

Occurrence and success of greater sage-grouse broods in relation to insect-vegetation community gradients

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Abstract: A community-level approach to identify important brood habitats of greater sage-grouse (*Centrocercus urophasianus*) may prove useful in guiding management actions because it acknowledges that important habitat components are not ecologically independent from each other. We used principal components analysis to combine insect and vegetation variables into community gradients and used logistic regression to link these components with brood survival and occurrence. We found that brood success was higher when broods occurred in specific insect-vegetation community types. A relationship between brood occurrence and insect-vegetation gradients was not apparent. The high resolution of the data and the solid validation performance suggest that identifying insect-vegetation communities is a promising technique for quantifying sage-grouse habitat relationships. This approach offers land managers a way of identifying important sage-grouse habitat that is ecologically aligned with traditional community-level land management practices (e.g., fire management, rotational grazing, vegetation manipulation, etc.).

Key words: brood occurrence, brood success, greater sage-grouse, habitat, human–wildlife conflicts, insect-vegetation community, multivariate analysis

THE GREATER SAGE-GROUSE (*Centrocercus urophasianus*; hereafter, sage-grouse) occurs in shrub-steppe habitat throughout portions of western North America. Populations have declined range-wide over the last several decades, leading to concern about the long-term status of the species (Connelly and Braun 1997, U.S. Fish and Wildlife Service [USFWS] 2010) and to widespread efforts to identify ways to conserve sage-grouse populations (Connelly et al. 2000, Doherty et al. 2008, Harju et al. 2010, Dzialak et al. 2011, Fedy and Aldridge 2011). Loss in quantity and quality of early brood-rearing habitat has been suggested as a contributing cause of population declines (Connelly and Braun 1997). Identifying

resources that enable sage-grouse chicks to survive is critical to providing knowledge and insight into patterns and processes affecting sage-grouse population dynamics (Gregg and Crawford 2009). Knowledge of critical resources can also be used to develop recommendations for managing large landscapes for the benefit of sage-grouse (Connelly et al. 2000, Dzialak et al. 2011).

A recent meta-analysis found some general patterns of selection for vegetation by sage-grouse with broods (Hagen et al. 2007). Selection for vegetation types may reflect balancing food needs with the security cover provided by structural vegetation features (Thompson et al. 2006). Forbs, and, particularly, insects

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Figure 1. Sage-grouse hen with transmitter.

associated with forbs, are crucial to the growth and survival of sage-grouse chicks for several weeks after hatching (Johnson and Boyce 1990, Drut et al. 1994, Jamison et al. 2002, Huwer et al. 2008, Gregg and Crawford 2009). While several studies have identified individual vegetation or insect features associated with increased chick survival and brood success, few studies have attempted to quantify existing gradients in insect-vegetation communities and then link these community gradients to the occurrence and success of sage-grouse broods (Dahlgren et al. 2010, Guttery 2011).

To supplement the existing body of knowledge on factors related to the occurrence and success of sage-grouse broods, we conducted a study investigating how vegetation and insect community gradients (i.e., variation in the associations of insect and vegetation species within an existing community) were related to the local-level occurrence and 2-week post-hatch success of sage-grouse broods. We focused on insect-vegetation community gradients, rather than investigating relationships between brood occurrence or success and each independent habitat variable (e.g., each insect order or plant species), to (1) account for correlation within insect-vegetation communities, (2) identify existing patterns in insect-vegetation community composition, and (3) provide inference on variables that are amenable to community-level monitoring and management by wildlife and land managers. Our goal was to identify factors associated with sage-grouse brood occurrence and success at a relatively small spatial scale during the early brood-rearing period (0 to 14 days post-hatch). We hypothesized that there was an underlying

structure (i.e., communities) to the spatial distribution and abundance of insect orders and vegetation species and that this underlying structure was related to sage-grouse brood occurrence and success. Specific objectives included: (1) quantifying insect and plant abundance and coverage; (2) integrating these variables to represent gradients among insect-vegetation communities (principal components analysis); (3) using the integrated variables as predictors of brood occurrence and success (logistic regression); (4) and validating the final logistic regression models using cross-validation techniques.

Study area

This study took place in Sheridan County, in northeastern Wyoming, USA. The area is classified as Level III Northwestern Great Plains and Level IV Mesic Dissected Plains Ecoregion. Habitat was predominately mixed-grass prairie with patches of low- to medium-density sagebrush; topography is rolling with moderately steep slopes. Elevation ranges from 1,038 to 1,443 m. Land-use is mainly grazing with irrigated cropland in the valley bottoms.

Methods

Field data collection

During March and April, 2008, we captured 32 sage-grouse hens around breeding leks and attached 30-g solar-powered Argos GPS PTT-100 satellite transmitters (Microwave Telemetry Inc., Columbia, Md.; accuracy ≤ 18 m) to each sage-grouse (Figure 1). During the brood-rearing period (May 15 to July 15), the transmitters recorded hen locations every hour between 0800 hours and 2200 hours. Nest locations were determined based on the spatial pattern of GPS locations. As soon as a hen left the nesting area, we determined the fate of the nest. A brood was included in the insect-vegetation sampling regime if ≥ 1 chick survived ≥ 2 days post-hatch. Broods were considered successful if ≥ 1 chick survived ≥ 35 days post-hatch (all successful broods still had ≥ 1 chick at the end of our monitoring 35 days post-hatch). Brood survival was determined by checking for the presence of ≥ 1 chick at least once per week between hatching and July 15. We made efforts to determine brood status (presence versus absence of a brood) without flushing females. A

brood was considered to have failed if no chick was detected on ≥ 2 occasions. All brood failures occurred within or shortly after the 2-week early brood-rearing window. All capture and handling activities were approved by the Wyoming Game and Fish Department (permit #649).

We randomly selected 1 GPS location per brooded hen per day for insect and vegetation sampling beginning with the first day post-hatch and continuing through 14 days post-hatch (i.e., we defined and monitored the early brood-rearing period separately for each bird). To minimize temporal variation, brood locations were sampled within 3 days of brood occurrence. We sampled insects and vegetation only at GPS locations prior to a successful brood check to ensure that we did not sample locations where the hen occurred after a brood failed. Each sample point was paired with a random location within a 200-m radius, which was also sampled for vegetation and insects. The paired location sampled for each nest location was generated in the field by selecting a random bearing and distance between 50 and 200 m. We used Daubenmire plot techniques (Daubenmire 1959) to sample vegetation at brood and paired locations. Using each point (used and random locations) as the center, we placed a measuring tape along a random orientation, with a second tape perpendicular to the first. We positioned standard Daubenmire plots (20 x 50-cm frames) 1, 4, 7, and 10 m from the center in each direction along both transects, resulting in 16 frames per plot. We identified forbs, grass, and shrubs to species and estimated percentage cover of each species.

We used standard pitfall trap techniques (Connelly et al. 2000) in which we distributed 10 pitfall traps within a 10 m radius of the sampling plot center. A soil sample drilling auger was used for trap placement and the pitfall traps (.45-kg-cups) were filled to 51 mm of water and rubbing alcohol to asphyxiate insects that fell into the traps. Variable soil conditions (i.e., rocky or compacted soil at some locations) and pitfall trap sample contamination from rainwater runoff resulted in more samples from brood locations than paired locations. The insects were collected and the traps moved to a new location every 3 days. We counted (abundance), dried, weighed (dry weight;

mg), and identified insects to order, with the exception of Chilopoda (centipedes) and Diplopoda (millipedes), which we identified to class.

Data analysis

There was a clear bimodal distribution for the occurrence of insect or and plant species within samples (e.g., taxa or species either occurred in nearly all samples or in almost none of the samples). To acknowledge that many taxa were rare and to minimize extraneous statistical noise from including variables that were unlikely to affect the response variables, we removed taxa or species from consideration if they occurred in $< 20\%$ of samples. To develop integrated insect-vegetation habitat variables, we conducted a principal components analysis and used Horn's procedure (Horn 1965) to select the number of principal components to retain for further analysis and discussion. We centered and standardized all variables prior to calculating the principal components.

We interpreted the retained principal components and subsequently used them as predictor variables in 2 separate logistic regressions: (1) available (nonuse, the random locations we sampled) versus use locations of all broods and (2) use locations of successful versus unsuccessful broods. In the occurrence analysis locations were classified with a 1 or a 0 if the location was used versus random, respectively; in the brood success analysis, used locations were classified with a 1 or a 0 if the location was from either a successful or failed brood, respectively. We used the logit link and assumed that the response variables followed a binomial distribution. We included a random brood effect in the occurrence analysis to remove potential pseudo-replication (e.g., multiple locations per brood) and to account for different sample sizes among broods. We were not able to include a random brood effect in the success analysis because brood success was nonidentifiable from the brood effect (i.e., brood success and brood identification both had consistent values for all locations within each brood).

We used information-theoretic methods (Burnham and Anderson 2002) for explanatory model selection. The candidate model set included a global model (all principal

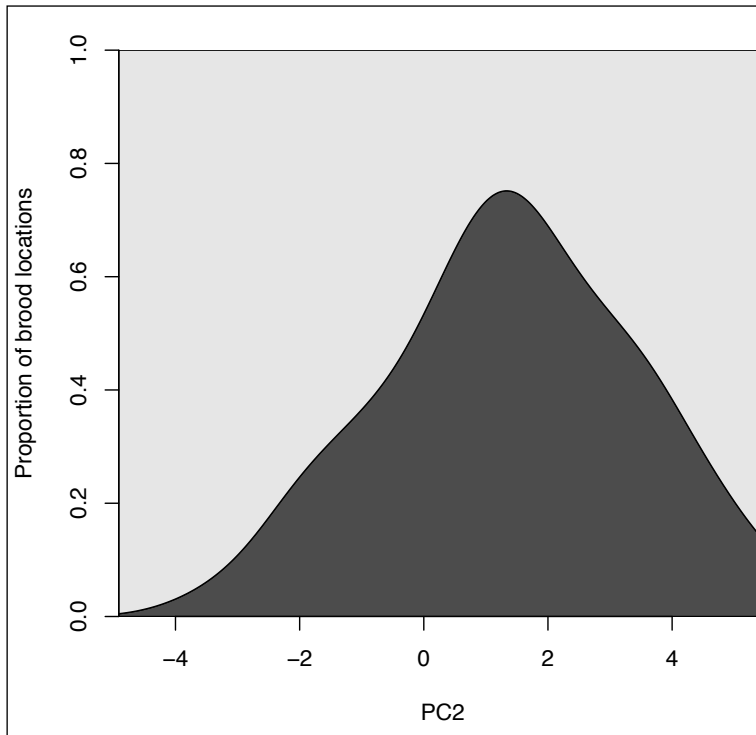


Figure 2. Conditional density plot of the smoothed relationship between greater sage-grouse (*Centrocercus urophasianus*) brood success and PC2 (insect-nonnative grassland). The light and dark grey regions represent the proportion of locations from successful and failed broods, respectively, for a given value of PC2. Locations at lower values of PC2 were characterized by increasing ant, beetle, and grasshopper abundance and dry weight. Locations at higher values of PC2 were characterized by increasing forb, western wheatgrass, and Japanese brome coverage.

components), reduced models (each single principal component), and an intercept-only model to assess model fit. For the brood success analysis, we also included the date that the GPS location was recorded as a nuisance variable in all models (except Intercept-only) because unsuccessful broods tended to have locations earlier in the sample period than successful broods. Following investigation of conditional density plots (a smoothing of the relationship between the observed binary response and an observed continuous predictor), we modeled PC2 as a quadratic polynomial (Figure 2). We also constructed a post-hoc model for brood success after analysis of the global model. We compared the strength of evidence for competing models using AICc and Δ AICc, model weights (w_i ; relative likelihood of a given model being the best among the candidate set), and evidence ratios (the strength of evidence that the top model is best versus each model in the candidate set; Burnham and Anderson 2002).

To assess the predictive capacity of the brood success model, we used a cross-validation technique that, unlike standard approaches, accounts for the hierarchical nature of the data wherein brood locations were nested within individual broods and, thus, brood fate was not independent among locations within a brood. Standard cross-validation techniques withhold individual observations or random subsets of observations as a validation set, build the model with the remaining observations (the training set), and measure how well the model predicts the known values of the validation set. This process was repeated iteratively until all observations have been used in a validation set. To better account for hierarchies in the data, we conducted cross-validation by hand. We withheld all locations from a single brood, built the model using the remaining broods, and then predicted the probability of brood success each location of the withheld brood. Next, we averaged the predicted probability of success across locations within the brood, and did this

Table 1. Principal component (PC) loadings for insect and vegetation variables in northern Wyoming, 2008, with principal component names at end of table. Boldface values highlight loadings $>|0.15|$.

Variable	Insect-vegetation principal component						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Total insect abundance ^a	-0.218	-0.22	-0.06	0.275	-0.113	0.079	-0.16
Hymenoptera	-0.045	-0.198	-0.149	0.283	-0.089	0.186	-0.222
Coleoptera	-0.142	-0.221	0.127	0.046	-0.155	-0.059	0.043
Orthoptera	-0.224	-0.154	0.136	-0.082	0.024	-0.189	-0.189
Aranae	-0.193	-0.019	0.034	0.201	-0.235	-0.129	0.123
Lepidoptera	-0.201	-0.065	0.157	-0.212	-0.064	0.232	0.203
Diptera	-0.199	-0.011	-0.058	0.168	-0.132	0.196	0.267
Total insect dry weight ^b	-0.264	-0.247	0.185	-0.081	-0.021	-0.093	-0.072
Hymenoptera	-0.097	-0.223	-0.155	0.26	-0.09	0.183	-0.23
Coleoptera	-0.179	-0.245	0.226	-0.073	-0.059	-0.102	0.037
Orthoptera.	-0.213	-0.182	0.121	-0.184	0.069	-0.099	-0.152
Aranae	-0.179	-0.039	0.107	0.231	-0.102	-0.257	0.036
Lepidoptera	-0.209	-0.037	0.163	-0.15	-0.005	0.174	0.232
Diptera	-0.198	-0.033	-0.08	0.2	-0.08	0.171	0.234
Bare ground ^c	0.185	-0.159	-0.023	-0.009	0.034	0.066	0.129
Litter ^c	-0.183	0.208	-0.02	0.092	0.084	-0.15	-0.121
Rock ^c	0.139	-0.067	-0.208	0.099	-0.097	0.042	0.191
Total vegetation ^c	-0.273	0.209	-0.264	-0.109	0.033	-0.001	0.008
Total forbs	-0.26	0.275	-0.184	0.011	0.068	0.006	0.027
<i>Achillea millefolium</i>	-0.169	0.042	-0.103	-0.021	0.121	0.007	0.114
<i>Alyssum desertorum</i>	-0.092	-0.036	-0.213	-0.116	-0.161	0.193	0.145
<i>Antennaria microphylla</i>	-0.046	-0.143	-0.054	-0.017	0.181	-0.152	0.336
<i>Cerastium arvense</i>	-0.039	-0.055	-0.117	-0.118	0.148	0.234	-0.186
<i>Gaura coccinea</i>	-0.094	-0.128	-0.185	0.039	0.279	-0.232	0.097
<i>Liatrix punctata</i>	-0.003	-0.111	-0.106	-0.072	0.317	0.158	0.053
<i>Phlox hoodii</i>	-0.071	-0.134	-0.287	-0.048	0.212	-0.177	0.124
<i>Psoralea esculenta</i>	0.015	-0.065	-0.035	-0.03	0.258	0.164	-0.319
<i>Sphaeralcea coccinea</i>	-0.09	0.072	0.174	0.021	0.304	0.081	0.078
<i>Taraxacum officinale</i>	-0.106	0.116	0.194	0.041	0.159	0.304	0.077
<i>Tragopogon dubius</i>	-0.08	0.095	0.228	0.058	0.223	0.179	0.045
<i>Vicia americana</i>	-0.068	-0.01	-0.096	-0.276	-0.067	-0.043	-0.003

Table 1 continued on next page.

Table 1 continued.

Variable	Insect-vegetation principal component						
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Total grass	-0.23	0.309	-0.125	0.04	-0.029	-0.028	-0.072
<i>Bromus japonicus</i>	-0.17	0.267	0.025	-0.051	-0.073	0.043	-0.11
<i>Carex filifolia</i>	0.001	-0.102	-0.095	-0.005	-0.038	0.206	0.176
<i>Elymus smithii</i>	-0.12	0.279	-0.123	0.106	-0.067	-0.121	-0.016
<i>Elymus spicatus</i>	0.121	-0.054	-0.157	0.151	0.052	-0.043	-0.005
<i>Koeleria macrantha</i>	-0.031	-0.056	-0.106	0.085	0.218	0.002	0.096
<i>Nassella viridula</i>	-0.086	-0.013	0.124	0.042	0.243	-0.115	0.094
<i>Poa secunda</i>	-0.145	-0.048	-0.184	-0.016	0.033	-0.116	-0.071
Total shrub	-0.085	-0.143	-0.266	-0.347	-0.09	-0.019	-0.052
<i>Artemisia cana</i>	-0.155	-0.102	-0.064	0.055	0.236	0.139	-0.257
<i>Artemisia frigida</i>	0.027	-0.11	-0.122	0.014	0.037	0.187	0.049
<i>Artemisia tridentata</i>	-0.032	-0.061	-0.158	-0.4	-0.233	0.002	-0.068
<i>Gutierrezia sarothrae</i>	0.055	-0.14	-0.134	0.097	0.15	-0.255	0.152
<i>Opuntia polyacantha</i>	-0.031	-0.023	-0.076	-0.046	-0.023	0.038	0.059
Proportion of variance explained	0.137	0.113	0.075	0.066	0.055	0.044	0.041

PC = biomass–emptiness; PC2 = insects–non-native grassland; PC3 = mixed sage–grassland–leafy-mesic forbs; PC4 = sagebrush–open bunchgrass rangeland; PC5 = insects–sagebrush–subshrubs–mixed forbs; PC6 = mixed forbs and grasshopper–spiders; mixed forbs and ants–caterpillars–flies; PC7 = mixed vegetation and ants–grasshoppers; mixed vegetation and caterpillars–flies.

^aNumber of individuals.

^bmg

^cBare ground, litter, rock, and all vegetation variables are proportion cover of that variable.

iteratively for all broods. We then compared the independent average predicted probability of success for each brood against its known fate to evaluate the robustness of the model in predicting the success of independent sage-grouse broods. We used R (R Development Core Team, v. 2.13.2, 2011) for all statistical analyses.

Results

We sampled insects and vegetation at 71 brood locations and 66 associated random locations from 11 broods (see Appendix Table 1 for summary of raw insect and vegetation data for used vs. available locations and successful vs. unsuccessful broods; see Appendix Table 2 for a list of all vegetation species encountered; see Appendix Table 3 for a list of all insect taxa encountered). Five broods were successful, and 6 broods were unsuccessful. Two of the unsuccessful broods failed shortly after the 2-week post-hatch period (i.e., <23 days post-hatch) and were retroactively classified as

unsuccessful during the early brood-rearing period because failure shortly after the 2-week post-hatch period may have been a function of cumulative resource selection choices by the hen during the 2-week post-hatch period. Additionally, we classified these 2 broods as failed because the failure happened close to the end of the 14-day post-hatch period. We did this because the use of 14-days post-hatch to classify the early brood-rearing period is a human-designed rule-of-thumb and did not capture the continuous process of chick development and because all successful broods survived at least until the end of our monitoring period (35 days post-hatch). Initial variable screening resulted in retaining: 6 insect taxa (both abundance and dry weight, as well as total insect abundance and dry weight), 24 vegetation species, 4 pooled vegetation types (browse, forb, grass, and total canopy cover), and cover of bare ground, litter, and rock, resulting in 45 variables for the integrated

vegetation–insect principal components analysis (Table 1).

The principal components analysis supported the hypothesis that there was underlying structure (i.e., communities) to the distribution and abundance of insect taxa and vegetation species. Horn's procedure suggested retaining the first 7 principal components that, in combination, explained 53% of the variation in the 45-variable dataset (Table 1). We labeled each principle component based on interpretation of the strength and sign of individual variable loadings to reflect elements of the larger insect–vegetation community where sage-grouse occurred. In Table 1 labels, the left-hand and right-hand sides of the hyphen represent opposite ends of a gradient as characterized by low and high values of the principal component. For example, for the first principal component (biomass–emptiness), low values represent high biomass, and high values represent emptiness (i.e., low biomass and high bare ground and rock). For the second principal component (insects–nonnative grassland), low values represent high insect abundance and dry weight and low coverage of nonnative grassland, and high values represent high coverage of nonnative grassland (and low insect abundance and dry weight).

The data did not support the hypothesis that sage-grouse brood occurrence was related to the measured insect–vegetation community gradients. Occurrence was not an apparent function of any of the 7 retained principal components, with the null model (i.e., intercept-only) explaining the data, as well as, or even slightly better than, models that included insect–vegetation community gradients as predictors (Table 2). The data did, however, support the hypothesis that sage-grouse brood success was related to variation along the PC2 (insect–nonnative grassland) and PC4 (sagebrush–open bunchgrass rangeland) community gradients (Table 3). All brood success candidate models performed noticeably better than the Intercept-

Table 2. Model selection results for insect–vegetation habitat gradients and greater sage-grouse (*Centrocercus urophasianus*) brood occurrence in northern Wyoming, USA, 2008. All models (except Intercept-only) contain a random effect for brood identification.

Model	K ^a	ΔAIC_c^b	w_i^c	ER ^d
Intercept only	1	0.00	0.236	
PC7	3	0.92	0.149	1.58
PC5	3	1.22	0.128	1.84
PC4	3	1.32	0.122	1.93
PC2	3	1.62	0.105	2.25
PC1	3	2.02	0.086	2.75
PC3	3	2.02	0.086	2.75
PC6	3	2.02	0.086	2.75
Global	9	11.86	0.001	375.28

^aNumber of parameters.

^bDifference in AIC_c from lowest AIC_c model.

^cModel weight.

^dEvidence ratio.

Table 3. Model selection results for greater sage-grouse (*Centrocercus urophasianus*) brood success in relation to insect–vegetation habitat in northern Wyoming, USA, 2008. All models contain an intercept term and all models except Intercept-only contain the nuisance date term. The PC2 model contains both the linear and quadratic PC2 term.

Model	K ^a	ΔAIC_c^b	w_i^c	ER ^d
Post-hoc	5	0.00	0.883	
PC2	4	4.62	0.088	10.08
PC4	3	8.14	0.015	58.59
Global	10	8.82	0.011	82.09
PC3	3	12.91	0.001	634.33
Date	2	14.11	0.001	1159.45
PC1	3	16.05	0.000	3061.21
PC6	3	16.20	0.000	3301.28
PC5	3	16.28	0.000	3420.58
PC7	3	16.29	0.000	3449.78
Intercept only	1	53.71	0.000	4.61E+11

^a Number of parameters.

^b Difference in AIC_c from lowest AIC_c model.

^c Model weight.

^d Evidence ratio.

only model, partially due to the inclusion of the nuisance variable date in all models. There was little model selection uncertainty between the post-hoc model (Date + PC2 + PC4), PC2, PC4) and the global ($\Delta AIC_c < 10$). We did not consider the global model further because it

was overparameterized, given the equivalent explanatory power of the post-hoc, PC2, and PC4 models. Given that the post-hoc model was a combination of the PC2 and PC4 models, and given its relatively high model weight and evidence ratios over the PC2 and PC4 models, we focus solely on the post-hoc model for inference (Table 4), with the caveat that it was derived after analysis of the data (Burnham and Anderson 2002).

The post-hoc model identified several important local-level community types with respect to brood success. Sage-grouse broods were more likely to succeed when they spent time in locations with open bunchgrass and high abundance of ants (Hymenoptera), spiders (Aranae), and flies (Diptera) and were less likely to succeed in areas with big sagebrush (*Artemisia tridentata*) and caterpillars (Lepidoptera). They were also more likely to succeed at either high or low portions of the PC2 community gradient (a quadratic relationship). This meant that brood success was higher in areas with high insect abundance per dry weight and low coverage of forbs, western wheatgrass (*Elymus smithii*), and the nonnative grass Japanese brome (*Bromus japonicus*), or in areas with high coverage of forbs, western wheatgrass and Japanese brome and low insect abundance per dry weight, but not in areas at intermediate portions of this gradient (Figure 2). Brood-level cross validation indicated that the post-hoc model was robust, accurately predicting the fate of 9 out of 11 independent broods (Figure 3).

Discussion

The use of principal components analysis to create variables that represent the composite structure of insect-vegetation communities provides a useful contribution to the management of sage-grouse broods. Management of landscapes is most practically achieved at the level of the community (Jamison et al. 2002) because management tools that are most effective and efficient focus on general processes over large areas (e.g., grazing management, preventing or prescribing fire, or managing anthropogenic development; Connelly et al. 2000, Hess and Beck 2012). Thus,

Table 4. Coefficient estimates from the top greater sage-grouse (*Centrocercus urophasianus*) brood success model (post-hoc) in northeastern Wyoming, USA, 2008.

Coefficient	Estimate ^a	SE	z value	Pr(> z)
Intercept	0.74	0.59	0.13	0.90
Date	0.22	0.07	3.39	0.001
PC2	-1.07	0.43	-2.50	0.01
PC2 ²	0.31	0.13	2.47	0.01
PC4	1.06	0.47	2.25	0.03

^aLog-odds

while previous work with sage-grouse broods has identified important habitat components (e.g., Drut et al. 1994), it has not addressed the difficulties with managing or identifying specific habitat components on the landscape, especially insects (Jamison et al. 2002). For example, Gregg and Crawford (2009) found that abundance of caterpillars (Lepidoptera) and frequency of Phlox were positively related to sage-grouse chick survival. The challenge with this information rests in application. How does a wildlife or land manager influence the abundance of caterpillars on the landscape? Alternatively, approaches that provide information on how entire communities may be managed to encourage a desired response (e.g., sage-grouse chick survival) more effectively lend themselves to application because such approaches are better aligned with the tools that are available to managers.

The importance of insects in the diet of young sage-grouse chicks has been repeatedly established (Peterson 1970, Johnson and Boyce 1990, Thompson et al. 2006, Dahlgren et al. 2010). Although we also found brood success was positively related to abundance and dry weight of several insect taxa (both PCs 2 and 4), our finding that brood survival was lower in areas with high caterpillar abundance and dry weight appears to contrast with that of Gregg and Crawford (2009) who found that chick survival was positively associated with caterpillar abundance. The apparent contrast raises an important point to consider when interpreting our results. We did not identify that brood success was negatively associated with caterpillar abundance or dry weight per se. Average caterpillar abundance and dry weight were only slightly higher at failed versus successful brood locations (Appendix Table 1).

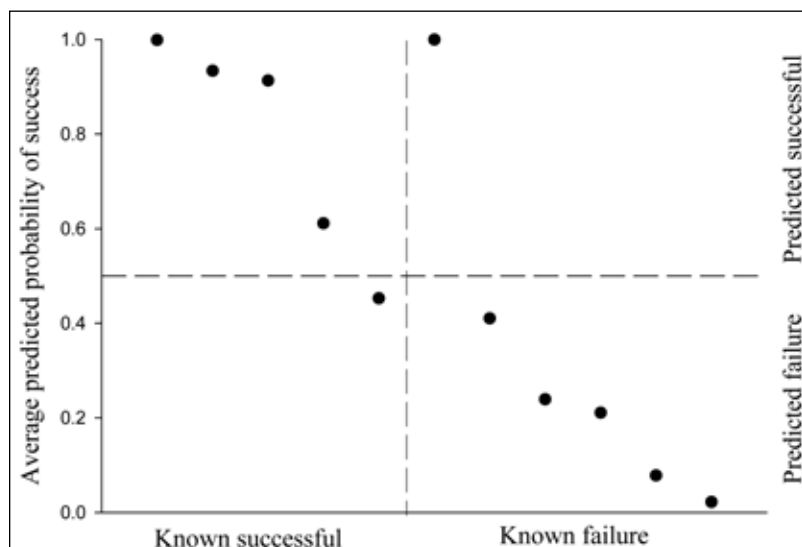


Figure 3. Cross-validation results comparing known fate of independent greater sage-grouse (*Centrocercus urophasianus*) broods with predicted fate. Predicted fate was derived from the insect–vegetation community gradient model Intercept + PC2 + PC2² + PC4 (developed using remaining broods). Each dot represents an individual brood. Broods are arranged horizontally in order of decreasing predicted probability of success, within each known state.

Rather, we found that there was a community type characterized by high coverage of big sagebrush and high abundance of caterpillars and that broods were less likely to succeed in these areas. Big sagebrush and caterpillars may not be causal mechanisms behind brood failure. For example, this habitat type may be associated with a lack of other critical food sources or, structurally, may increase the success of brood predators. The lack of causal mechanisms in our results does not detract from their utility. Regardless of how areas characterized by big sagebrush and caterpillars are related to brood failure, we found that they are nonetheless associated with failure, presenting potential implications for land management.

Lower success among broods that used areas with higher coverage of big sagebrush is supported by several previous studies where, during the early brood-rearing period, broods avoided areas with dense big sagebrush (Klebenow 1969, Drut et al. 1994, Sveum et al. 1998; but see Thompson et al. 2006). We also found that brood success was higher in communities characterized by high coverage of forbs, western wheatgrass, and the invasive annual grass, Japanese brome. It is surprising that high coverage of an invasive grass would appear to be positively associated with brood success, especially considering that the raw

data show coverage of Japanese brome was 1.8 times higher at locations of failed broods (22% coverage) than those of successful broods (11.83% coverage; Appendix Table 1). The forb-wheatgrass-brome end of this community gradient was also devoid of insects (contrary to Ostoja et al. 2009). Increased brood success in this community type may have been the result of non-insect food benefits (e.g., forbs), structural safety from predation (e.g., western wheatgrass), or spatial proximity of opposite ends of this community gradient (e.g., broods selecting for 1 end of the gradient occasionally occurring in the spatially proximate but compositionally opposite end of the gradient). Thus, Japanese brome may be a harmful component within an otherwise beneficial vegetation community.

Unexpectedly, we found no association between the occurrence of sage-grouse with broods and integrated insect-vegetation community gradients. Several studies have found that sage-grouse with broods select habitats non-randomly, and during the early brood-rearing period, they generally choose locations with lower shrub cover, higher forb or grass cover, and higher insect abundance (Klebenow 1969, Drut et al. 1994, Sveum et al. 1998, Thompson et al. 2006). Places with these attributes typically are limited in spatial

extent and are patchily distributed throughout larger sage-steppe areas. The project area in this study is more grassland-dominated with higher moisture levels and broadly-distributed mesic conditions than most sage-steppes, and possibly early brood-rearing habitat selection may occur on a larger spatial scale than either we measured or than occurs in other portions of the range of sage-grouse. However, brood success was related to these community gradients at the spatial scale we used. Alternatively, sage-grouse may have selected locations with respect to other variables that we did not measure (e.g., specific habitat components rather than the community gradients we measured) or our sample of sage-grouse selected locations on the landscape randomly. Given the large number of studies that have found nonrandom habitat selection during early brood-rearing, the latter possibility is unlikely. Regardless, patterns in occurrence may not reflect the processes driving population demography, and, thus, stronger management implications are derived from understanding how brood success is related to environmental factors (Aldridge and Boyce 2007, Gregg and Crawford 2009, Dzialak et al. 2011, Guttery 2011).

The increasing incorporation of high-resolution GPS collars into sage-grouse research has provided more precise data on sage-grouse locations and fate than was previously available (Dzialak et al. 2011, Webb et al. 2012). Thus, although we were able to collect data for only a single brood-rearing season in this study, through the combination of data with high spatial and temporal precision and an alternative conceptual model, we demonstrate how investigating animal–habitat relationships can benefit from a multivariate approach. Multivariate approaches have the advantage of seeing the larger picture of the ecology of a single species in relation to associated plant-animal communities. This contrasts with advantages of univariate approaches, including seeing important bivariate relationships that may be masked by community-level interactions. We, therefore, suggest that multivariate approaches to modeling animal–habitat relationships provide an important and useful contrast to existing univariate approaches.

The insect-vegetation community gradients we identified in northeastern Wyoming provide

preliminary community-level information for wildlife and land managers to consider when identifying, monitoring, and manipulating landscapes to benefit early brood survival of greater sage-grouse. We acknowledge that results were based on a small sample from a single year, limiting their direct implications for management. We believe that the solid performance of this approach under cross-validation indicates that it may be a useful tool for wildlife managers to quantify insect-vegetation communities that function as high- or low-quality habitat, particularly with respect to critical population-regulating mechanisms (e.g., mortality, reproductive success, etc.). Identifying important or deleterious communities may facilitate sage-grouse management by aligning research results with the ecological scale at which management actions are most effective (e.g., grazing management, fire management, herbicide application, mowing, etc.)

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Landscape features and weather influence nest survival of a ground-nesting bird of conservation concern, the greater sage-grouse, in human-altered environments. *Ecological Processes* 1:4

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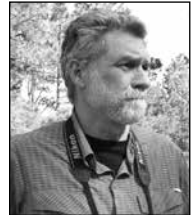
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Appendix

Appendix Table 1. Mean (SD) of raw data for insect and vegetation taxa collected at greater sage-grouse (*Centrocercus urophasianus*) brood use-available locations and fate of sage-grouse broods (success versus failure) in 2008 in northern Wyoming, USA.

	Used locations	Available locations	Successful broods	Failed broods
Total insect abundance ^a	186.42 (212.25)	187.61 (194.08)	231.42 (240.13)	117.32 (137.55)
Hymenoptera abundance	108.49 (198.17)	114.55 (183.33)	139.44 (227.15)	60.96 (132.99)
Coleoptera abundance	28.27 (17.75)	23.74 (16.32)	32.98 (19.04)	21.04 (12.77)
Orthoptera abundance	20.73 (30.78)	20.56 (28.47)	27.44 (37.87)	10.43 (6.53)
Aranae abundance	12.86 (11.06)	12.11 (8.3)	15.42 (12.76)	8.93 (6.12)
Lepidoptera abundance	5.34 (6.7)	5.24 (7.11)	4.98 (6.32)	5.89 (7.35)
Diptera abundance	9.54 (7.96)	10.35 (11.95)	10.28 (7.86)	8.39 (8.12)
Total insect dry weight ^b	3.73 (3.21)	3.54 (3.03)	4.29 (3.85)	2.88 (1.51)
Hymenoptera	0.23 (0.51)	0.25 (0.53)	0.29 (0.59)	0.13 (0.33)
Coleoptera	1.8 (1.51)	1.59 (1.57)	2.02 (1.72)	1.47 (1.05)
Orthoptera	1.31 (1.87)	1.33 (1.64)	1.57 (2.31)	0.9 (0.7)
Aranae	0.19 (0.24)	0.18 (0.18)	0.24 (0.24)	0.12 (0.21)
Lepidoptera	0.17 (0.2)	0.16 (0.19)	0.14 (0.18)	0.22 (0.23)
Diptera	0.01 (0.01)	0.02 (0.02)	0.02 (0.01)	0.01 (0.01)
Bare ground ^c	18.67 (10.85)	18.7 (14.94)	19.63 (11.35)	17.2 (10.06)
Litter	37.07 (19.9)	42.12 (22.88)	38.71 (20.63)	34.56 (18.81)
Rock	2.45 (4.76)	2.47 (4.49)	2.62 (4.9)	2.2 (4.62)
Total vegetation	70.86 (28.15)	69.29 (31.59)	68.16 (30.56)	74.99 (23.92)
Total forbs	55.66 (26.31)	55.71 (29.64)	54.56 (29.13)	57.36 (21.67)
<i>Achillea millefolium</i>	0.97 (1.59)	1.12 (2.68)	0.79 (1.59)	1.25 (1.58)
<i>Alyssum desertorum</i>	3.37 (3.51)	4.52 (4.67)	3.01 (4.03)	3.91 (2.46)
<i>Antennaria microphylla</i>	0.21 (0.58)	0.15 (0.46)	0.3 (0.71)	0.06 (0.18)
<i>Cerastium arvense</i>	0.55 (1.38)	0.24 (0.65)	0.57 (1.57)	0.51 (1.03)
<i>Gaura coccinea</i>	0.6 (1.51)	0.56 (1.28)	0.67 (1.81)	0.48 (0.88)
<i>Liatris punctata</i>	0.65 (0.95)	0.5 (0.89)	0.69 (1.05)	0.58 (0.8)
<i>Phlox hoodii</i>	2.61 (2.63)	2.24 (3.03)	2.95 (2.78)	2.09 (2.33)
<i>Psoralea esculenta</i>	0.72 (1.05)	0.52 (1.13)	0.82 (1.22)	0.56 (0.73)
<i>Sphaeralcea coccinea</i>	0.6 (1.03)	0.54 (1)	0.52 (0.92)	0.71 (1.2)
<i>Taraxacum officinale</i>	1.28 (2.86)	0.77 (1.34)	0.71 (1.35)	2.16 (4.13)
<i>Tragopogon dubius</i>	0.45 (1.06)	0.5 (1.18)	0.25 (0.39)	0.76 (1.59)
<i>Vicia americana</i>	1.6 (2.13)	1.38 (1.75)	1.03 (1.27)	2.48 (2.81)
Total grass	37.03 (22.04)	39.6 (25.16)	35.94 (22.15)	38.7 (22.17)
<i>Bromus japonicus</i>	15.69 (17.77)	18.51 (18.58)	11.83 (14.86)	21.61 (20.37)
<i>Carex filifolia</i>	0.76 (2.08)	0.58 (1.76)	0.8 (2.2)	0.69 (1.93)
<i>Elymus smithii</i>	10.22 (12.55)	9.78 (12.95)	10.93 (15.22)	9.11 (6.76)
<i>Elymus spicatus</i>	1.95 (3.93)	1.52 (3.06)	2.98 (4.74)	0.35 (0.89)
<i>Koeleria macrantha</i>	1.07 (1.98)	0.67 (1.17)	1.16 (1.92)	0.93 (2.1)
<i>Nassella viridula</i>	0.91 (2.23)	1.36 (2.94)	1.12 (2.58)	0.59 (1.54)
<i>Poa secunda</i>	3.3 (5.3)	3.68 (6.75)	3.74 (5.51)	2.63 (4.96)
Total shrub	15.19 (10.52)	13.58 (9.95)	13.6 (10.65)	17.64 (10.02)
<i>Artemisia cana</i>	1.22 (2.83)	1.81 (2.97)	1.63 (3.39)	0.58 (1.47)
<i>Artemisia frigida</i>	0.57 (0.76)	0.48 (1.01)	0.7 (0.82)	0.36 (0.61)

Appendix Table 1 continued on next page.

Appendix Table 1 continued.

	Used locations	Available locations	Successful broods	Failed broods
<i>Artemisia tridentata</i>	10.92 (10.02)	9.43 (10.21)	7.85 (8.7)	15.63 (10.22)
<i>Gutierrezia sarothrae</i>	1.3 (2.62)	0.37 (0.84)	1.93 (3.14)	0.34 (0.93)
<i>Opuntia polyacantha</i>	0.17 (0.5)	0.24 (0.82)	0.06 (0.22)	0.34 (0.72)

^aNumber of individuals.

^bmg

^cBare ground, litter, rock, and all vegetation variables are proportion cover of that variable.

Appendix Table 2. List of all plant species encountered during sage-grouse (*Centrocercus urophasianus*) early brood-rearing period in 2008 in northern Wyoming, USA.

Scientific name	Common name	Plant type
<i>Achillea millefolium</i>	Western yarrow	Forb
<i>Agoseris glauca</i>	False dandelion	Forb
<i>Allium textile</i>	Textile onion	Forb
<i>Alyssum desertorum</i>	Alyssum	Forb
<i>Antennaria microphylla</i>	Littleleaf pussytoes	Forb
Apiaceae spp.	Carrot	Forb
<i>Arabis glabra</i>	Tower rockcress	Forb
<i>Arnica fulgens</i>	Shining arnica	Forb
<i>Artemisia ludoviciana</i>	Cudweed or Louisiana sagewort	Forb
<i>Astragalus bisulcatus</i>	Two-grooved milkvetch	Forb
<i>Astragalus lentiginosus</i>	Freckled milkvetch	Forb
<i>Astragalus mollissimus</i>	Wolly locoweed	Forb
<i>Astragalus plattensis</i>	Platte River milkvetch	Forb
<i>Astragalus spatulatus</i>	Spoonleaf milkvetch	Forb
<i>Astragalus</i> spp.	Milkvetch	Forb
<i>Astragalus tenellus</i>	Pulse milkvetch	Forb
<i>Barbarea vulgaris</i>	Yellow rocket	Forb
Boraginaceae spp.	Borage family	Forb
<i>Calochortus nuttallii</i>	Sego lily	Forb
<i>Calylophus serrulatus</i>	Yellow evening primrose	Forb
<i>Camelina microcarpa</i>	Littlepod false flax	Forb
<i>Cardaria chalapensis</i>	Lenspod whitetop	Forb
<i>Cardaria draba</i>	Hoary cress	Forb
<i>Castilleja sessiliflora</i>	Downy paintbrush	Forb
<i>Cerastium arvense</i>	Chickweed	Forb
<i>Ceratoides lanata</i>	Winterfat	Forb
<i>Cirsium arvense</i>	Canada thistle	Forb
<i>Cirsium undulatum</i>	Wavyleaf thistle	Forb
<i>Collomia linearis</i>	Slenderleaf collomia	Forb
<i>Collinsia parviflora</i>	Maiden blue eyed Mary	Forb
<i>Comandra umbellata</i>	Bastard toadflax	Forb
<i>Convolvulus arvensis</i>	Field bindweed	Forb
<i>Crepis runcinata</i>	Fiddleleaf hawksbeard	Forb
<i>Cymopterus acaulis</i>	Plains springparsley	Forb
<i>Cynoglossum officinale</i>	Hound's tongue	Forb
<i>Dalea enneandra</i>	Slender dalea	Forb
<i>Delphinium bicolor</i>	Larkspur	Forb
<i>Descurainia pinnata</i>	Pinnate tansy mustard	Forb
<i>Descurainia sophia</i>	Tansy mustard	Forb
<i>Echinadea angustifolia</i>	Purple coneflower	Forb
<i>Erigeron strigosus</i>	Daisy fleabane	Forb
<i>Erysimum asperum</i>	Western wallflower	Forb
<i>Euphorbia agraria</i>	Urban spurge	Forb
<i>Euphorbia esula</i>	Leafy spurge	Forb
<i>Galium boreale</i>	Bedstraw	Forb
<i>Gaura coccinea</i>	Scarlet gara	Forb
<i>Geum triflorum</i>	Prairie smoke	Forb
<i>Grindelia squarrosa</i>	Curlycup gumweed	Forb
<i>Heterotheca villosa</i>	Hairy false goldenaster	Forb

Appendix Table 2 continued on next page.

Appendix Table 2 continued.

Scientific name	Common name	Plant type
<i>Ipomopsis congesta</i>	Ballhead gilia	Forb
<i>Lactuca serriola</i>	Prickly lettuce	Forb
<i>Lathyrus polymorphus</i>	Manystem pea	Forb
<i>Lepidium densiflorum</i>	Prairie pepperweed	Forb
<i>Lesquerella ludoviciana</i>	Silver bladderpod	Forb
<i>Leucocrinum montanum</i>	Common starfily - sandlily	Forb
<i>Liatris punctata</i>	Dotted gayfeather	Forb
Liliaceae spp.	Lilly	Forb
<i>Linum lewisii</i>	Blue flax	Forb
<i>Lithospermum incisum</i>	Narrowleaf gromwell	Forb
<i>Lomatium foeniculaceum</i>	Desert biscuitroot	Forb
<i>Lupinus argenteus</i>	Silvery lupine	Forb
<i>Lygodesmia juncea</i>	Skeletonweed	Forb
<i>Machaeranthera grindelioides</i>	Rayless tansyaster	Forb
<i>Medicago sativa</i>	Alfalfa	Forb
<i>Melilotus officinal</i>	Yellow sweetclover	Forb
<i>Melilotus</i> spp.	Sweetclover	Forb
<i>Mertensia</i> spp.	Bluebell	Forb
<i>Musineon divaricatum</i>	Wild parsley	Forb
<i>Oxytropis lambertii</i>	Lambert or Purple locoweed	Forb
<i>Oxytropis sericea</i>	White locoweed	Forb
<i>Oxytropis</i> spp.	Locoweed	Forb
<i>Penstemon albidus</i>	White beardtongue	Forb
<i>Penstemon procerus</i>	Littleflower penstemon	Forb
<i>Phacelia linearis</i>	Threadleaf phacelia	Forb
<i>Phlox hoodii</i>	Hood's phlox	Forb
<i>Plantago patagonica</i>	Indianwheat	Forb
<i>Polygonum</i> spp.	Smartweed	Forb
<i>Potentilla recta</i>	Sulphur cinquefoil	Forb
<i>Psoralea argophylla</i>	Silverleaf scurfpea	Forb
<i>Psoralea esculenta</i>	Breadroot scurfpea	Forb
<i>Ratibida columnifera</i>	Prairie coneflower	Forb
<i>Rumex acetosella</i>	Sheep sorrel	Forb
<i>Senecio canus</i>	Gray ragwort	Forb
<i>Senecio integerrimus</i>	Lambstongue groundsel	Forb
<i>Senecio</i> species	Groundsel	Forb
<i>Sisyrinchium montanum</i>	Blue-eyed grass	Forb
<i>Smilacina stellata</i>	Starry false Solomon's seal	Forb
<i>Solidago</i> spp.	Goldenrod	Forb
<i>Sphaeralcea coccinea</i>	Scarlet globemallow	Forb
<i>Taraxacum officinale</i>	Dandelion	Forb
<i>Thlapsin arvense</i>	Stinkweed	Forb
<i>Thermopsis rhomifolia</i>	Goldenpea or Goldenbanner	Forb
<i>Tragopogon dubius</i>	Goatsbeard	Forb
<i>Tradescantia occidentalis</i>	Prairie spiderwort	Forb
<i>Veronica arvensis</i>	Corn speedwell	Forb
<i>Veronica peregrina</i>	Neckweed	Forb
<i>Veronica</i> species	Speedwell/Neckweed	Forb
<i>Vicia americana</i>	American vetch	Forb
<i>Viola nuttallii</i>	Nuttals violet	Forb
<i>Viola</i> spp.	Violet	Forb
<i>Zigadenus venenosus</i>	Deathcamus	Forb
<i>Agropyron cristatum</i>	Crested wheatgrass	Grass; grasslike
<i>Elymus repens</i>	Quackgrass	Grass; grasslike
<i>Agrostis stolonifera</i>	Redtop	Grass; grasslike
<i>Schizachyrium scoparium</i>	Little bluestem	Grass; grasslike
<i>Aristida purpurea</i>	Red threeawn	Grass; grasslike
<i>Bouteloua curtipendula</i>	Sideoats grama	Grass; grasslike
<i>Bouteloua gracilis</i>	Blue grama	Grass; grasslike
<i>Bromus inermis</i>	Smooth brome	Grass; grasslike
<i>Bromus japonicus</i>	Japanese brome	Grass; grasslike
<i>Bromus tectorum</i>	Cheat grass	Grass; grasslike

Appendix Table 2 continued on next page.

Appendix Table 2 continued.

Scientific name	Common name	Plant type
<i>Buchloe dactyloides</i>	Buffalograss	Grass; grasslike
<i>Carex filifolia</i>	Threadleaf sedge	Grass; grasslike
<i>Danthonia unispicata</i>	Onespike danthonia	Grass; grasslike
<i>Elymus smithii</i>	Western wheatgrass	Grass; grasslike
<i>Elymus spicatus</i>	Bluebunch wheatgrass	Grass; grasslike
<i>Festuca idahoensis</i>	Idaho fescue	Grass; grasslike
<i>Hesperastipa comata</i>	Needleandthread	Grass; grasslike
<i>Hordeum jubatum</i>	Foxtail barley	Grass; grasslike
<i>Koeleria macrantha</i>	Prairie junegrass	Grass; grasslike
<i>Nassella viridula</i>	Green needlegrass	Grass; grasslike
<i>Poa bulbosa</i>	Bulbous bluegrass	Grass; grasslike
<i>Poa pratensis</i>	Kentucky bluegrass	Grass; grasslike
<i>Poa secunda</i>	Sandberg bluegrass	Grass; grasslike
<i>Sporobolus cryptandrus</i>	Sand dropseed	Grass; grasslike
<i>Vulpia octoflora</i>	Sixweeks fescue	Grass; grasslike
<i>Artemisia cana</i>	Silver sagebrush	Woody
<i>Artemisia tridentata</i>	Big sagebrush	Woody
<i>Ericameria nauseosus</i>	Rubber rabbitbrush	Woody
<i>Juniperus horizontales</i>	Creeping juniper	Woody
<i>Juniperus scopulorum</i>	Rocky Mountain juniper	Woody
<i>Prunus virginiana</i>	Chokecherry	Woody
<i>Rhus glabra</i>	Smooth sumac	Woody
<i>Rhus spp.</i>	Sumac	Woody
<i>Rhus trilobata</i>	Skunkbrush sumac	Woody
<i>Ribes oxycanthoides</i>	Gooseberry	Woody
<i>Rosa woodsii</i>	Woods' rose	Woody
<i>Symphoricarpos occidentalis</i>	Western snowberry	Woody
<i>Toxicodendron rydbergii</i>	Western poison ivy	Woody
<i>Artemisia frigida</i>	Fringed sagewort	Woody
<i>Gutierrezia sarothrae</i>	Broom snakeweed	Woody
<i>Yucca glauca</i>	Yucca	Woody
<i>Opuntia polyacantha</i>	Plains pricklypear	Woody
<i>Pediocactus simpsonii</i>	Barrel cactus	Woody
<i>Acer negundo</i>	Boxelder	Woody

Appendix Table 3. List of insect orders collected during early sage-grouse (*Centrocercus urophasianus*) brood-rearing period during 2008 in northern Wyoming, USA.

Order	Generic names of species
Araneae	Spiders
Chilopoda	Centipedes
Coleoptera	Beetles
Dermaptera	Earwigs
Diplopoda	Millipedes
Diptera	Flies, mosquitos
Hemiptera	True bugs
Homoptera	Cicadas, leafhoppers, treehoppers
Hymenoptera	Ants, bees, wasps
Lepidoptera	Butterflies, moths
Microcoryphia	Jumping bristletails
Neuroptera	Antlions, lacewings, mantidflies
Orthoptera	Grasshoppers, crickets, katydids
Thysanoptera	Thrips
Zoraptera	Zorapterans