock and bare ground. Based on stepwise multiple linear regression, the strongest model describing WEME ($r^2 = 0.53$, $P = 0.000$) included the following variables: PTSHCOV ($t = 2.342$, $P = 0.023$), TOTSCAT ($t = -4.240$, $P = 0.000$) and LITTER ($t = 3.289$, $P = 0.002$).

DISCUSSION

Several relationships between elk habitat selection and vegetation structure were identified during the study. Shrubsteppe areas in the park receiving higher grazing pressure from elk generally had lower shrub cover and vertical complexity, and understories with lower herbaceous cover and higher cryptogamic soil, rock, and bare ground cover. Because this study did not take a manipulative approach, however, a strict cause and effect relationship cannot be established from these data. Elk may be altering the shrubsteppe structure in areas where they graze intensively. Hobbs et al. (1996), for example, found that herbaceous dry matter declined in linear relation to elk density. The amount of bare ground and exposed rock has also been shown to increase with grazing (Singer and Harter 1996, Singer et al. 1998). Other studies, however, have documented positive or neutral responses of vegetation to intermediate levels of grazing. Singer and Harter (1996) found that forb biomass was higher on grazed sites than on ungrazed sites. Singer et al. (1998) found no differences in aboveground standing-crop biomass of plants between grazed and ungrazed areas.

An alternative hypothesis, however, is that elk are selecting habitats with low shrub cover and certain understory characteristics and hence the structure of those areas is independent of elk use. We controlled for major differences due to soil type, however more subtle differences in soil type or microclimatic conditions may be influencing the vegetation structure in the park. Edge et al. (1987) found, however, that elk make broad use of available habitats and that site-specific habitat selection was not evident in their study. In another study, moreover, McCorquodale (1987) found that elk were more selective of foraging habitats than bedding habitats and that elk selected areas without sagebrush because there was a higher availability of forage there. In the current study the percent of herbaceous cover varied independently of shrub cover and if anything was higher in areas with higher shrub cover. The overall availability (biomass) of forage in the understory, however, may indeed be higher in areas with lower shrub cover because of the higher availability of soil substrate.

Shrubsteppe areas in GTNP with high bitterbrush cover were largely unutilized by elk despite evidence that bitterbrush is high quality forage for wild ungulates (Reiner and Urness 1982, Austin et al. 1984, Kucera 1997) albeit more so during the fall and winter months. A possible explanation for this is that areas with high densities of bitterbrush tended to have high overall shrub cover which could limit herbaceous plant availability and/or elk mobility, or that high bitterbrush sites were farther from optimal daytime refugia. Both forage production and avoidance of human disturbance have been shown to be important with respect to elk habitat selection (Irwin and Peek 1983).

Contrary to a priori predictions, elk use was not related to the prevalence of noxious weed species. This result contradicts studies showing that overgrazing on western rangelands has led to widespread changes in plant composition and has facilitated the invasion of introduced species (DiTomaso 2000). This suggests that either the elk grazing intensity in GTNP has not reached levels that would effect such changes (i.e. does not constitute "overgrazing"), wild ungulate grazing regimes affect the soil substrates differently than cattle, or the spread of noxious weeds in the park is still more localized in areas with human-induced soil disturbance. The former hypothesis is corroborated by Singer et al's (1998) data showing that native ungulates in Yellowstone had no effect on the presence of exotic plant species. Furthermore, the current study probably did not effectively answer the question of whether elk might be facilitating the spread of noxious weeds. To more effectively answer this, the spread of known weed patches in high versus low density elk areas should be compared over time. Weed infestations in the park tend to be located in areas that have experienced anthropogenic soil disturbance somewhat recently. For example, at the southeast end of Timbered Island (a small forested "island") a substantial patch of musk thistle is located where there used to be an old gravel-mining pit (see Appendix I.). Elk regularly travel through this area because it lies in between foraging areas in the shrubsteppe and daytime forested refugia. In effect, elk may indeed facilitate the spread of musk thistle, but this is only the proximate problem. Ultimately, the issue is the original human disturbance to the soil and conducting more effective mitigation to sites that might be susceptible to weed invasion.

Intensive elk grazing may also directly or indirectly impact the shrubsteppe breeding bird community. Total breeding bird abundance, avian species richness, and abundance of several species individually (Brewer's Sparrow, Green-tailed Towhee, Sage Thrasher, and Western Meadowlark) decreased with increasing elk grazing. Causal mechanisms for this relationship, however, have not been explored in this study or in others.

Several studies similarly suggest that birds respond to habitat changes caused by grazing by livestock, both in the form of decreased avian abundance (Douglas et al. 1992, Sutter et al. 1995, Bradford et al. 1998, Popotnick and Giuliano 2000) and diversity (Sutter et al. 1995, Bradford et al. 1998, Poptnik and Giuliano 2000). Furthermore, this result is consistent across a wide array of avian species and habitat types including shrubsteppe (Bradford et al. 1998), montane riparian (Douglas et al. 1992, Ammon and Stacey 1997), pinyon-juniper (Goguen and Mathews 1998), native grassland (Kantrud 1981), native prairie (Sutter et al. 1995), and ponderosa pine forest (Rumble and Anderson 1993).

Grazing effects on vegetation may impact birds via decreasing the availability of suitable nesting substrates (Ammon and Stacey 1997, Popotnik and Giuliano 2000), or preferred song post sites (Sutter et al. 1995). Avian nesting success may also be reduced because of increased detection rates of nests by predators (Ammon and Stacey 1997) or the augmentation of nest predator assemblages (Ammon and Stacey 1997, Chalfoun et al. *in press*) or brood parasites (Goguen and Mathews 1998). Another possibility is that vegetation changes induced by grazing alter insect populations which affects avian food availability (Rumble and Anderson 1993, Rambo and Faeth 1999). No studies were found, however, examining the effects of native ungulate grazing regimes on birds, which further precludes the development of more definitive hypotheses regarding the impacts of grazing on nesting birds.

Regardless of exactly why, shrubsteppe birds in the current study showed preferences for certain habitat characteristics. Overall bird abundance and species richness were higher in areas with higher structural complexity (density) and vertical complexity (height) in the shrub layer, and with dense herbaceous understories. Habitat heterogeneity has long been recognized as an important factor in structuring the composition of bird communities (Rotenberry and Wiens 1980, Blake and Hoppes 1986) and shrubsteppe bird species diversity has been shown to increase as the complexity of the plant community increases (McAdoo et al. 1989). Birds may also at least partly select habitats based on microclimatic conditions that affect fitness either through physiology or indirectly via the availability of food (Karr and Freemark 1983). Areas with denser vegetation may facilitate the retention of soil moisture and/or may moderate fluctuations of basal temperatures by providing more shade. Shrubsteppe birds may thus experience reduced abiotic stress in areas of denser vegetation.

Brewer's Sparrow abundance was positively related to shrub cover, height, and forb cover. Other studies corroborate this result. Knopf et al. (1990) concluded that Brewer's Sparrows were more abundant in landscapes dominated by sagebrush. Wiens and Rotenberry (1981) similarly found strong associations between Brewer's Sparrows and shrub coverage and local site floristics. And Vander Haegen et al. (2000) reported that Brewer's Sparrows were strongly related to shrub characteristics in a fragmented landscape in Washington. Brewer's Sparrows nest off the ground in sagebrush, and thus probably benefit from high shrub density for nest site selection and concealment from nest predators.

Green-tailed Towhees were only present on sites with high shrub density and complexity, and were strongly associated with the density of bitterbrush. Knopf et al. (1990) similarly described Green-tailed Towhee habitats as ecotones between sagebrush and other shrub species. Berry and Bock (1998) also report that Green-tailed Towhees selected habitats on the basis of local shrub characteristics and heterogeneity. Green-tailed Towhees nest either on the ground or off the ground in shrubs and thus would benefit from overall vegetation structure and complexity for increased nesting opportunities and concealment from predators.

Sage Thrashers were most abundant in areas with high sagebrush cover and height, and higher herbaceous ground cover. Moreover, in a study in central Utah, Castrale (1982) found that Sage Thrashers were only found in habitat patches containing the largest shrubs and hypothesized that nesting requirements best explained this result. Thrashers nest either on the ground at the base of or in sagebrush plants. The males of this species prefer elevated perches from which to sing while establishing and defending territories (Ehrlich et al. 1988).

Vesper Sparrows by contrast preferred more habitats with lower shrub density. Vesper Sparrows are typically considered a more open habitat species, and are even sometimes referred to as “grassland” species (Castrale 1982, Wiens and Rotenberry 1985). One surprising result, however, was that Vesper Sparrow abundance decreased with increasing grass cover and showed no relationship with amount of forb cover. Vesper Sparrows are ground-nesters and require understory vegetation for nest concealment.

Another somewhat surprising result was that Western Meadowlarks were only found in areas with high shrub density, and especially in areas with high amounts of bitterbrush. This contrasts results of other studies and the common association of Meadowlarks with open grasslands and meadows (Castrale 1982, Knick and Rotenberry 1995).

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

The results of this study exemplify the interconnectedness of ecosystems, and the importance of considering these relationships in management strategies (Fig. 17). Although this study cannot definitively assert that elk are significantly affecting the vegetation of the shrubsteppe in Grand Teton National Park, the results suggest this possibility and the need to more experimentally and quantitatively assess this relationship. This is especially important in terms of maintaining vegetation conditions that maximize the habitat quality for a wide array of shrubsteppe-obligate species, especially those such as passerine birds which have been showing marked population declines due to habitat alteration in other parts of the Intermountain West and throughout the Great Basin.

My recommendations are thus as follows. Initiate or encourage research that experimentally tests the relationship between elk grazing intensity and nesting birds, by for example, excluding elk from portions of the shrubsteppe and monitoring trends in bird communities over time. Because it is not enough, moreover, to know that birds exist in an area but rather whether they are also reproducing successfully, monitoring efforts should include an assessment of nesting success. Management of the shrubsteppe in the park should include consideration of maintaining areas with a dense, diverse, and complex shrub layer and dense herbaceous cover in the understory, to maximize shrubsteppe bird abundance and species richness. This will also probably have beneficial effects for Sage Grouse, a species of high conservation concern, and that similarly require high sagebrush and forb cover to successfully nest and rear their young. Finally, to determine whether high elk densities could in the future have a detrimental impact via helping to spread noxious weeds, the size of known weed patches in areas with and without high elk densities should be monitored over time.

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Table 1. Definitions of elk, bird, and habitat variables calculated from data collected at each

site ($N = 60$) during 2001 in the shrubsteppe of Grand Teton National Park, Wyoming.

Variable	*Definition*
TOTSCAT	Index of elk habitat use/grazing intensity (pellet groups/ha)
TOTABUND	Index of total avian abundance (mean detections per survey visit)
RICHNESS	Total avian species richness (# of species)
BRSP	Index of Brewer’s Sparrow abundance (mean detections per survey visit)
VESP	Index of Vesper Sparrow abundance (mean detections per survey visit)
GTTO	Index of Green-tailed Towhee abundance (mean detections per survey visit)
SATH	Index of Sage Thrasher abundance (mean detections per survey visit)
WEME	Index of Western Meadowlark abundance (mean detections per survey visit)
BRBL	Index of Brewer’s Blackbird abundance (mean detections per survey visit)
TOTSHCOV	% shrub cover (all species combined)
ATSHCOV	% shrub cover of Big Sagebrush
AASHCOV	% shrub cover of Low Sagebrush
PTSHCOV	% shrub cover of Antelope Bitterbrush
TOTHT	Mean shrub height (all species combined)

ATHT	Mean shrub height of Big Sagebrush
BUNCH	% ground cover of bunch grass species
SOD	% ground cover of sod-forming grass species
GRASS	% ground cover of all grass combined
FORBS	% ground cover of forbs
FOGR	% ground cover of herbaceous plants (forbs + grass)
LITTER	% ground cover of litter
MOLI	% ground cover of cryptogamic soil (includes moss, lichen)
ROCK	% ground cover of exposed rock
BARE	% bare ground exposed
Variable	*Definition*
BASVEG	% Basal ground cover of live vegetation
BASLITTER	% Basal ground cover of litter
BASROCK	% Basal ground cover of rock
BASBARE	% Basal bare ground

Table 2. Results of Pearson correlations between TOTSCAT (elk habitat use) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. $N = 60$ sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	-.593	.000
ATSHCOV	-.478	.000
AASHCOV	.196	.133
PTSHCOV	-.328	.010
TOTHT	-.524	.000
ATHT	-.540	.000
Understory		
BUNCH	-.381	.000
SOD	-.090	.495
GRASS	-.428	.000
FORBS	-.439	.000
FOGR	-.673	.000

MOLI	.462	.000
LITTER	-.002	.988
ROCK	.461	.000
BARE	.410	.001

Table 3. Results of Pearson correlations between TOTSCAT (elk habitat use) and breeding bird abundance/species richness in GTNP, Wyoming, 2001. $N = 60$ sites.

	Correlation Coefficient	*P*
Overall		
TOTABUND	-.558	.000
RICHNESS	-.588	.000
Individual Species (Abundance)		
BRSP	-.436	.000
VESP	.415	.001
GTTO	-.544	.000

SATH	-.521	.000
WEME	-.507	.000

Table 4. Results of Pearson correlations (2-tailed) between TOTABUND (total breeding bird abundance) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001.

N = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.569	.000
ATSHCOV	.446	.000
AASHCOV	-.113	.390
PTSHCOV	.338	.008
TOTHT	.474	.000
ATHT	.439	.000
Understory		
BUNCH	-.089	.497
SOD	.041	.758
GRASS	-.050	.705
FORBS	.487	.000

FOGR	.348	.006
MOLI	-.611	.000
LITTER	.092	.483
ROCK	-.056	.669
BARE	-.084	.523

Table 5. Results of Pearson correlations (2-tailed) between RICHNESS (avian species richness) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.515	.000
ATSHCOV	.407	.001
AASHCOV	-.368	.004
PTSHCOV	.391	.002
TOTHT	.544	.000
ATHT	.438	.000
Understory		
BUNCH	.156	.235
SOD	-.047	.719
GRASS	.143	.277
FORBS	.319	.013
FOGR	.369	.004

MOLI	-.441	.000
LITTER	.200	.126
ROCK	-.322	.012
BARE	-.265	.041

Table 6. Results of Pearson correlations (2-tailed) between BRSP (abundance of Brewer's Sparrows) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.564	.000
ATSHCOV	.506	.000
AASHCOV	-.007	.956
PTSHCOV	.198	.130
TOTHT	.333	.009

ATHT	.340	.008
Understory		
BUNCH	-.158	.229
SOD	-.121	.359
GRASS	-.202	.121
FORBS	.535	.000
FOGR	.252	.052
MOLI	-.440	.000
LITTER	.018	.890
ROCK	.119	.366
BARE	.018	.889

Table 7. Results of Pearson correlations (2-tailed) between VESP (abundance of Vesper Sparrows) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*

Overstory		
TOTSHCOV	-.543	.000
ATSHCOV	-.124	.346
AASHCOV	.279	.031
PTSHCOV	-.681	.000
TOTHT	-.410	.001
ATHT	-.408	.001
Understory		
BUNCH	-.329	.010
SOD	-.093	.481
GRASS	-.337	.009
FORBS	.122	.355
FOGR	-.150	.252
MOLI	.056	.670
LITTER	-.440	.000
ROCK	.477	.000
BARE	.452	.000

Table 8. Results of Pearson correlations (2-tailed) between GTTO (abundance of Green-tailed Towhees) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.668	.000
ATSHCOV	.294	.023
AASHCOV	-.291	.024
PTSHCOV	.688	.000
TOTHT	.604	.000
ATHT	.622	.000
Understory		
BUNCH	.158	.228
SOD	.129	.328
GRASS	.185	.156
FORBS	.121	.357
FOGR	.250	.054

MOLI	-.357	.005
LITTER	.321	.012
ROCK	-.301	.019
BARE	-.344	.007

Table 9. Results of Pearson correlations (2-tailed) between SATH (abundance of Sage Thrashers)and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.285	.027
ATSHCOV	.288	.026
AASHCOV	-.268	.039
PTSHCOV	.234	.071
TOTHT	.257	.047
ATHT	.093	.480
BUNCH	.247	.057
SOD	-.186	.156
GRASS	.209	.110
FORBS	.182	.163
FOGR	.263	.043

MOLI	-.261	.044
LITTER	.183	.163
ROCK	-.297	.021
BARE	-.282	.029

Table 10. Results of Pearson correlations (2-tailed) between WEME (abundance of Western Meadowlarks) and shrubsteppe vegetation structure measurements in GTNP, Wyoming, 2001. *N* = 60 sites.

	Correlation Coefficient	*P*
Overstory		
TOTSHCOV	.436	.000
ATSHCOV	.098	.457
AASHCOV	-.239	.066
PTSHCOV	.563	.000
TOTHT	.294	.022
ATHT	.176	.178
Understory		
BUNCH	.243	.061
SOD	.081	.541
GRASS	.306	.018
FORBS	-.126	.336
FOGR	.153	.243

MOLI	-.269	.038
LITTER	.472	.000
ROCK	-.445	.000
BARE	-.473	.000

FOR ADDITIONAL TABLES AND GRAPHS FOR THIS REPORT, PLEASE CONTACT KATHY TONNESSEN, kat@forestry.umt.edu 406-243-4449