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

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Abstract: A community-level approach to identify important brood habitats of greater sagegrouse (*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 longterm 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 sagegrouse 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 insect-vegetation broods. We focused on 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 insectvegetation 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 crossvalidation 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 mixedgrass prairie with patches of low- to mediumdensity 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 insectvegetation sampling regime if ≥1 chick survived ≥2 days post-hatch. Broods were considered successful if ≥1 chick survived ≥35 days posthatch (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 ≥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 posthatch and continuing through 14 days posthatch (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;; 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

	Insect-vegetation principal component						
Variable	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
The first state of the state of	0.0(4	0.045	0.105	0.001	0.001	0.002	0.072
Iotal insect dry weight	-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	-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
Tatal (asha	0.96	0.075	0 104	0.011	0.000	0.007	0.027
	-0.20	0.275	-0.104	0.011	0.068	0.006	0.027
Achilieu millefolium	-0.109	0.042	-0.103	-0.021	0.121	0.007	0.114
Alyssum aesertorum	-0.092	-0.036	-0.213	-0.116	-0.161	0.193	0.145
Antennaria microphylia	-0.046	-0.143	-0.054	-0.017	0.181	-0.152	0.336
Cerastium arvense	-0.039	-0.055	-0.117	-0.118	0.148	0.234	-0.186
Gaura coccinea	-0.094	-0.128	-0.185	0.039	0.279	-0.232	0.097
Liatris puncata	-0.003	-0.111	-0.106	-0.072	0.317	0.158	0.053
Phlox hoodii	-0.071	-0.134	-0.287	-0.048	0.212	-0.177	0.124
Psoralea esculenta	0.015	-0.065	-0.035	-0.03	0.258	0.164	-0.319
Sphaeralcea coccinea	-0.09	0.072	0.174	0.021	0.304	0.081	0.078
Taraxacum officinale	-0.106	0.116	0.194	0.041	0.159	0.304	0.077
Tragopogon dubius	-0.08	0.095	0.228	0.058	0.223	0.179	0.045
Vicia americana	-0.068	-0.01	-0.096	-0.276	-0.067	-0.043	-0.003

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|.

Table 1 continued on next page.

Table 1 continued.

	Insect-vegetation principal component						
Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Total grass	-0.23	0.309	-0.125	0.04	-0.029	-0.028	-0.072
Bromus japonicus	-0.17	0.267	0.025	-0.051	-0.073	0.043	-0.11
Carex filifolia	0.001	-0.102	-0.095	-0.005	-0.038	0.206	0.176
Elymus smithii	-0.12	0.279	-0.123	0.106	-0.067	-0.121	-0.016
Elymus spicatus	0.121	-0.054	-0.157	0.151	0.052	-0.043	-0.005
Koeleria macrantha	-0.031	-0.056	-0.106	0.085	0.218	0.002	0.096
Nassella viridula	-0.086	-0.013	0.124	0.042	0.243	-0.115	0.094
Poa secunda	-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
Artemisia cana	-0.155	-0.102	-0.064	0.055	0.236	0.139	-0.257
Artemisia frigida	0.027	-0.11	-0.122	0.014	0.037	0.187	0.049
Artemisia tridentata	-0.032	-0.061	-0.158	-0.4	-0.233	0.002	-0.068
Gutierrezia sarothrae	0.055	-0.14	-0.134	0.097	0.15	-0.255	0.152
Opuntia polyacantha	-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-leafymesic forbs; PC4 = sagebrush-open bunchgrass rangeland; PC5 = insects-sagebrush-subshrubsmixed 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

Bare 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 sagegrouse 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 (biomassemptiness), 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 (insectnonnative 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	Ka	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 AICc from lowest AIC, 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	Kª	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.

^bDifference in AIC, from lowest AIC, model.

° 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 (Δ 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 sagegrouse (*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 (Lepidopterans) 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 forbwheatgrass-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, sagegrouse 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 highresolution GPS collars into sage-grouse research has provided more precise data on sagegrouse locations and fate than was previously available (Dzialak at el. 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 modeling animal-habitat relationships to 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 crossvalidation indicates that it may be a useful tool for wildlife managers to quantify insectvegetation 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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Appendix

Appendix Table 1. Mean (SD) of raw data for insect and vegetation taxa collected at greater sagegrouse (*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)
abundance	108.49 (198.17)	114.55 (183.33)	139.44 (227.15)	60.96 (132.99)
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)
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)
Achillea millefolium	0.97 (1.59)	1.12 (2.68)	0.79 (1.59)	1.25 (1.58)
Alyssum desertorum Antennaria	3.37 (3.51)	4.52 (4.67)	3.01 (4.03)	3.91 (2.46)
microphylla	0.21 (0.58)	0.15 (0.46)	0.3 (0.71)	0.06 (0.18)
Cerastium arvense	0.55 (1.38)	0.24 (0.65)	0.57 (1.57)	0.51 (1.03)
Gaura coccinea	0.6 (1.51)	0.56 (1.28)	0.67 (1.81)	0.48 (0.88)
Liatris puncata	0.65 (0.95)	0.5 (0.89)	0.69 (1.05)	0.58 (0.8)
Phlox hoodii	2.61 (2.63)	2.24 (3.03)	2.95 (2.78)	2.09 (2.33)
Psoralea esculenta	0.72 (1.05)	0.52 (1.13)	0.82 (1.22)	0.56 (0.73)
Sphaeralcea coccinea	0.6 (1.03)	0.54(1)	0.52 (0.92)	0.71 (1.2)
Iaraxacum officinale	1.28 (2.86)	0.77(1.34)	0.71 (1.35)	2.16 (4.13)
Iragopogon dubius Vicia americana	0.45 (1.06) 1.6 (2.13)	0.5(1.18) 1.38(1.75)	0.25(0.39) 1.03(1.27)	0.76 (1.59) 2.48 (2.81)
Total grass	37.03 (22.04)	39.6 (25.16)	35.94 (22.15)	38.7 (22.17)
Bromus japonicus	15.69 (17.77)	18.51 (18.58)	11.83 (14.86)	21.61 (20.37)
Carex filifolia	0.76 (2.08)	0.58 (1.76)	0.8 (2.2)	0.69 (1.93)
Elymus smithii	10.22 (12.55)	9.78 (12.95)	10.93 (15.22)	9.11 (6.76)
Elymus spicatus Koeleria macrantha	1.95(3.93) 1.07(1.98)	1.52(3.06) 0.67(1.17)	2.98(4.74) 1.16(1.92)	0.35(0.89) 0.93(2.1)
Nassella viridula	0.91 (2.23)	1.36 (2.94)	1.12 (2.58)	0.59 (1.54)
Poa secunda	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)
Artemisia cana	1.22 (2.83)	1.81 (2.97)	1.63 (3.39)	0.58 (1.47)
Artemisia frigida	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.
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	Used locations	Available locations	Successful broods	Failed broods
Artemisia tridentata	10.92 (10.02)	9.43 (10.21)	7.85 (8.7)	15.63 (10.22)
Gutierrezia sarothrae	1.3 (2.62)	0.37 (0.84)	1.93 (3.14)	0.34 (0.93)
Opuntia polyacantha	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 a	ll plant species encountered during sage-gro	ouse (Centrocercus uropha-
<i>sianus</i>) early brood-rearing _]	period in 2008 in northern Wyoming, USA.	

Scientific name	Common name	Plant type
Achillea millefolium	Western varrow	Forb
Aonseris olauca	False dandelion	Forb
Allium textile	Textile onion	Forb
Alussum desertorum	Alvssum	Forb
Antennaria micronhulla	Littleleaf pussytoes	Forb
Aniaceae spp	Carrot	Forb
Arahis olahra	Tower rockcress	Forb
Arnica fulgens	Shining arnica	Forb
Artemisia Indoniciana	Cudweed or Louisiana sagewort	Forb
Aetragalue hieulcatue	Two-grooved milkyetch	Forb
Aetragalus lentigingeus	Freekled milkvetch	Forb
Aetragalus mollissimus	Wolly locoweed	Forb
Astragalus nlattoneis	Platta River millevotch	Forb
Astragalus piutensis	Spoonloof millwotch	Forb
Astragalus sputututus	Millwotch	Forb
Astragalus spp.	Pulso millayotch	FOID
Astrugulus tenetius	Yellow reaket	FOID
Burbureu Oulguris	Remove forestla	FOID
<i>Coloringinuceue</i> spp.	Correction for the second seco	FOID
	Sego my	FOID
Calylophus serrulatus	reliow evening primrose	Forb
Camelina microcarpa	Littlepod false flax	Forb
Caraaria chalapensis	Lenspod whitetop	Forb
Cardaria draba	Hoary cress	Forb
Castilleja sessiliflora	Downy paintbrush	Forb
Cerastium arvense	Chickweed	Forb
Ceratoides lanata	Wintertat	Forb
Cirsium arvense	Canada thistle	Forb
Cirșium undulatum	Wavyleaf thistle	Forb
Collomia linearis	Sienderleaf collomia	Forb
Collinsia parviflora	Maiden blue eyed Mary	Forb
Comandra umbellata	Bastard toadflax	Forb
Convolvulus arvensis	Field bindweed	Forb
Crepis runcinata	Fiddleleaf hawksbeard	Forb
Cymopterus acaulis	Plains springparsley	Forb
Cynoglossum officinale	Hound's tongue	Forb
Dalea enneandra	Slender dalea	Forb
Delphinium bicolor	Larkspur	Forb
Descurainia pinnata	Pinnate tansy mustard	Forb
Descurainia sophia	Tansy mustard	Forb
Echinadea angustifolia	Purple coneflower	Forb
Erigeron strigosus	Daisy fleabane	Forb
Erysimum asperum	Western wallflower	Forb
Euphorbia agraria	Urban spurge	Forb
Euphorbia esula	Leafy spurge	Forb
Galium boreale	Bedstraw	Forb
Gaura coccinea	Scarlet gara	Forb
Geum triflorum	Prairie smoke	Forb
Grindelia squarrosa	Curlycup gumweed	Forb
Heterotheca villosa	Hairy false goldenaster	Forb

Appendix Table 2 continued.

Scientific name	Common name	Plant type
Ipomopsis congesta	Ballhead gilia	Forb
Lactuca serriola	Prickly lettuce	Forb
Lathyrus polymorphus	Manystem pea	Forb
Lepidium densiflorum	Prairie pepperweed	Forb
Lesquerella ludoviciana	Silver bladderpod	Forb
Leucocrinum montanum	Common starlily - sandlily	Forb
Liatris puncata	Dotted gayfeather	Forb
Liliaceae spp.	Lilly	Forb
Linum lewiŝii	Blue flax	Forb
Lithospermum incisum	Narrowleaf gromwell	Forb
Lomatium foeniculaceum	Desert biscuitroot	Forb
Lupinus argenteus	Silvery lupine	Forb
Lygodesmia juncea	Skeletonweed	Forb
Machaeranthera grindelioides	Rayless tansyaster	Forb
Medicago sativa	Altalta	Forb
Melilotus officinal	Yellow sweetclover	Forb
Melilotus spp.	Sweetclover	Forb
Mertensia spp.		Ford
Niusineon atoaricatum	Villa parsiey	FOID
Oxytropis lumbertii	White locowood	FOID
	L ageruand	FOID
Oxytropsis spp.	White board tongue	FOID
Pensiemon niolaus	Littleflower penstemon	Forb
Pensiemon procerus Phacelia linearic	Threadleaf phacelia	Forb
Phlor hoodii	Hood's phlox	Forb
Plantago natagonica	Indianwheat	Forb
Polygonum spp	Smartweed	Forb
Potentilla recta	Sulphur cinquefoil	Forb
Psoralea aroonhulla	Silverleaf scurfpea	Forb
Psoralea esculenta	Breadroot scurfpea	Forb
Ratihida columnifera	Prairie coneflower	Forb
Rumex acetosella	Sheep sorrel	Forb
Senecio canus	Grav ragwort	Forb
Senecio integerrimus	Lambstongue groundsel	Forb
Senecio species	Groundsel	Forb
Sisyrinchium montanum	Blue-eyed grass	Forb
Smilacina stellata	Starry false Solomon's seal	Forb
Solidago spp.	Goldenrod	Forb
Sphaeralcea coccinea	Scarlet globemallow	Forb
Taraxacum officinale	Dandelion	Forb
Thlapsin arvense	Stinkweed	Forb
Thermopsis rhomifolia	Goldenpea or Goldenbanner	Forb
Tragopogon dubius	Goatsbeard	Forb
Iradescantia occidentalis	Prairie spiderwort	Forb
Veronica arvensis	Corn speedwell	Forb
Veronica peregrina	Neckweed	Forb
Veronica species	Speedwell/Neckweed	Forb
Vicia americana	American vetch	Forb
Viola nuttallii	Nuttals Violet	Ford
Viola spp.	Violet	FOID
Agromuron gristatum	Crosted wheatgrass	Cross: grasslike
	Crested wheatgrass	Grass, grasslike
Liymus repens Agrostic stolonifera	Quackgrass	Grass; grasslike
Schizachurium scongrium	Little bluestem	Grass, grasslike
Aristida nurnurea	Red threeawn	Grass, grasslike
Bouteloug curtinendula	Sideoate grama	Grass, grasslike
Bouteloug gracilic	Blue grama	Crace: gracelike
Bromus inermis	Smooth brome	Grass grasslike
Bromus japonicus	Japanese brome	Grass; grasslike
Bromus tectorum	Cheat grass	Grass: grasslike

Appendix	Table	2	continued.	
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Scientific name	Common name	Plant type
Buchloe dactuloides	Buffalograss	Grass: grasslike
Carex filifolia	Threadleaf sedge	Grass; grasslike
Danthonia unispicata	Onespike danthonia	Grass; grasslike
Elymus smithii'	Western wheatgrass	Grass; grasslike
Elymus spicatus	Bluebunch wheatgrass	Grass; grasslike
Festuca idahoensis	Idaho fescue	Grass; grasslike
Hesperastipa comata	Needleandthread	Grass; grasslike
Hordeum jubatum	Foxtail barley	Grass; grasslike
Koeleria macrantha	Prairie junegrass	Grass; grasslike
Nassella viridula	Green needlegrass	Grass; grasslike
Poa bulbosa	Bulbous bluegrass	Grass; grasslike
Poa pratensis	Kentucky bluegrass	Grass; grasslike
Poa secunda	Sandberg bluegrass	Grass; grasslike
Sporobolus cryptandrus	Sand dropseed	Grass; grasslike
Vulpia octoflora	Sixweeks fescue	Grass; grasslike
Artemisia cana	Silver sagebrush	Woody
Artemisia tridentata	Big sagebrush	Woody
Ericameria nauseosus	Rubber rabbitbrush	Woody
Juniperus horizontiales	Creeping juniper	Woody
Juniperus scopulorum	Rocky Mountain juniper	Woody
Prunus virginiana	Chokecherry	Woody
Rhus glabra	Smooth sumac	Woody
Rhus spp.	Sumac	Woody
Rhus trilobata	Skunkbrush sumac	Woody
Ribes oxyacanthoides	Gooseberry	Woody
Rosa woodsii	Woods' rose	Woody
Symphoricarpos occidentalis	Western snowberry	Woody
Toxicodendron rydbergii	Western poison ivy	Woody
Artemisia frigida	Fringed sagewort	Woody
Gutierrezia sarothrae	Broom snakeweed	Woody
Yucca glauca	Yucca	Woody
Opuntia polyacantha	Plains pricklypear	Woody
Pediocactus simpsonii	Barrel cactus	Woody
Acer negundo	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	