The availability of Sage-grouse prey during brood-rearing varied among years and with vegetation structure

Lusha M. Tronstad, George Jones and Joy Handley

Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming 82071

Suggested citation: Tronstad, L.M., G.P. Jones and J. Handley. 2021. The availability of Sage-grouse prey during brood-rearing varied among years and with vegetation structure. Report prepared by the Wyoming Natural Diversity Database, University of Wyoming, Laramie, Wyoming for the Wyoming State Office of the Bureau of Land Management.

Abstract

The low availability of invertebrate prey may be a leading cause of the decline of Greater Sage-grouse (*Centrocercus urophasianus*), but few studies addressed the question. Chicks of Sage-grouse primarily eat beetles, ants, grasshoppers and caterpillars; however, the density and biomass of these insects during the brood-rearing period likely varies with weather and vegetation structure. We investigated insects during the first 2 weeks of June when Sage-grouse chicks were hatching in central Wyoming from 2018-2021. We measured vegetation characteristics in 25 x 25 m plots and within 3 microplots (5 x 5 m) in four shrub cover classes. Concomitantly, we counted beetles, grasshoppers and ant mounds in the entire plot, and sampled shrubs and litter in microplots to investigate how invertebrate density and biomass were related to vegetation characteristics. The shrub cover classes divided plots according to ground measurements of shrub cover and density. Many characteristics of vegetation did not vary among shrub cover classes, but canopy cover of forbs and live shrubs, and rock soil cover differed among some shrub cover classes. Beetles, ants, grasshoppers and caterpillars were the most abundant and had the highest biomass of insects we captured suggesting that the primary prey of Sage-grouse chicks is also the most available. We counted more grasshoppers in denser stands of shrubs, more ant mounds in sparser stands of shrubs and we observed the most beetles in intermediate shrub cover. Insects in litter were denser and had higher biomass in denser shrub stands. Insects in shrubs were more abundant and had higher biomass in sparser shrub stands. Taller shrubs with larger variance in heights, more litter, and higher shrub canopy cover were areas with the densest insects and the highest invertebrate biomass. The insects available as prey varied among years with the fewest individuals and lowest biomass during wetter years, and more insects in shrubs during warmer years. Sagebrush communities with differing vegetation characteristics likely offer different dominant insects that may be preyed upon, but taller sagebrush with a diversity of heights offered the most prey.

Introduction

The range-wide decline of Greater Sage-grouse (*Centrocercus urophasianus*; Sage-grouse hereafter) is likely explained by a variety of interacting factors. Research suggests that the viability of Sage-grouse populations largely depended on chick recruitment into the adult cohort, a population constraint that appears to be common for grouse worldwide (Hannon and Martin 2006, Connelly et al. 2011). Mortality of Sage-grouse is highest during the first two weeks of life, with cold weather, predation and lack of food, particularly invertebrate prey, as the primary causes of mortality (Hannon and Martin 2006). Invertebrate prey is vital to chick survival (Johnson and Boyce 1990, Drut et al. 1994, Thompson et al. 2006). Hens typically prefer brooding habitat with higher densities of insects (Fischer 1996). Additionally, invertebrate availability of Lepidoptera was positively related to brood survival in Nevada and Oregon (Gregg and Crawford 2009). Several studies (Connelly and Braun 1997, Sveum et al. 1998) point to low-quality brood-rearing habitat as a general limit to Sage-grouse populations, and low availability of invertebrate prey may be the primary factor. Furthermore, many proximate causes of chick mortality, such as succumbing to cold weather or predators, may result from poor body condition that is ultimately caused by low availability of invertebrate prey (Beckerton and Middleton 1982).

A large proportion of the diet of Sage-grouse chicks is insects (Patterson 1952, Klebenow and Gray 1968, Johnson and Boyce 1990, Blomberg et al. 2013). Insects provide a rich source of protein for rapidly growing chicks. Previous studies found that chicks mainly eat ants (Formicidae, Hymenoptera), beetles (Coleoptera), grasshoppers and crickets (Orthoptera; Patterson 1952, Klebenow and Gray 1968).

Patterson (1952) collected Sage-grouse chicks widely within Wyoming and discovered that insects were equally important in chick diets as forbs during the entire first two months of life (June and July). For example, 55% of the diet of one week old chicks was ants. In southeastern Idaho, 75-100% of Sage-grouse-chicks ate insects during the first month of life, and ants and beetles were the most common diet items (Klebenow and Gray 1968). Adult Sage-grouse also rely on the same prey taxa. In fact, adults eat insects from May through September each year, and insects account for 12% of their annual diet (Patterson 1952). In central Montana, 15% of Sage-grouse adults ate true bugs (Hymenoptera), 27% ate grasshoppers and crickets, and 3% ate beetles (Wallestad et al. 1975).

Throughout most Sage-grouse range, and especially in the high-elevation basins of Wyoming, the egg-laying and brood-rearing seasons are quite cold and late spring snowstorms are common. Cold springs limit plant growth and fewer insects may also emerge compared to springs with warmer temperatures. Wet springs bring the needed moisture for new plant growth, but low temperatures inhibit growth. More moisture may increase the likelihood of fungal infections in insects and warmer temperatures are usually crucial during spring for their success. Insect populations likely vary among years depending on climate, conditions during the previous year and other variables. Insects are a critical protein source for Sage-grouse and other vertebrates in the sagebrush steppe making insects a limited resource (Stiven 1961). The egg-laying and brood-rearing seasons are the times when protein requirements of Sage-grouse hens (producing eggs) and chicks (rapid growth) are at their highest (Beckerton and Middleton 1982). Insects provide much more protein for foraging chicks than plants, even later in the brood-rearing season when primary production increases (Stiven 1961). The need for protein in late spring and early summer by Sage-grouse may be common among vertebrates in the Intermountain region.

Scientists and wildlife managers are well-aware that Sage-grouse need sagebrush and forbs in their diet (Huwer et al. 2008), and much effort has been committed to researching and mapping those resources. In contrast, the relationships between habitat characteristics and invertebrate prey, especially early in the brood-rearing period, have received little attention. Managers and policy makers currently use a variety of Sage-grouse habitat maps in attempts to integrate Sage-grouse conservation with a suite of other important land uses. A major piece of the picture is missing; models describing the availability of insects vital to Sage-grouse during the early brood-rearing period. We modelled the abundance and biomass of insects available as prey to Sage-grouse during the early brood-rearing period as a function of landscape, climate and vegetation in the Greater South Pass Sage-grouse Core Area of Wyoming. Our primary goal was to provide insight into insect availability during a season when insects are a critical resource to Sage-grouse. By developing the information, we will fill critical gaps in both ecological knowledge and management effectiveness. Our objective was to investigate relationships between the availability of insect prey needed by Sage-grouse as a function of vegetation during the early brood-rearing season.

Study Area

We conducted the study in the Greater South Pass Core Area for Sage-grouse (Figure 1) identified by the State of Wyoming in its policy on management of Sage-grouse (Office of the Governor 2011). The specific areas that we studied within the Greater South Pass Core Area were chosen after examining data on Sage-Grouse brood-rearing habitat (Kurt Smith, unpublished data).

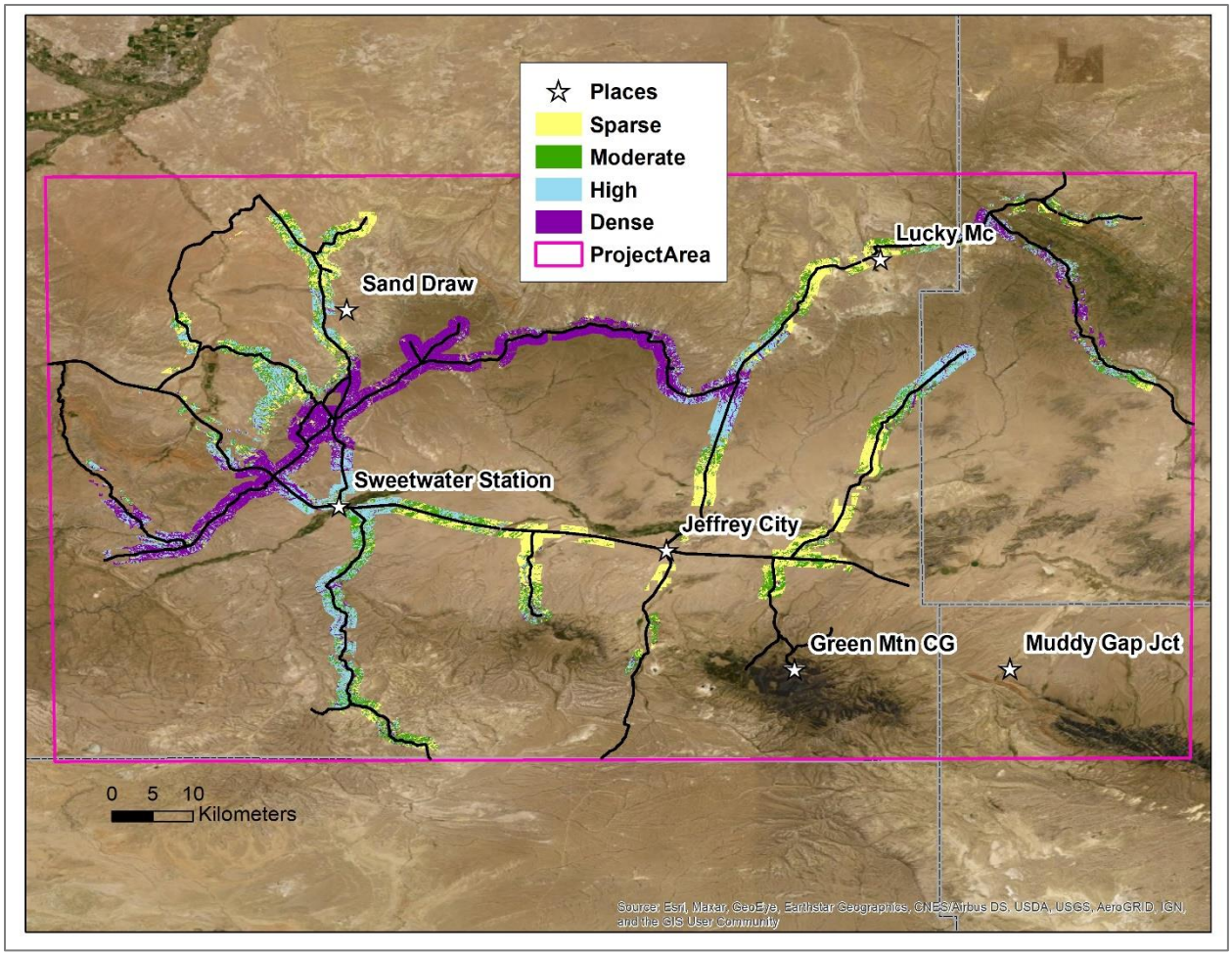


Figure 1. Map of the study area in central Wyoming depicting the four classes of shrub cover classes sampled during the study. Black lines are roads.

Methods

Climate

We used climate data from the Jeffrey City, Wyoming, weather station (484925) tabulated on the Western Regional Climate Center (WRCC) website https://wrcc.dri.edu/summary/Climsmwy.html to estimate how air temperatures and precipitation alters insect availability. Spring precipitation was obtained from the monthly total precipitation table and mean air temperature was from the monthly average of average temperature table.

Plot selection

We stratified the Greater South Pass Core Area based on the dominant land cover types using the GAP Ecological Systems layer (Davidson et al. 2009). The stratification was based on shrub canopy density using a 30-meter resolution raster layer in the project area. The pixels of that raster were sorted by amount of canopy cover and were divided into quarters using the quartiles. Sparse was 0 to 25% of maximum density, moderate was 25 to 50% of maximum density, high was 50 to 75% of maximum density and dense was >75% of maximum density (Figures 1, 2). We used ArcGIS to clip the stratified layer to a buffer within 1000 m of public roads in the project area and to exclude lands not administered by the BLM. In ArcMap, about 20 locations were randomly placed on public land each year of the study, using a spatially balanced method to allocate them proportionally to the area occupied by each of the major land-cover types and to avoid repeating plots from previous years. Potential sampling points were organized into pairs with a primary point and a secondary point at each location within 50 meters of each other. We selected a second point in case the primary option was judged to be unsuitable in the field (too close to a road, fence, livestock gathering area such as a mineral block, or other human disturbance). One plot was 25 x 25 m. We selected 6 core plots that were sampled annually for insect characteristics to estimate how spring weather altered insect availability.

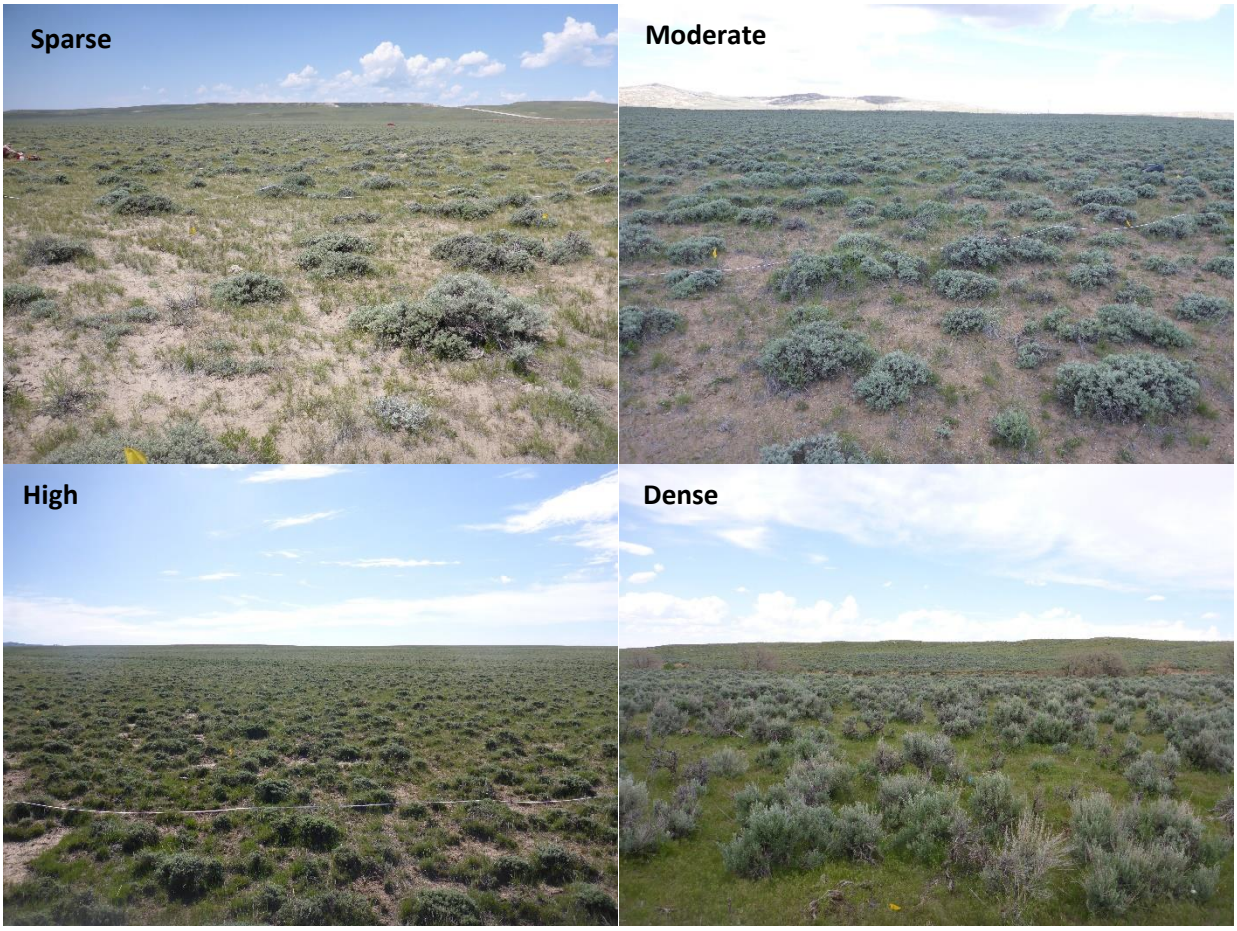


Figure 2. Examples of shrub cover classes sampled during our study in central Wyoming.

Plot and vegetation characterization

At each site, we marked a 25 x 25 m plot within which we collected our data. Within each plot, we laid out three parallel transects with a reel tape stretched taut and anchored at each end. We also marked the corners of three microplots measuring 5 x 5 m. Each microplot was randomly placed along a transect using a random number generator that selected numbers between 0 and 20, the distance at which the microplot began. We recorded the coordinates of the plot. We recorded information to characterize the physical setting of the plot (Herrick et al. 2016).

We used the point-intercept method to collect data about percent plant canopy cover, percent litter cover and percent ground cover (Herrick et al. 2016). Plant heights were measured at different points along the transects. A plant species list was made from the point-intercept data augmented by a search of the entire plot. We identified plants to species when possible. For plants that could not be identified in the field, we pressed specimens to identify later. We measured plants at 75 points along three transects in 2018 and 2019, and we measured 25 points along one transect in 2021.

Percent cover

Percent plant canopy cover was sampled at 100 cm apart along the transects using the point intercept method. At each point, a wire 1.5 mm in diameter was lowered to the ground, with the wire held vertical and allowed to fall to the ground without being guided by the observer. Each intercepted plant was recorded as alive or dead. Live plants were those that were rooted and had produced live tissue in the year of measurement. They included parts of perennial herbaceous plants or of woody plants that supported live canopy, even if the part of the canopy touched by the pin appeared to be dead. Dead plants were those that did not appear to have produced live tissue during the year of measurement. If the same species of plant was intercepted 2 or more times at a point, only one intercept was recorded. If both live and dead canopies of the same species were intercepted at a point, only the live intercept was recorded.

Percent plant canopy cover was estimated as the proportion of the intercept points at which plant canopy was intercepted at any level. For each plot, we estimated three percent cover values: cover of herbaceous plants, woody plants and of all plants. Each estimate was calculated using the intercept points in the plot (that is, the points from all the transects in a plot were combined for the calculation).

Percent litter cover and percent ground cover were sampled using the same intercept points as were used for plant canopy cover. Herbaceous litter consisted of detached plant parts $\leq$ 5 mm in diameter and dung. Woody litter consisted of detached plant parts >5 mm in diameter. Ground cover was the material that the pin intercepted at the soil surface and consisted of these seven categories: plant base (living or dead plant material rooted in the soil), cyanobacterial crust, moss, lichen attached to the soil, vagrant lichen, rock (fragments > 5 mm in diameter but not apparently continuous beneath the plot), bedrock (rock that appeared to be continuous beneath the plot) and bare soil (including rock fragments $\leq$ 5 mm in diameter). Percent litter cover was estimated as the proportion of the intercept points in the plot at which plant litter was intercepted at any level. We examined total litter cover, herbaceous litter cover and woody litter cover separately. Percent ground cover for a given category was estimated as the proportion of the intercept points in the plot at which each type of ground cover was intercepted.

We analyzed and prepared plots showing how canopy and soil cover differed among shrub cover classes in Program R (version 4.0.3; R Project for Statistical Computing, Vienna, Austria). We made histograms and selected the distribution that best fit the data for each variable. Most variables best fit a gamma distribution, but a few were normally distribution and meet statistical assumptions. For normally distributed data, we used analysis of variance (aov) to estimate how each variable differed among shrub cover classes. For other variables, we used generalized linear models (glm; package lme4) to estimate how each type of cover varied with shrub cover classes run with a gamma distribution (Bates et al. 2015). We used emmeans to estimate differences among shrub cover classes (Lenth 2021).

Plant heights

We measured the height of plants using the point-intercept method along transects and in microplots. Heights of herbaceous and woody plants in the point-intercept method were measured at points 200 cm apart along each transect and lying 15 cm to one side of the transect. The points lay 15 cm from the right edge of the tape, looking from the beginning of the transect (the 0 point on the tape) to the end. At each point, a rod was held vertically, and a 15-cm long rule was turned around the rod to describe a cylinder 30 cm in diameter, centered on the point and extending upward from the ground surface. The heights of the tallest herbaceous plant part and of the tallest woody plant part within the cylinder were recorded. The plants did not have to be rooted in the cylinder. The maximum height of ≤30 shrubs in each microplot were measured using a meter stick.

Heights were measured as the perpendicular distance (relative to the Earth's center) from the soil surface at the point (i.e., at the center of the cylinder), regardless of the slope or the unevenness of the ground. Plant parts were not straightened or held upright for the measurements. Heights up to 2 meters tall were recorded to the nearest centimeter. The identity of each measured plant was recorded, and it was noted as being alive or dead.

We analyzed and prepared plots showing how woody and herbaceous plant heights differed among shrub cover classes in Program R (version 4.0.3; R Project for Statistical Computing, Vienna, Austria). We calculated mean height and the standard deviation for each plot or microplot and date. We made histograms and selected the distribution that best fit each variable. Both variables best fit a gamma distribution. We used generalized linear models (glm; package lme4) to estimate how plant heights varied with shrub cover classes run with a gamma distribution (Bates et al. 2015). We used emmeans to estimate differences among shrub cover classes (Lenth 2021).

Shrub density and volume

Shrub density and volume were calculated from measurements taken within each microplot. Shrub density was estimated from counting the number of shrubs rooted in each of the microplots divided by 25 m^2 (area of microplot). The identity of each shrub was recorded, and we measured the height to the nearest cm. We measured the volume of one shrub at the corner of each microplot (n = 4). Three measurements were made on each shrub: the thickness of the canopy (the distance between the bottom and the top of the canopy), the length the canopy (measured along the longest axis), and

the width of the canopy (measured along the axis perpendicular to the longest axis). Volume was calculated as the product of canopy thickness, length and width.

Insect sampling

We estimated the availability of insects using four collection methods: shrub samples (Figure 3a), litter samples (Figure 3b), ant mound counts (Figure 3c) and whole-plot searches for large insects with emphasis on grasshoppers and beetles (Figure 3d, e). Shrubs and litter were collected in each of three microplots (5 m x 5 m). We counted ant mounds and large insects by walking transects 3 m apart, immediately after marking out the plot (Beever and Herrick 2006). To estimate the availability of insects living in shrubs, we selected one shrub (usually a sagebrush) in each of three microplots. We placed a bag over the selected sagebrush and cut the stem. Ethanol was poured over the shrub, and the black bag was sealed, hung and placed in the sun for at least two hours. We struck the main stem of the shrub with a hammer 20 times to dislodge insects and we collected the material in the bottom of the bag for analysis. We measured three dimensions (width, depth and height) of the shrub to estimate area and volume of the canopy to investigate relationships between invertebrate availability and shrub characteristics. To measure availability of insects in the litter layer, we collected litter samples from under each shrub sampled using a 43 cm x 43 cm frame with 1 mm^2 mesh sewed over the top to inhibit insects from escaping (Ausden and Drake 2006). We identified, counted and measured the length of all insects in the laboratory. Large insects and ant mounds were counted in the entire plot. Walking transects flushed grasshoppers and we observed scurrying ground insects (e.g., Tenebrionidae and Scarabaeidae) for easy counting. We measured air temperature and wind speed using a Kestral unit before walking transects.

We processed litter and shrub samples in the laboratory to estimate the availability of insects. Insects were separated from debris and generally identified to family using a dissecting microscope and available keys. All insects were counted and measured for length to estimate biomass using published length-mass regressions, $Mass = 0.0305 \times Length^{2.62}$, where mass is in mg and length is in mm (Rogers et al. 1976, Jarosik 1989). To estimate invertebrate density in litter, we counted the number of individuals per sample and calculated the density (ind/m^2) using the size of the frame. For shrub sampling, we calculated the density of insects based on shrub area (width x depth; ind/m^2).

We analyzed the number of grasshoppers and beetles in plots and included shrub cover class, wind speed and air temperature in the model using glm (Bates et al. 2015). The number of ant mounds was analyzed using shrub cover class only, because ant mounds should not vary by weather on the day of observation. We used emmeans to estimate differences in the number of insects or mounds among shrub cover classes (Lenth 2021). We analyzed the density and biomass of insects in litter and shrub samples using mixed effect models where shrub cover class, air temperature, wind speed and year were fixed effects and site was a random effect (glmer models). We used emmeans to estimate if categorical variables with ≥3 levels differed from one another in Program R (version 4.0.3; R Project for Statistical Computing, Vienna, Austria).

We sampled insects at 6 sites during all years to estimate how weather altered their availability. We sampled 1 site in the sparse cover class, 2 sites in the moderate and high cover classes and 1 site in the dense cover class. We used mixed effect models (glmer) where year, total spring precipitation,

mean spring temperature (March to May) were fixed effects and site was a random effect to investigate invertebrate characteristics (Bates et al. 2015). We analyzed the number of grasshoppers and active ant mounds per plot, as well as the density and biomass of insects in litter and shrub samples. We did not analyze beetles because they were not systematically counted in 2018.

Figure 3. We collected insects on sagebrush (a) and in litter (b), and we counted ant mounds (c) beetles (d) and grasshoppers (e) in whole plots.

Relationship between insects and vegetation

We used correlation and information criterion to investigate what vegetation characteristics best explained insect density and biomass. We calculated and plotted pearson's correlations using the package corrgram (Wright 2021). We used Akaike information criterion (AIC; Anderson et al. 2000) to select the vegetation characteristics that best explained total invertebrate density and biomass (sum of shrub and litter samples) using the lme4 package (Bates et al. 2015) in R (version 4.0.3; R Project for Statistical Computing, Vienna, Austria). We used mixed effect models (glmer) where vegetation characteristics were fixed effects, and year and site were random effects. We used our knowledge of insects, vegetation and the ecosystem to make a priori models. The model with the smallest AIC value was the model that best explained the invertebrate characteristics. We included fewer models for invertebrate biomass because several of the models would not converge.

Results

We collected 60 samples at 43 plots between 2018 and 2021 during the first 2 weeks of June when Sage-grouse chicks hatched. Precipitation did not vary among years (t = -0.33, p = 0.75), but the amount that fell varied among some months (Figure 4a). March, April, May and June received more precipitation than most other months of the year (glm, t > 2.6, p< 0.01). 2019 was the wettest year we collected data and the most spring precipitation fell that year. The driest spring that we collected samples was in 2021. Mean temperature did not vary among years (t = 0.86, p = 0.39), but mean temperature differed between most months (t > 2.2,p < 0.03; Figure 4b). The coolest spring was 2019 and 2018 was the warmest spring.

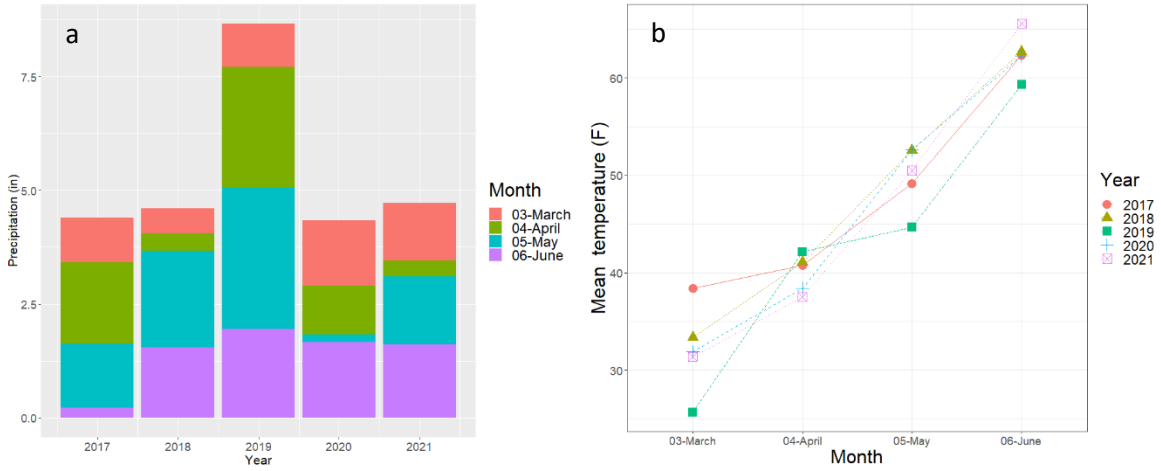


Figure 4. Spring precipitation (a) and mean air temperature (b) recorded by month at a weather station at Jeffrey City, Wyoming between 2017 and 2021.

Vegetation

All plots were in sagebrush steppe vegetation and dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), black sagebrush (*Artemisia nova*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*) or rubber rabbitbrush (*Ericameria nauseosa*). Graminoids generally shared dominance with shrubs (in terms of canopy cover). The common graminoids among plots were Sandberg bluegrass (*Poa secunda*), western wheatgrass (*Pascopyrum smithii*), thickspike wheatgrass (*Elymus lanceolatus*), prairie Junegrass (*Koeleria macrantha*), threadleaf sedge (*Carex filifolia*), squirrel tail (*Elymus elymoides*), needle and thread (*Hesperostipa comata*), sixweeks fescue (*Vulpia octoflora*), bluebunch wheatgrass (*Pseudoroegnaria spicata*) and Indian ricegrass (*Achnatherum hymenoides*). Cheatgrass (*Bromus tectorum*). Common forbs included spiny phlox (*Phlox hoodii*), stemless mock goldenweed (*Stenotus acaulis*), woolly plantain (*Plantago patagonica*), and species of sandwort (*Arenaria*), desert parsley (*Lomatium*), and fleabane (*Erigeron*).

Plant and soil canopy cover

Plant canopy cover differed among some shrub cover classes. Total canopy cover averaged 72% among plots, and there was more live (71%) than dead plants (<1%) in the canopy. Total (aov, F = 2.7, p = 0.05; Tukey's HSD, p = 0.05) and live (aov, F = 2.7, p = 0.05; Tukey's HSD, p = 0.05) canopy cover were

higher in the dense cover class compared to the moderate cover class (Figure 5). Dead (glm, t = 0.03-1.4, p = 0.16-0.97), annual grass (glm, t = 0.03-0.66, p = 0.51-0.975) and perennial forb (glm, t = 0.87-2.1, p = 0.04-0.39; emmeans, p > 0.14) canopy cover did not differ among shrub cover classes. Perennial grass had the highest cover of all the types we measured (51%), but the proportion of canopy cover did not vary among shrub cover classes (glm, t = 0.8-1.5, p = 0.13-0.45). We measured higher canopy cover of forbs in the dense shrub cover classes compared to the moderate shrub cover class (glm, t = 2.3-2.8, p < 0.03; emmeans, p = 0.03). The dense shrub cover class had the lowest proportion of points that lacked any type of canopy or ground cover (glm, t = 2.1-3.8, p < 0.05; emmeans, p = 0.0009). Shrub canopy cover was highest in the dense cover class (glm, t = 2.7-3.6, p < 0.002; emmeans, p < 0.04; Figure 6) demonstrating that our dense shrub cover class had the highest shrub canopy cover. The cover of herbaceous (glm, t = 0.5-1.4, p = 0.17-0.63) and woody litter canopy cover (glm, t = 0.5-1.6, p = 0.12-0.62) did not differ among shrub cover classes.

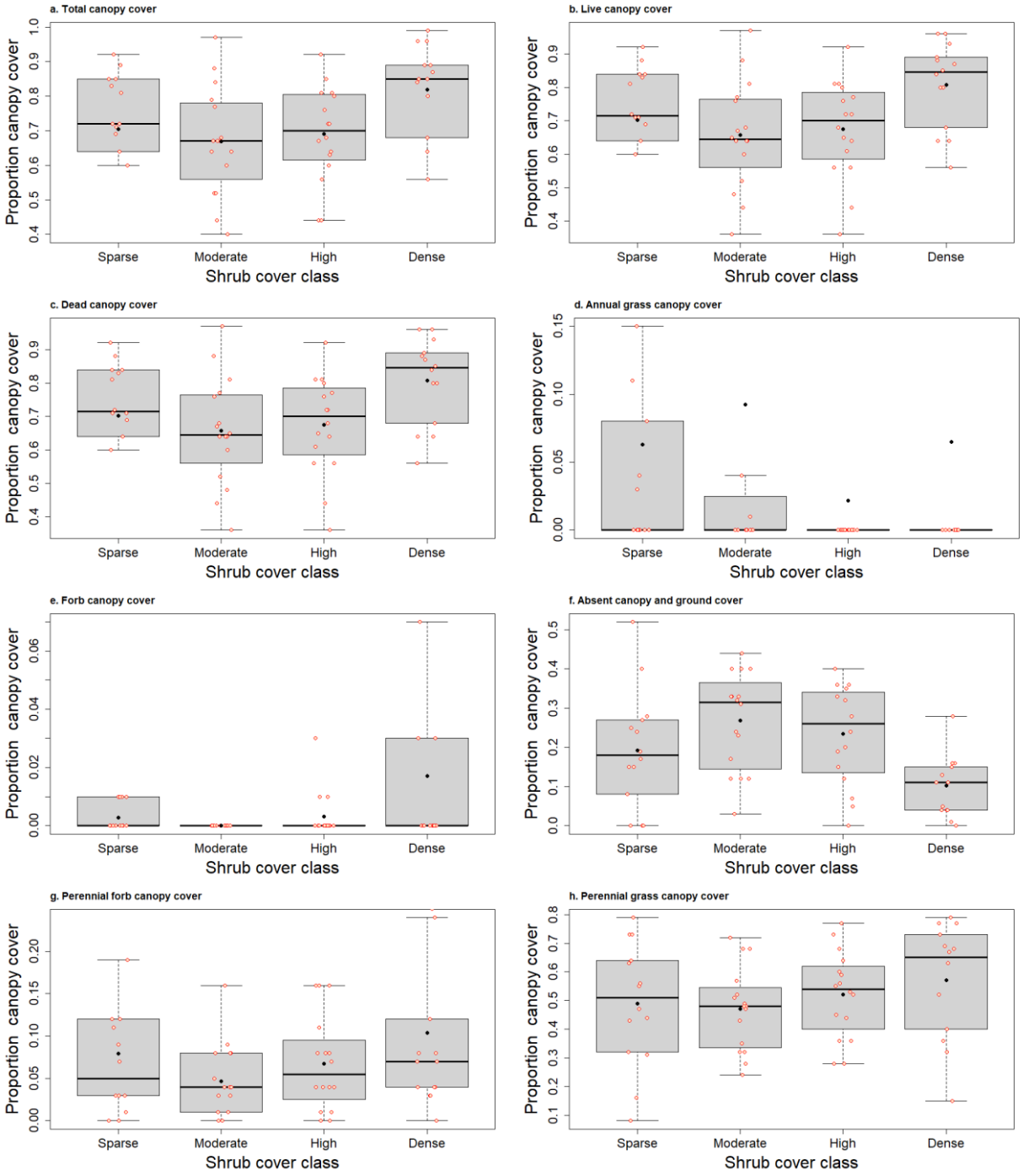


Figure 5. Total (a), live (b) and dead (c) canopy covered measured in each shrub cover class. We also measured annual grass (d), forb (e), absence of cover (f), perennial forb (g) and perennial grass canopy cover (h) in each shrub cover class. Bold line is the median, black circle is the mean, lower and upper edges of the box are the 25th and 75th percentiles, whiskers are the lower and upper limits of the data excluding outliers and open circles are the data points (one data point per plot).

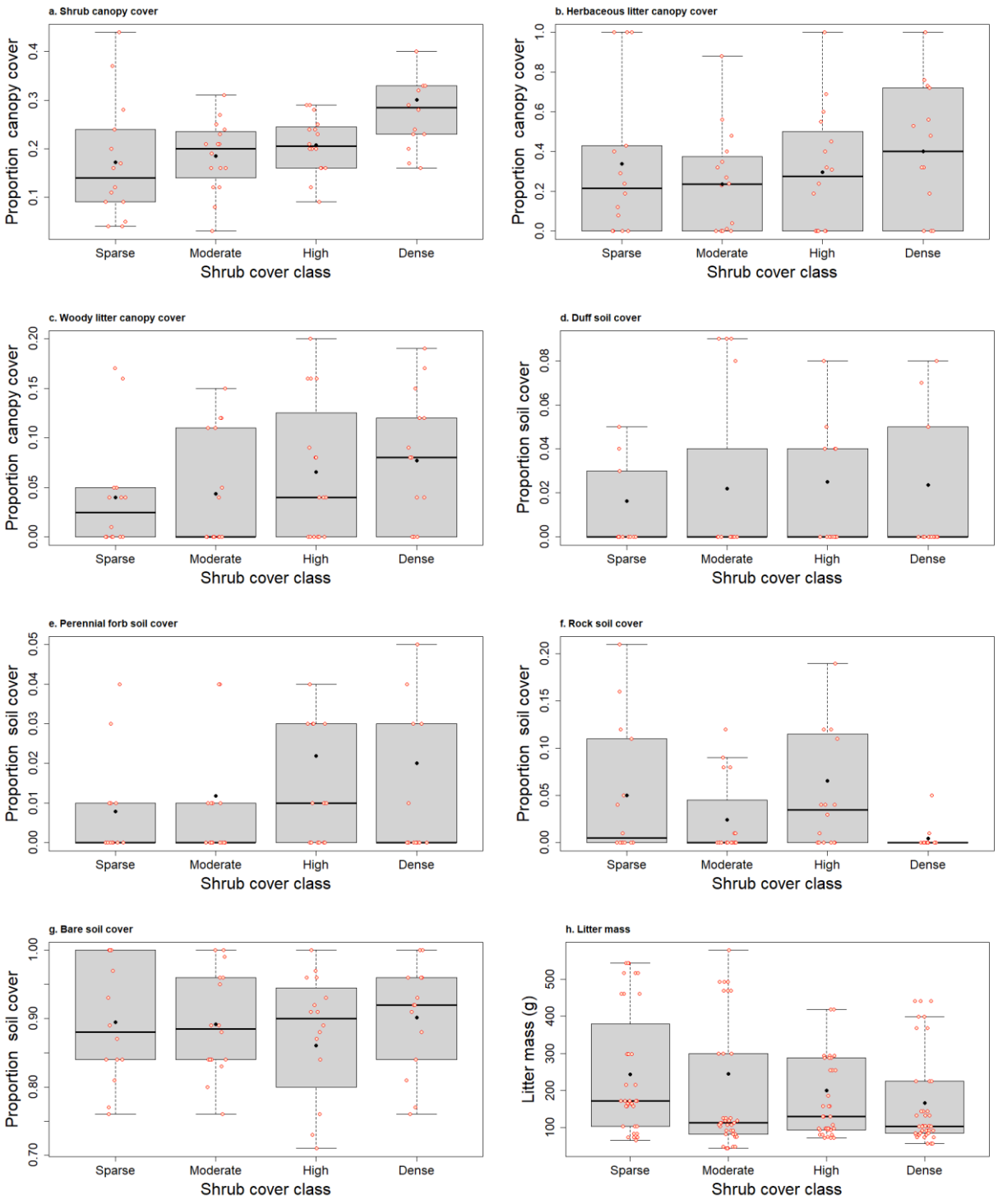


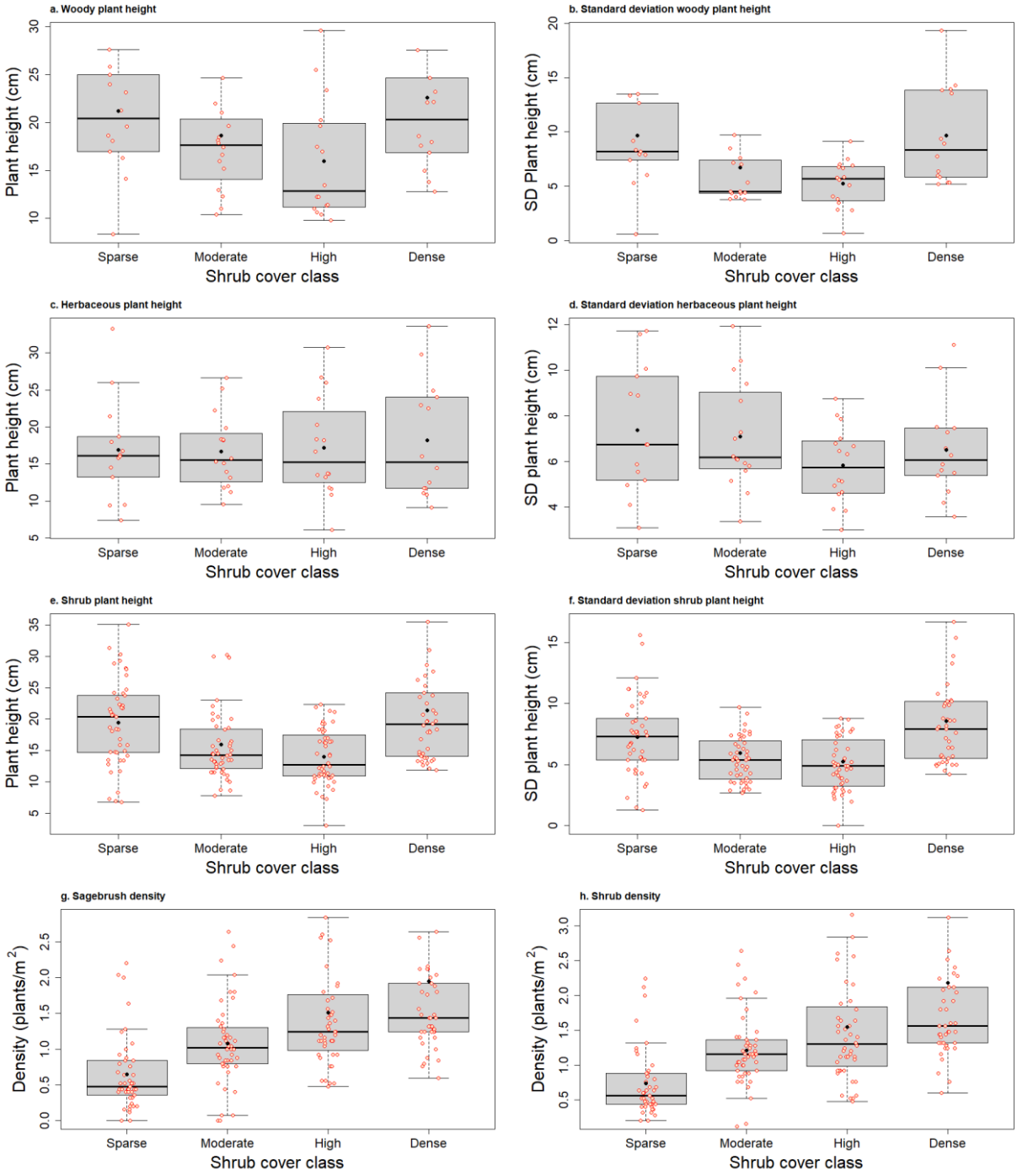
Figure 6. Shrub (a), herbaceous litter (b) and woody litter (c) canopy covered measured in each shrub cover class. We also measured soil cover of duff (d), perennial forb (e), rock (f) and bare soil (g), and the mass of litter (h) in each shrub cover class. Bold line is the median, black circle is the mean, lower and upper edges of the box are the 25th and 75th percentiles, whiskers are the lower and upper limits of the data excluding outliers and open circles are the data points (one data point per plot).

Soil cover in the sagebrush steppe of central Wyoming was primarily bare ground (89%). The proportion of duff covering the soil did not differ among shrub cover classes (glm, t = 0.4-0.6, p = 0.55-0.70; Figure 6). The proportion of lichen covering the soil was ≤8% and typically absent, and did not vary among shrub cover classes (glm, t = 0.7-1.7, p = 0.10-0.49). Similarly, the proportion of moss covering the soil was ≤3% and typically absent, and did not vary among shrub cover classes (glm, t = 0.3-1.5, p = 0.15-0.77). Soil cover by perennial forbs (glm, t = 0.2-1.2, p = 0.25-0.86) did not differ among shrub cover classes. We measured more rock on the ground in the high shrub cover class compared to the dense cover class (glm, t = 0.9-2.7, p = 0.01-0.38; emmeans, p = 0.04). The amount of bare ground did not vary among shrub cover classes (glm, t = 0.2-1.2, p = 0.24-0.84). The mass of litter did not vary among shrub cover classes (glmer, t = 0.45-1.2, p = 0.25-0.64 (Figure 6h).

Canopy height and volume

The average height of wood plants in the study was 19.5 cm and herbaceous plants averaged 17.2 cm. Using the point-line intercept, woody plants were taller in the dense shrub cover class compared to the high shrub cover class (glm, t = 0.4-2.4, p = 0.02-0.67; emmeans, p = 0.07; Figure 7a). The height of wood plants in the high shrub cover class were more uniform (smaller standard deviation) compared to the sparse and dense shrub cover classes (glm, t = 0.013-3.0, p = 0.004-0.98; emmeans, p <0.02; Figure 7b). Herbaceous plant height did not differ among shrub cover classes (glm, t = 0.4-0.6, p = 0.0.52-0.68; Figure 7c). The heights of herbaceous plants were fairly uniform among shrub cover classes (standard deviation did not differ; glm, t = 0.72-0.99, p = 0.32-0.48).

The height of shrubs measured in microplots were shorter in the high shrub cover class compared to the sparse and dense cover class (glm, t = 1.1-5.2, p < 0.0001-0.24; emmeans, p < 0.06) and the shrubs in the dense cover class were taller than those in the high and moderate cover classes (emmeans, p < 0.002; Figure 7e). Shrub height varied more in the dense shrub cover class than the moderate and high cover classes (glm, t = 1.4-2.8, p = 0.005-0.16; emmeans, p < 0.02) and the sparse cover class varied more than the high cover class (emmeans, p = 0.03; Figure 7f). The height and standard deviation of shrubs measured along transects followed the same pattern as height measured in microplots. Shrub volumes were largest in the sparse and dense shrub cover classes (glmer, t = 1.9-7.2, p < 0.0001-0.06; emmeans, p < 0.003; Figure 7i).


a. Woody plant height
Plant height (cm)
Sparse
Moderate
High
Dense
Shrub cover class
b. Standard deviation woody plant height
SD Plant height (cm)
c. Herbaceous plant height
d. Standard deviation herbaceous plant height
SD plant height (cm)
e. Shrub plant height
f. Standard deviation shrub plant height
g. Sagebrush density
Density (plants/m 2)
h. Shrub density

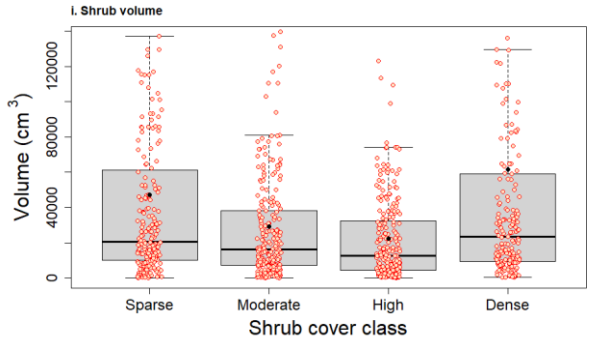


Figure 7. The height (a) and standard deviation (b) of woody plants in each shrub cover class measured using the point-intercept method, and the height (c) and standard deviation (d) of herbaceous plants. We observed the same pattern of shrub heights (e) and their standard deviation (f) in microplots. The density of sagebrush (g) and all shrubs (h) were highest in the dense shrub cover class. Bold line is the median, black circle is the mean, lower and upper edges of the box are the 25th and 75th percentiles, whiskers are the lower and upper limits of the data excluding outliers and open circles are the data points (one point per plot for transects ,three points per plot for microplots and all bush volume measurements shown).

Shrub Density

The density of sagebrush and all shrubs agreed with the shrub cover classes. The density of sagebrush was lowest in the sparse shrub cover class (glm, t = 1.5-5.2, p = <0.0001-0.14; emmeans, p < 0.0005), but the sparse and moderate classes did not differ (emmeans, p = 0.14; Figure 7g). The density of sagebrush was highest in the dense class and differed from the sparse and moderate shrub cover classes (emmeans, p < 0.008). Other shrubs growing in the plots were rabbitbrush and winterfat (*Krascheninnikovia lanata*), but these shrubs were typically much less dense than sagebrush. The density of all shrubs were lowest in the sparse shrub cover class (glm, t = 3.1-6.6, p = <0.0001-0.002; emmeans, p < 0.009). The high shrub cover class had denser shrubs than the moderate shrub cover class (emmeans, p = 0.002). Therefore, the shrub cover class layer we used to select plots appeared to seeperate shrub density on the landscape.

Insects

The number of grasshoppers in an entire plot did not vary with shrub cover class (glm, t = 0.2-1.6, p = 0.11-0.79, emmeans, p = 0.36-0.99; Figure 8a), but we observed increasing variance in denser cover classes. We did observe more grasshoppers at lower wind speeds (t = 2.1, p = 0.04) and lower temperatures (t = 2.4, p = 0.02). The number of beetles we observed did not vary with shrub cover class (glm, t = 0.03-0.65, p = 0.52-0.97, emmeans, p = 0.62-1.0; Figure 8b), but we observed more beetles at intermediate shrub cover. The number of beetles did not vary with wind speed (t = 0.74, p = 0.46) or air temperature (t = 0.61, p = 0.55). We counted more ant mounds in lower shrub cover classes than the higher shrub cover classes (glm, t = 0.69-2.5, p = 0.02-0.50, emmeans, p < 0.008-0.12; Figure 8c).

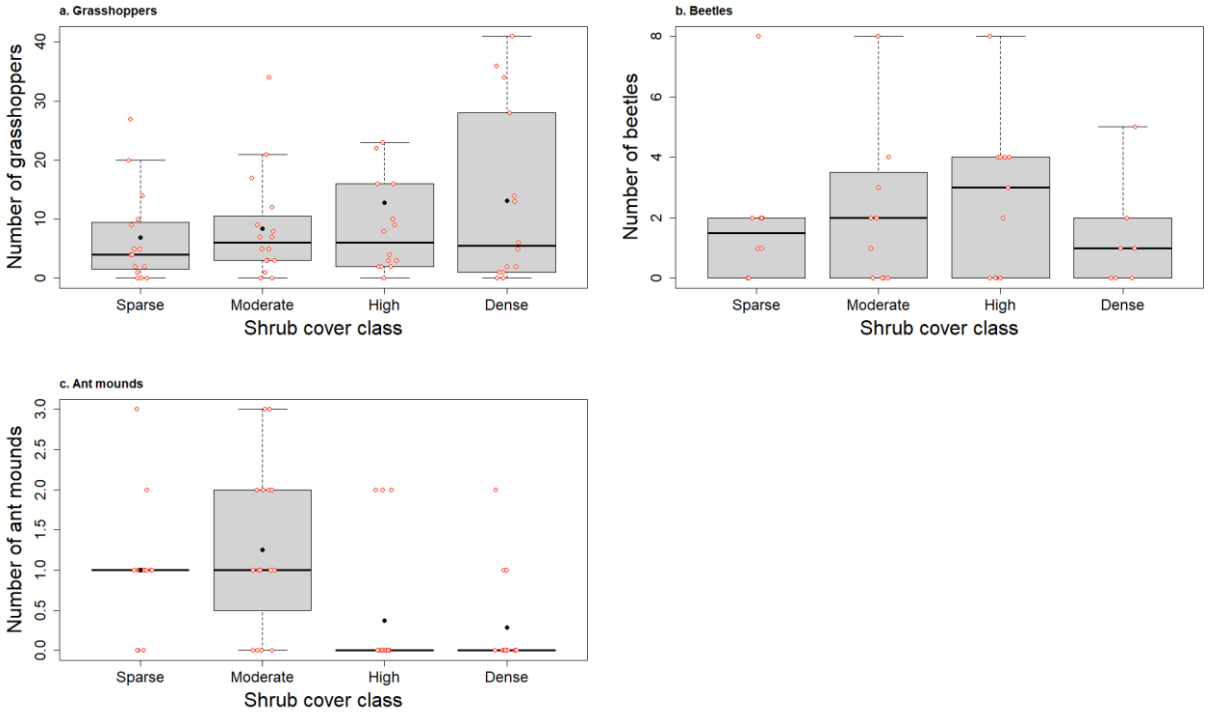


Figure 8. The number of grasshoppers (a) was highest in the dense shrub cover class, beetles (b) were more abundant at intermediate shrub cover and we observed more ant mounds (c) in areas with lower shrub cover.

Insects were 8.5x more abundant than arachnids in the litter. Beetles (Coleoptera) were the dominant order of insects found in the litter followed by Hymenoptera (primarily ants), Lepidoptera (caterpillars), pseudoscorpions, true bugs (Hemiptera), spiders and flies (Diptera). The most abundant families of insects were ants (Formicidae), ground beetles (Carabidae), weevils (Curculionidae) and darkling beetles (Tenebrionidae). The biomass of insects was >135x higher than spiders. Beetles had the highest biomass in litter followed by caterpillars and Hymenoptera. Ground beetles had the highest biomass of any family followed by darkling beetles, ants, weevils and click beetles (Elateridae). We identified 12 families of insects in 7 orders and members of the spider class (Arachnida; Table 1).

Insects in the litter had higher densities in the dense shrub cover class (glmer, t = 3.7-4.0, p < 0.0002; emmeans, p < 0.002; Figure 9a). Similarly, the biomass of insects was highest in the dense shrub cover class (glmer, t = 0.25-1.85, p = 0.06-0.80; emmeans, p = 0.08-0.38; Figure 9b). Invertebrate density did not vary with temperature (glmer, t = 0.15, p = 0.88) or wind speed (glmer, t = 1.3, p = 0.21). Invertebrate biomass varied with air temperature (glmer, t = 2.8, p = 0.005) but not wind speed (glmer, t = 0.07, p = 0.94). Neither invertebrate density (glmer, t = 0.25-1.7, p = 0.1-0.8) nor biomass (glmer, t = 0.05-0.2, p = 0.84-0.96) varied among years. The mass of litter did not vary with invertebrate density (glmer, t = 0.29, p = 0.77), but we observed higher biomass of insects in samples with more litter (glmer, t = 1.9, p = 0.06; Figure 9c).

Insects were nearly 10x more abundant than arachnids in shrubs. Hymenoptera were the densest order of insects followed by true bugs, beetles, spiders, and butterflies and moths. Ants were the most abundant family followed by plant bugs (Miridae). In terms of biomass, insects had >12x more

biomass in shrubs compared to spiders. Hymenoptera had the highest biomass followed by caterpillars, beetles, true bugs and spiders. Ants had by far the highest biomass followed by ground beetles, weevils, plant bugs and darkling beetles. We identified 28 families of insects in 11 orders and members of the spider class (Arachnida; Table 2).

Insects were densest in shrubs within the sparse shrub cover class (glmer, $t = 0.9\text{-}2.4$, $p = 0.02\text{-}0.36$, emmeans, $p = 0.007\text{-}0.80$; Figure 9d). The density of insects in shrubs was lowest in 2019 (glmer, $t = 0.38\text{-}4.4$, $p < 0.0001\text{-}0.70$; emmeans, $p < 0.0006$; Figure 9e). Invertebrate density was highest at lower air temperatures (glmer, $t = 2.5$, $p = 0.01$), but wind speed did not effect densities (glmer, $t = 0.9$, $p = 0.38$). Invertebrate biomass did not differ among shrub cover classes (glmer, $t = 0.56\text{-}1.4$, $p = 0.17\text{-}0.58$; emmeans, $p > 0.29$; Figure 9f). Invertebrate biomass was higher at lower air temperatures (glmer, $t = 1.8$, $p = 0.07$), but wind speed did not alter invertebrate biomass (glmer, $t = 1.4$, $p = 0.15$). The biomass of insects was far lowest in 2019 (glmer, $t = 0.4\text{-}4.2$, $p < 0.0001\text{-}0.66$; emmeans, $p = 0.0001$; Figure 9g).

Table 1. The density (ind/m^2), biomass (mg/m^2) and associated standard deviations (SD) of invertebrate taxa collected in litter in each shrub cover class.

	Mean density				SD density				Mean biomass				SD biomass		
	Dense	**High**	**Moderate**	**Sparse**	**Dense**	**High**	**Moderate**	**Sparse**	**Dense**	**High**	**Moderate**	**Sparse**	**Dense**	**High**	**Moderat**
Araneae	**16**	**16**	**16**	**16**	**0**				**21**	**0**	**81**	**5**	**0**		
Gnaphosidae				16								5			
Philodromidae			16								81				
Salticidae	16								54						
Thomisidae	16	16							6	0					
Coleoptera	**25**	**17**	**28**	**30**	**21**	**2**	**16**	**40**	**230**	**235**	**255**	**119**	**301**	**258**	**17**
Carabidae	32	19	49	16	32	7	23	0	265	228	348	81	235	158	24
Curculionidae	16	16	24	73	0	0	16	80	38	70	116	119	45	52	12
Dermestidae	16								3						
Elateridae	22				9				131				32		
Scarabaeidae	16			16					0			234			
Tenebrionidae	24	15	16	16	11	2			98	153	333	44	91	156	
Diptera				**16**								**333**			
Hemiptera	**24**	**41**	**16**	**32**	**0**	**34**			**15**	**19**	**6**	**7**	**5**	**20**	
Lygaeidae				16								6			
Miridae			16								8				
Scutelleridae	16				0				23				5		
Hymenoptera	**23**	**26**	**19**	**20**	**14**	**16**	**7**	**18**	**29**	**27**	**34**	**505**	**30**	**28**	**4**
Formicidae	23	26	19	23	14	16	7	18	29	27	34	48	30	28	4
Lepidoptera	**70**	**16**		**16**	**102**				**1322**	**180**		**1627**	**1656**		
Pseudoscorpiones	**25**	**16**			**16**	**0**			**6**	**2**			**4**	**2**	

Table 2. The density (ind/m^2), biomass (mg/m^2) and associated standard deviations (SD) of invertebrate taxa collected in shrub samples in each shrub cover class.

	Density				SD density				Biomass				SD biomass		
	Dense	High	Moderate	Sparse	Dense	High	Moderate	Sparse	Dense	High	Moderate	Sparse	Dense	High	Moderate
Araneae	14	6	8	14	5	1	6	2	8	8	12	3	5	2	15
Clubionidae	27	9	12		20		5		3	3	1		2		0
Dictynidae	15				9				4				1		
Gnaphosidae	3		4	31					0		0	6			
Linyphiidae			10								1				
Miturgidae		4								28					
Oxyopidae	6	9	11	5	2		8		16	19	53	4	13		55
Philodromidae	39		8	7			3	2	29		7	2			2
Pisauridae			5								10				
Salticidae	13	6	12	5	6	2	12	2	10	6	22	6	15	4	11
Theridiidae	5	5		5	0	1		1	1	0		1	1	1	
Thomisidae	6	6	4	31	2	0	1		2	3	5	3	1	2	6
Coleoptera	10	14	7	40	3	6	3	27	64	54	15	77	33	17	10
Carabidae	10				2				170				83		
Cleridae	6								8						
Coccinellidae	14	30		84				46	17	100		155			
Curculionidae	22	14	7	30	9	9	3	28	72	12	10	61	48	5	10
Scolytidae	4			37					1			19			
Tenebrionidae	11	7		32		2			177	77		88		28	
Collembola	3								1						
Diptera			12	37			6				6	45			0
Culicidae				37								45			
Hemiptera	8	22	8	68	4	15	7	45	3	17	6	34	1	4	3
Cicadellidae	5	39	4	3				1	2	82	1	6			
Coccidae		35	5	4		54	2	1		7	3	1		11	3
Lygaeidae	3		5	58				45	4		4	32			

Miridae		5	25	275		1	15	174		6	10	154		5	5
Ortheziidae	8	38			3				1	5			1		
Psylidae	15	5							4	2					
Reduviidae	3		4	56					1		18	6			
Hymenoptera	86	65	34	365	254	58	24	577	124	51	38	159	332	36	27
Formicidae	167	65	34	365	254	58	24	577	198	51	38	159	332	36	27
Vespidae	5								49						
Ixodida				7											
Ixodidae				7											
Lepidoptera		7	12	37		4	6	18		37	69	191		34	59
Orthoptera		36	5	19						59	12	4			
Pseudoscorpiones	12								3						
Psocoptera				6								3			

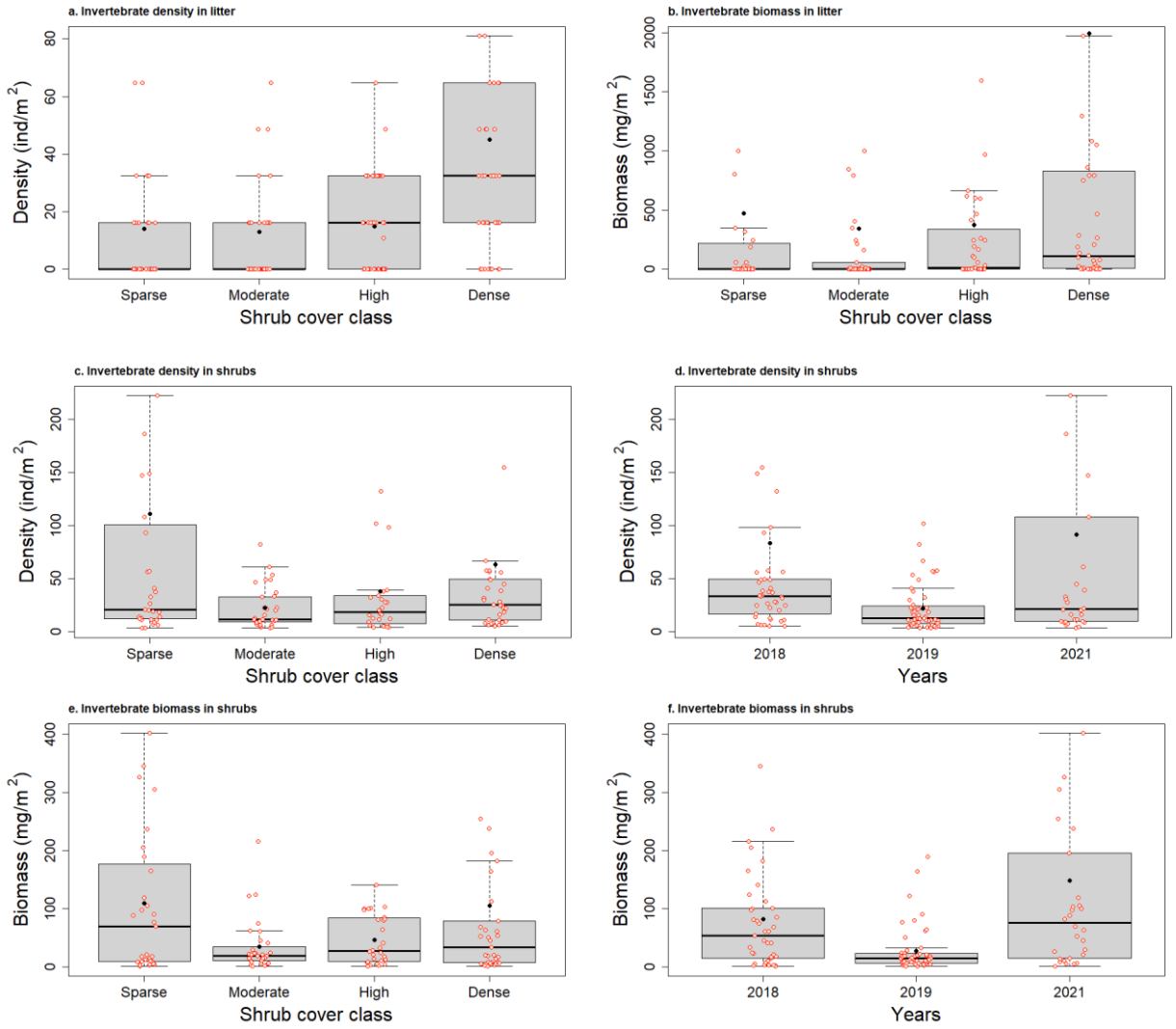


Figure 9. The density (a) and biomass (b) of insects in litter were highest in the dense shrub cover class. Insects were densest in the sparse shrub cover class (c) and densities were lowest in 2019 (d). Invertebrate biomass did not differ among shrub cover classes (e), but biomass was lowest in 2019 (f).

Insects among years

The number of grasshoppers differed among years and was highest in 2021 (glmer, t = 2.0-6.2, p <0.0001-2.4; emmeans, p < 0.05) and lowest during warmer springs (glmer, t = 2.8, p = 0.006), but the abundance did not vary with precipitation (glmer, t = 0.6, p = 0.53). The number of ant mounds did not vary among years (glmer, t = 0.2-1.4, p = 0.18-0.83; emmeans, p = 0.44-0.96).

The density of insects in the litter was lowest in 2021 (glmer, t = 1.2-2.1, p = 0.035-0.64; emmeans, p = 0.09). Neither mean spring temperature (glmer, t = 1.5, p = 0.14) nor total spring precipitation (glmer, t = 0.9, p = 0.35) explained the density of insects in litter. The biomass of insects in litter did not vary among years (t = 0.03-0.7, p = 0.47-0.97), but was highest in 2019. Neither spring mean temperature (glmer, t = 0.7, p = 0.46) nor total spring precipitation altered the biomass of insects

(glmer, t = 0.9, p = 0.37) in litter. The density of insects in shrubs was lowest in 2019 (glmer, t = 0.8-2.2, p = 0.03-0.44; emmeans, p = 0.02-0.07). Neither mean spring temperature (glmer, t = 1.3, p = 0.21) nor total spring precipitation (glmer, t = 1.5, p = 0.14) altered invertebrate density in shrubs. The biomass of insects in shrubs was also lowest in 2019 (glmer, t = 0.57-3.8, p < 0.001-0.57; emmeans, p < 0.001). Biomass of insects in shrubs was highest when mean spring temperatures were higher (glmer, t = 3.2, p = 0.003) and when total spring precipitation was lower (glmer, t = 3.6, p = 0.001).

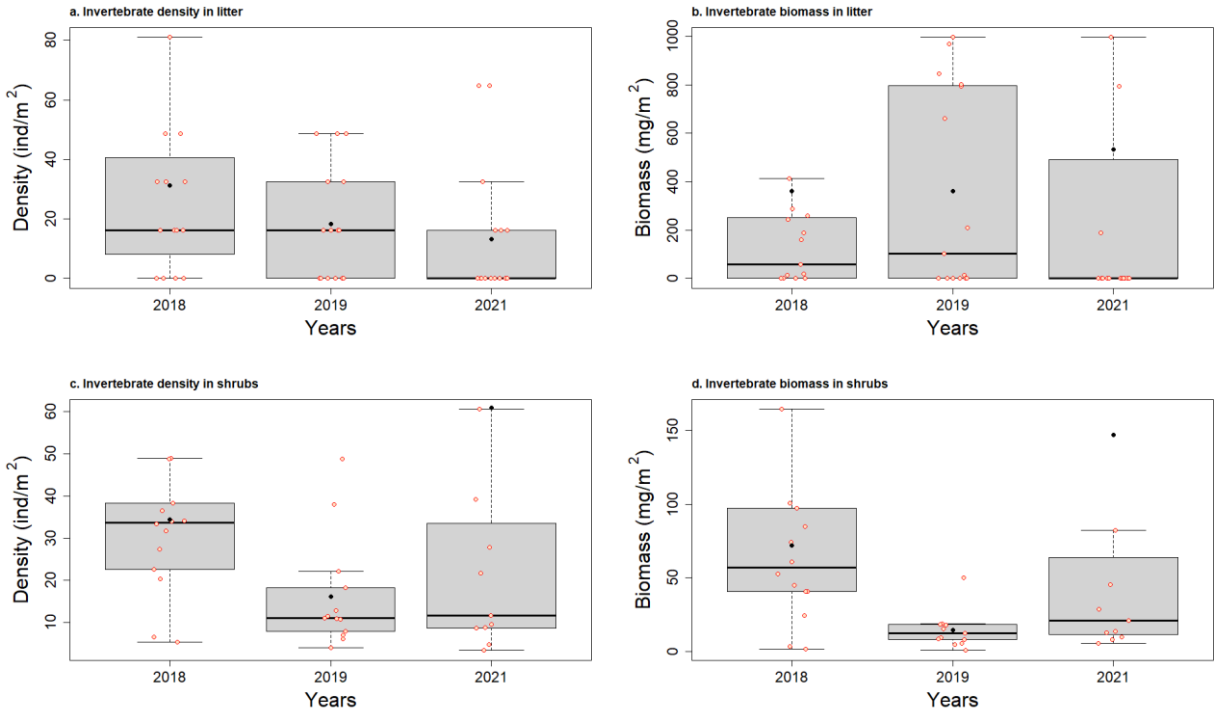


Figure 10. Invertebrate density (a, c) and biomass (b, d) in litter (a, b) and shrubs (c, d) among years.

Invertebrate and vegetation characteristics

Few invertebrate metrics were highly correlated (> 0.8) with vegetation characteristics (Figure 11). Invertebrate density was best explained in a model that contained the mean height and standard deviation of woody shrubs, the mass of litter and shrub cover (Table 3). Replacing shrub cover with total canopy cover increased the AIC value slightly. The height and standard deviation of woody plants, and mass of litter reduced the AIC values immensely compared to other potential models and was a competing model. Insect biomass was best explained by the mean height and standard deviation of woody plants, mass of litter and total canopy cover. No other models were close competitors. The mean and standard deviation of woody plant heights, litter mass and shrub cover were positively related to the total density and biomass of insects.

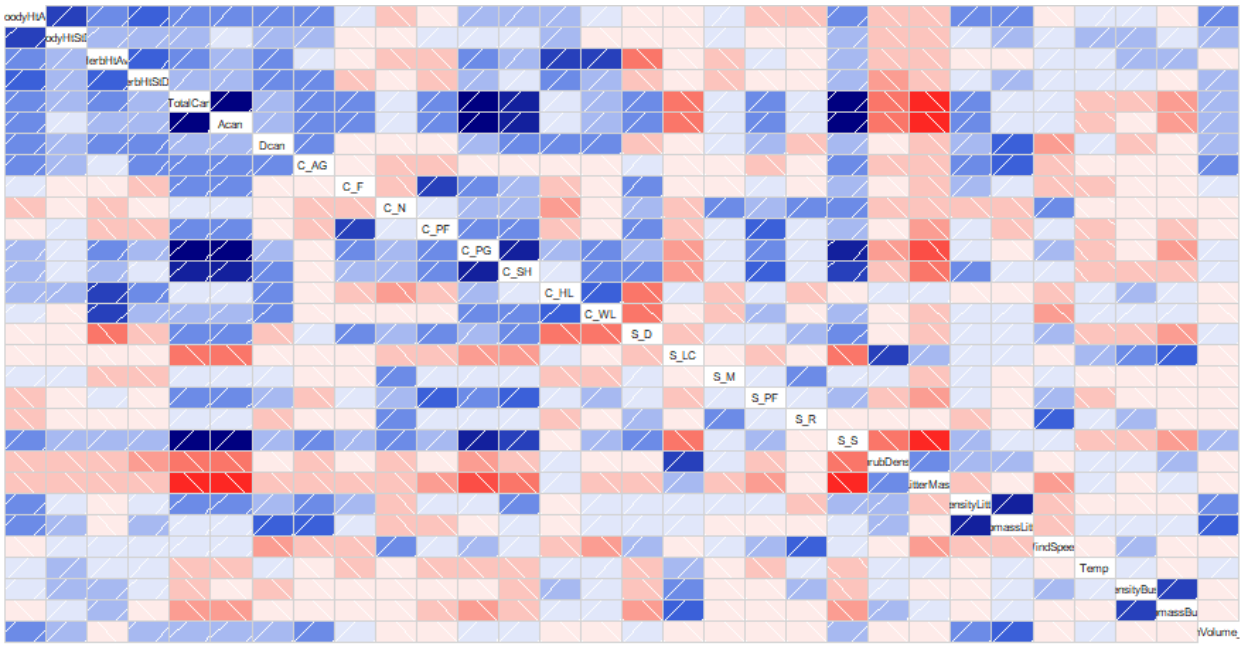


Figure 11. Pearson's correlations among vegetation characteristics, and invertebrate density and biomass. Darker blues indicate stronger positive correlation and darker reds indicate stronger negative correlations. Abbreviations starting in the upper left are mean height and standard deviation of woody shrubs, mean height and standard deviation of herbaceous plants, total canopy cover, live (Acan) and dead (Dcan) canopy cover, annual grass (C_AG), forbs (C_F), lack of canopy cover (C_N), perennial forbs (C_PF), perennial grass (C_PG), shrubs (C_SH), herbaceous litter (C_HL) and woody litter (C_WL), soil cover of duff (S_D), lichen (S_LC), moss (S_M), perennial forbs (S_PF), rock (S_R) and bare soil (S_S), shrub density, litter mass, density and biomass of insects in litter, wind speed, air temperature, density and biomass of insects in shrub, the total insects density and biomass (litter plus shrub) of insects in litter and shrub volume.

Table 3. Model selection to investigate vegetation characteristics that best explained insect density and biomass in litter and shrubs. We used mixed effect models where site and year were random variables.

Model	AIC	ΔAIC
Invertebrate density (ind/m^2; shrub + litter)		
Mean height woody shrub + SD height woody shrubs + litter mass + shrub cover	400.2	
Mean height woody shrub + SD height woody shrubs + litter mass + total canopy cover	403.2	3.0
Mean height woody shrub + SD height woody shrubs + litter mass	403.7	3.5
Mean height woody shrub + SD height woody shrubs	413.4	13.2
Litter mass	420.2	20.0
Mean height woody shrub + SD height woody shrubs + litter mass + annual grass canopy cover	437.3	37.1
Shrub cover class	440.0	39.8
Mean height woody shrubs	442.0	41.8
Mean height herbaceous plants	444.8	44.6
Mean height herbaceous plants + SD height herbaceous plants	445.3	45.1
Duff soil cover	448.0	47.8
Perennial grass canopy cover	449.7	49.5
Live canopy cover	450.5	50.3
Shrub cover	450.8	50.6
Rock soil cover	450.8	50.6
Total canopy cover	451.3	51.1
Bare soil cover	451.3	51.1
Herbaceous litter cover	451.6	51.4
Annual grass canopy cover	451.8	51.6
Live perennial forb cover	451.9	51.7
Lack of canopy and litter cover	451.9	51.7
Perennial forb canopy cover	451.9	51.7
Shrub density	455.3	55.1
Annual grass cover	494.3	94.1
Invertebrate biomass (mg/m^2; shrub + litter)		
Mean height woody shrub + SD height woody shrubs + litter mass + total canopy cover	7478.9	
Mean height woody shrub + SD height woody shrubs + litter mass + annual grass cover	7570.5	91.6
Mean height woody shrub + SD height woody shrubs + litter mass + total shrub cover	7592.2	113.3
Mean height woody shrub + SD height woody shrubs + litter mass + perennial forb cover	7658.6	179.7
Mean height woody shrub + SD height woody shrubs	7936.8	457.9
Shrub density	8280.8	801.9
Lack of canopy and litter cover	8411.9	933.0
Live canopy cover	8560.8	1081.9
Total canopy cover	8592.1	1113.2
Lack of canopy	8594.1	1115.2
Annual grass cover	8707.6	1228.7
Mean height woody shrub + shrub cover class	8791.8	1312.9
Mean height woody shrub + SD height woody shrubs + live canopy cover	8933.9	1455.0

Perennial grass canopy cover	8933.9	1455.0

Discussion

Insects can increase the growth and survival of Sage-grouse chicks, especially during the first two weeks of life (Thompson et al. 2006, Blomberg et al. 2013, Harju et al. 2013). Our intent was to measure vegetation characteristics to identify relationships between vegetation and the availability of invertebrate food to Sage-grouse during the early brood-rearing period. Our results suggest that taller woody plants, less uniform woody plant height, more litter and more shrub cover were vegetation structures that increased invertebrate density and biomass. Sage-grouse chicks eat insects that are on or near the ground, such as ants, beetles and grasshoppers. We generally observed more grasshoppers in denser stands of sagebrush, which is the opposite of what Hagen et al. (2005) reported. Beetles were more abundant in moderate and high shrub cover classes. We counted more ant mounds in the sparser shrub cover classes. Therefore, different insects are likely available to Sage-grouse chicks depending on the vegetation characteristics of the nesting location. Perhaps no single vegetation community will provide the maximum available insects of all orders for chicks. Overall, we measured more insects and higher biomass of insects in the litter within denser stands of sagebrush and more litter. Conversely, we estimated invertebrate densities in shrubs were higher in sparser shurbs stands, perhaps because of less available shrub cover.

Many studies measured the characteristics of vegetation that Sage-grouse nest in and the meaningful attributes differed among studies. For example, Sage-grouse in the Great Basin of Nevada and California tended to nest in locations with higher herbaceous cover and near water (Coates et al. 2020). Sage-grouse in Utah used sites with lower shrub cover and higher grass cover (Baxter et al. 2017). Conversely, Gunnison Sage-grouse (*Centrocercus minimus*) used areas with at least 10% sagebrush cover (Aldridge et al. 2012) and Sage-grouse in Wyoming selected sites with higher shrub cover, grass cover and taller grass (Holloran et al. 2010). Additionally, another study in Wyoming reported that Sage-grouse nest in locations with lower forb cover and higher sagebrush cover (Hansen et al. 2016). Taller vegetation has been associated with more protection from predators (Hansen et al. 2016), but taller vegetation can also have the benefit of more insects to feed on (e.g., grasshoppers and insects in litter). The height of shrubs was one of the main predictors in our model indicating more insects and higher invertebrate biomass. Therefore, taller sagebrush communities (within the bounds of our study) may provide more invertebrate prey for Sage-grouse chicks. Overall, Sage-grouse nest in a variety of vegetation structures and differences among studies may be due to differences in the landscape, available habitat, and other abiotic and biotic factors.

Vegetation characteristics have also been used to describe areas with higher chick survival. In Wyoming, higher survival of Sage-grouse chicks was associated with taller grass and sagebrush cover >30% (Hansen et al. 2016). Mean canopy cover in our dense shrub cover class was 30%. We measured more insects on the ground in areas with denser sagebrush and more grasshoppers, which may partially explain higher chick survival. In California, a higher percentage of chicks survived in areas with more non-sagebrush shrubs. At most sites in our study, shrubs were dominated by sagebrush, but rabbitbrush were more abundant at some sites and we also observed winterfat. Another Wyoming study showed that higher survival of chicks was associated with fewer caterpillars, lower density of sagebrush and more forbs. Caterpillars typically had lower abundance in our study, but Gregg and Crawford (2009) reported caterpillars being associated with higher survival. Lower density of sagebrush was associated with more ant mounds in our study. Ants are small insects with small individual biomass, but collectively they had some of the highest densities and biomass we measured. Ants are not limited

to mounds; many species make small colonies that were often dense in our study area (L. Tronstad, personal observation). Ants were common in both litter and shrub samples. Ants appear to be an abundant, readily available food source for chicks. Our study did not reveal a strong association between forbs and insects; however, Sage-grouse chicks readily eat forbs (Blomberg et al. 2013). Higher forb cover may provide more food for chicks along with the needed protein from insects as well as cover for protection from predators. Thompson et al. (2006) found a relationship between higher survival of chicks in areas with more Hymenoptera (presumably ants) and beetles, and more grass and herbaceous cover. Protein from insects is needed for chicks to survive the first few weeks of life (Johnson and Boyce 1990, Drut et al. 1994 Thompson et al. 2006), thus the global decline of insects could negatively affect survival (Sanchez-Bayo and Wyckhuys 2019).

Most vegetation characteristics did not vary among shrub cover classes. Total, live and dead canopy cover did not vary among shrub cover classes. In general, live canopy cover ranged between 35 to nearly 100%, and dead canopy cover was generally <5%. The canopy cover of annual grasses was highest in the sparse shrub cover class, but this variable did not explain the variation in invertebrate density or biomass. Forb canopy cover was generally low (<10%) but peaked in the dense shrub cover class. Most studies found higher chick survival in denser sagebrush and more forbs provide more food. All other measures of forb and grass cover did not vary among shrub cover classes. The shrub cover layer we used to select sites divided areas by shrub canopy cover; however, the moderate and high classes were nearly identical. The density of sagebrush and shrubs we measured showed that the spatial layer did a good job of dividing the sites among classes. We expected overlap as the vegetation across the landscape varies, even within 30 x 30 m pixels. Most soil cover did not differ among shrub cover classes, except we observed less rock and more perennial forbs in the denser shrub cover classes. The height of shrubs varied in surprising ways with the tallest shrubs in the sparse and dense shrub cover classes, and the most uniform heights in the medium shrub cover classes. The height of herbaceous plants varied little among shrub cover classes. Sage-grouse typically nest in areas with vegetation heights between 23 and 46 cm (Hansen et al. 2016). The height of woody plants varied between 7 and 30 cm in our study and the height of herbaceous plants varied between 7 and 35 cm, thus a portion of our sites had vegetation within the height window for Sage-grouse nesting. In addition to the added protection from taller vegetation, we found more insects in areas with taller woody plants.

Annual weather appeared to play a large role in the availability of insects in early June. The high plains of Wyoming are well-known for late snowstorms that can drop up to a meter of snow on the ground throughout the spring and into early June. The wet, cold conditions caused by late snowstorms can directly increase mortality of Sage-grouse chicks. Such conditions can also alter the density and biomass of insects available for chicks. Spring is late to arrive in central Wyoming with elevations >1900 m and the insects are often beginning to emerge. Conditions can vary widely among years in terms of precipitation and temperature. For example, 2019 had intermediate mean spring temperature, but the highest precipitation compared to the other years. The density and biomass of insects was lowest in 2019. The wet spring may have reduced the insects available as prey. Grasshoppers are more likely to perish from fungal infection during wet, cool springs. Additionally, such conditions may cause insects to emerge later. Warmer, drier springs likely result in the highest densities and biomass of insects available to Sage-grouse chicks after hatching. The year 2018 had the highest mean spring temperatures, but 2021 had the highest temperatures in early June. A combination of spring temperatures and temperatures during sampling likely contribute to the insects we captured. We expect that invertebrate

availability likely increased over the time period we sampled, such that a 3 week old chick likely has more invertebrate prey available than a day old chick. Interestingly, insects in litter did not vary among years, perhaps because being on the ground and in the litter buffers these individuals from changes in air temperature.

Sage-grouse food matched with the insects that were most dense and with the highest biomass on the landscape. Sage-grouse chicks mainly eat ants, beetles, grasshoppers and caterpillars (Patterson 1952, Klebenow and Gray 1968, Gregg and Crawford 2009). In our study, we found that beetles, ants and caterpillars had the highest densities and biomass in litter. Similarly, ants, beetles and caterpillars had the highest densities and biomass in shrub samples. Therefore, Sage-grouse chicks are likely eating the insects that are most available to them. Beetles, grasshoppers and caterpillars tend to have larger individual biomass and we collected fewer individuals compared to ants who had lower individual biomass but were exceptionally common. The density of insects in litter and shrubs was similar, but we counted much higher densities in some of the shrub samples. Mean invertebrate biomass was higher in shrubs, but values in litter had higher variance. The lower densities yet higher biomass in litter indicated that mean individual body mass was higher in litter than shrubs. Both shrubs and litter offer preferred prey items for Sage-grouse chicks.

Our study suggested that various vegetation characteristics offer different dominant prey items to Sage-grouse chicks during the early brood-rearing period. For example, we observed more grasshoppers in dense shrubs, more ant mounds in sparser shrubs and more beetles in shrubs with intermediate cover. Grasshoppers, ants and beetles are all preferred prey items for chicks (Patterson 1952, Klebenow and Gray 1968). Model selection clearly indicated that taller shrubs with more variation in heights, higher litter mass and more canopy cover had the highest invertebrate densities and biomass. Studies investigated the degree to which treating sagebrush with mowing or burning may alter Sage-grouse habitat selection (e.g., Baxter et al. 2017); however, our study indicated that taller stands of shrubs had more insects available to chicks. Activities that reduce the height of shrubs (e.g., mowing or burning) may reduce the insect prey. Hess and Beck (2014) showed that most invertebrate measures were not enhanced by burning or mowing in central Wyoming.

Acknowledgements

We thank the Wyoming Bureau of Land Management for partnering on this project. Matt Green performed laboratory work. Lindsey Washkoviak, Oliver Wilmot, Hannah Gurrieri and Kamaile DeLong collected data in the field.

Literature Cited

Aldridge, C. L., D. J. Saher, T. M. Childers, K. E. Stahlnecker, and Z. H. Bowen. 2012. Crucial nesting habitat for gunnison sage-grouse: A spatially explicit hierarchical approach. Journal of Wildlife Management **76**:391-406.

Anderson, D. H., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management **64**:912-923.

Ausden, M., and M. Drake. 2006. Ecologicl Census Techniquest: A Handbook.*in* W. Sutherland, editor. Cambridge University Press.

Bates, D., M. Machler, B. M. Bolker, and S. E. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1-48.

Baxter, J. J., R. J. Baxter, D. K. Dahlgren, and R. T. Larsen. 2017. Resource Selection by Greater Sage-Grouse Reveals Preference for Mechanically-Altered Habitats. Rangeland Ecology & Management **70**:493-503.

Beckerton, P., and A. Middleton. 1982. Effects of dietary protein levels on ruffed grouse reproduction. Journal of Wildlife Management **43**:569-579.

Beever, E. A., and J. Herrick. 2006. Effects of feral horses in Great Basin landscapes on soils and ants: direct and indirect mechanisms. Journal of Arid Environments **66**:96-112.

Blomberg, E. J., S. R. Poulson, J. S. Sedinger, and D. Gibson. 2013. Prefledging diet is correlated with individual growth in greater sage-grouse (*Centrocercus urophasianus*). Auk **130**:715-724.

Coates, P. S., B. E. Brussee, M. A. Ricca, J. P. Severson, M. L. Casazza, K. B. Gustafson, S. P. Espinosa, S. C. Gardner, and D. J. Delehanty. 2020. Spatially explicit models of seasonal habitat for greater sage-grouse at broad spatial scales: Informing areas for management in Nevada and northeastern California. Ecology and Evolution **10**:104-118.

Connelly, J., and C. Braun. 1997. Long-term changes in sage grouse Centrocercus urophasianus populations in western North America. Wildlife Biology **3**:229-234.

Connelly, J. W., E. T. Rinkes, and C. E. Braun. 2011. Characteristics of Greater Sage-Grouse Habitats A LANDSCAPE SPECIES AT MICRO- AND MACROSCALES.

Davidson, A., J. Aycrigg, E. Grossmann, J. Kagan, S. Lennartz, S. McDonough, and T. Miewald. 2009. Digital Land Cover Map for the Northwestern United States., Northwest Gap Analysis Project, USGS GAP Analysis Program, Moscow, Idaho.

Drut, M. S., W. H. Pyle, and J. A. Crawford. 1994. Technical Note - Diets and Food Selection of Sage Grouse Chicks in Oregon. Journal of Range Management **47**:90-93.

Fischer, R. 1996. An investigation on fire effects within xeric Sagegrouse brood habitat. Journal of Range Management **49**:194-198.

Gregg, M. A., and J. A. Crawford. 2009. Survival of Greater Sage-Grouse Chicks and Broods in the Northern Great Basin. Journal of Wildlife Management **73**:904-913.

Hagen, C. A., G. C. Salter, J. C. Pitman, R. J. Robel, and R. D. Applegate. 2005. Lesser prairie-chicken brood habitat in sand sagebrush: invertebrate biomass and vegetation. Wildlife Society Bulletin **33**:1080-1091.

Hannon, S., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology **269**:422-433.

Hansen, C. P., L. A. Schreiber, M. A. Rumble, J. J. Millspaugh, R. S. Gamo, J. W. Kehmeier, and N. Wojcik. 2016. Microsite Selection and Survival of Greater Sage-Grouse Nests in South-Central Wyoming. Journal of Wildlife Management **80**:862-876.

Harju, S. O., CV, L. Foy-Martin, S. Webb, and M. Dzialak. 2013. Occurrence and success of greater sage-grouse broods in relation to insect-vegetation community gradients. Human-Wildlife Interactions **7**:214-229.

Herrick, J., J. Van See, S. McCord, E. Courtright, J. Karl, and L. Burkett. 2016. Monitoring Manual for Grassland, Shrubland, and Savanna Ecosystems. USDS ARS Journal of Experimenal Range, Las Cruces, New Mexico.

Hess, J. E., and J. L. Beck. 2014. Forb, Insect, and Soil Response to Burning and Mowing Wyoming Big Sagebrush in Greater Sage-Grouse Breeding Habitat. Environmental Management **53**:813-822.

Holloran, M. J., B. Heath, A. Lyon, S. Slater, J. Kuipers, and S. Anderson. 2010. Greater Sage-grouse nesting habitat selection and success in wyoming. Journal of Wildlife Management **69**:638-649.

Huwer, S., D. Anderson, T. Remington, and G. White. 2008. Using human-imprinted chicks to evaluate the importance of forbs to Sage-grouse. Journal of Wildlife Management **72**:1622-1627.

Jarosik, V. 1989. Mass vs length relationship for carabid beedtles. Pedobiologia **33**:87-90.

Johnson, G., and M. S. Boyce. 1990. Feeding trails with insects in the diet of Sage Grouse hicks. Jounal of Wildlife Management **54**:89-91.

Klebenow, D. A., and G. M. Gray. 1968. Food Habits of Juvenile Sage Grouse. Journal of Range Management **21**:80-&.

Lenth, R. 2021. emmeans: estimated mearginal means, aka least-squares means.

Patterson, R. 1952. The Sage Grouse of Wyoming. Sage Books Incorporated, Denver, Colorado.

Rogers, L., H. WT, and R. Buschbom. 1976. A general weight vs. length relationship for insects. Annals of the Entomological Society of America **69**:387-389.

Sanchez-Bayo, F., and K. A. G. Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biological Conservation **232**:8-27.

Stiven, A. 1961. Effects of dietary protein levels on ruffed grouse reproduction. Ecology **42**:547-553.

Sveum, C., J. Crawford, and W. Edge. 1998. Use and selection of brood-rearing habitat by sage grouse in south central Washington. Great Basin Naturalist **58**:344-351.

Thompson, K. M., M. J. Holloran, S. J. Slater, J. L. Kuipers, and S. H. Anderson. 2006. Early brood-rearing habitat use and productivity of greater sage-grouse in Wyoming. Western North American Naturalist **66**:332-342.

Wallestad, R., J. Peterson, and R. Eng. 1975. Effects of dietary protein levels on ruffed grouse reproduction. Journal of Wildlife Management **39**:628-630.

Wright, K. 2021. corrgram: plot a correlogram.