ESTIMATING THE OCCUPANCY, ABUNDANCE, AND DENSITY OF DUSKY GROUSE: DEVELOPING METHODS OF UNBIASED POPULATION

MONITIORING IN MONTANA

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**EXECUTIVE SUMMARY**

This report summarizes the results of the first quarter (September – December 2018) of a four-year (2018 – 2022) research project conducted by researchers at Montana State University’s Wildlife Habitat Ecology Lab to develop methods for unbiased population monitoring for Dusky grouse (*Dendragapus obscurus*; previously “blue grouse”) in Montana.

This first quarter focused on building and evaluating a statewide model of relative habitat suitability for dusky grouse in Montana. We obtained dusky grouse observations collected during the past nine springs (April–June, 2009–2018) from the Integrated Monitoring in Bird Conservation (IMBCR) program and extracted habitat information for detected/not-detected locations using remotely-sense geospatial datasets. We evaluated relative habitat use with resource selection functions calibrated using generalized linear mixed models. Candidate models representing hypothesized relationships between grouse detections/non-detections and habitat conditions (e.g. forest type and coverage, relative elevation, slope) were compared using multi-model inference based on information theory. Vegetation types were classified by specific type and by groupings. The groups consisted of conifer forest, riparian areas, sparsely vegetated areas, mountain shrub, barren, agriculture, developed, grassland, hardwood, and Douglas fir forest. We found the following spatially-explicit habitat attributes to have a significant effect on whether or not a dusky grouse was detected at a site: proportion of rocky mountain subalpine montane mesic meadow, proportion of northern Rocky mountain dry-mesic montane mixed conifer forest, proportion of Douglas fir forest, proportion of area with shrubs 0.5–1 meter in height, average elevation, proportion of northern Rocky Mountain ponderosa pine woodland and savanna, average slope, proportion of riparian area, distance to the edge of conifer forest, and proportion of total conifer forest. Preliminary results suggested that relative use for dusky grouse was higher in areas with higher proportions of mixed conifer forest (β = 1.86 ± 1.53) and subalpine meadows (β = 3.89 ± 1.10). Relative use was lower as the distance to conifer forest increased (β = -0.002 ± 0.006) and in areas with higher proportions of riparian area (β = -3.33 ± 5.31). Relative use by dusky grouse was maximized when the proportion of shrub coverage (woody vegetation 0.5–1 meter in height) was 0.05, and when average elevation of a 250-m area was between 1600 and 1700 m. Relative use also exhibited positive non-linear relationships with the proportional coverage of the Douglas fir forest (β = 0.29 ± 0.23), in which relative use increased rapidly until about 40% of the 20-ha survey area was classified as Douglas fir forest, and proportion of conifer forest (β = 0.14 ± 0.30), in which relative use increased rapidly until 40–50 % of the survey area was classified as conifer forest Relative use also exhibited a positive non-linear relationship with average slope (β = 0.24 ± 0.41), in which relative use increased rapidly until average slope was about 20º, and with proportion of ponderosa pine forest (β = 0.16 ± 0.22), in which relative use increased until about 20–30% of the survey area was classified as ponderosa pine forest.

We conducted a series of statistical simulations to evaluate the efficacy of potential survey protocols and N-mixture models for monitoring dusky grouse populations. Based on discussions with FWP Region 3 personnel, an acceptable monitoring program would produce an unbiased index of annual population in each administrative region. In addition, the annual estimate or index should have a coefficient of variation (CV) of less than 15% in order to be useful for management. We simulated sixteen data sets of dusky grouse abundance across various survey protocols, including 2–3 replicated surveys within a period of population closure at 50, 100, 200, and 500 independent survey sites. Each simulation was parameterized with a unique combination of number of survey sites and number of replicate surveys (2 or 3), under two specifications of mean local abundance per site (1.25 grouse per survey site, and 0.625 grouse per survey site) based on preliminary results from a Utah study. Results of our simulations revealed that 3 replicate surveys at each of 100 independent survey sites yielded unbiased and relatively precise (< 15% CV) indices of regional population abundance when site-specific abundance was at least 0.625 grouse and average probability of detection was 0.5.

A secondary objective is that our survey protocol and analytical framework can be used with little modification to evaluate the associations between dusky grouse abundance and habitat conditions or management actions (e.g., effects of beetle-kill or timber harvest). We therefore developed four additional datasets to evaluate the effects of a hypothetical habitat condition on dusky grouse abundance. An acceptable sampling protocol would yield unbiased estimates of 1) the true regional population size, and 2) the effect of the habitat covariate on local dusky grouse abundance. We evaluated two scenarios in which the hypothetical habitat condition (X) had a strong effect on site-specific abundance (β = -1.0), reflecting a 50% decrease in local abundance for every 0.1 increase in the habitat covariate (e.g., proportion beetle killed forest). We evaluated a weaker, but still negative, effect (β = -0.5) of the habitat covariate on local abundance in two additional scenarios. Generally, all parameters were unbiased (their 95% CrI of posterior distributions overlapped the true slope coefficient), and allowed correct inference to be made regarding the effects of the covariate. A scenario where 100 sites are surveyed three times yielded unbiased estimates of estimates of regional population size and unbiased estimates of the effect size when the true effect of the habitat covariate was either strong or weak. As expected, however, the precision of the total population abundance estimate was reduced when a habitat treatment covariate was added to the model. For example, the probability that the N-mixture model and protocol of 100 sites surveyed 3 times yields a total population estimate with < 15% CV is 0.66 and 0.76 when the effect is strong and weak, respectively. If 200 sites are surveyed 3 times, the model produces unbiased estimates of all parameters, as well as precise estimates of total population size. Overall, results of our simulations suggest that a survey protocol in which at least 100 independent sites are surveyed 3 times per year will yield unbiased and acceptably precise estimates of regional dusky grouse populations and allow for evaluation of associations between local grouse abundance and a habitat covariate or management action. Evaluation of relationships between local abundance and habitat covariates may require additional survey sites, depending on the strength of the relationship.

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MONITIORING IN MONTANA

2018 Annual Report

**OBJECTIVES**

**Objective 1: Generate a predictive model of habitat suitability for dusky grouse throughout their range in Montana**

*Accomplishments*

The goal of this quarter was to develop and test a predictive model of habitat suitability for dusky grouse that can be used to identify appropriate survey sites. We obtained dusky grouse observation data from the Integrated Monitoring in Bird Conservation Regions monitoring program (hereafter, IMBCR) administered by the Bird Conservancy of the Rockies. The collaborative IMBCR program conducts avian point count surveys between May and July at randomly selected locations in Montana and other states (Hanni et al. 2018). We obtained observation data from Spring 2009 through Spring 2018 for survey sites located in Montana. We reduced observations from the IMBCR point counts to detected/ not detected data that we then used to represent sites that were used (detected) and available (not-detected); it is possible that birds were present but not detected at available sites. We assumed that all birds assigned to point count locations were detected within 250 m of the point.

We extracted habitat information within a 250-m buffer drawn around each survey point using remotely-sensed geospatial datasets. We used digital elevation models (DEMs) from U.S. Geological Survey, ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands, CA) and geospatial modeling environment (GME) to measure average elevation, aspect, and slope of the 250 m radii area (Beyer 2015, U.S. Geological Survey 2017). We calculated the average distance of the 250 m radii area to the nearest stream and to the nearest road using the spatial analyst tools of ArcGIS applied to the Montana Spatial Data Infrastructure (MSDI) Transportation Framework and Hydrography datasets downloaded from the Montana state library and GME (Beyer 2015, Montana Spatial Data Infrastructure 2017, 2018). We used the 2012 LANDFIRE vegetation datasets with a spatial resolution of 30 × 30 m (LANDFIRE 2013), including layers for existing vegetation canopy (EVC), existing vegetation height (EVH), existing vegetation type (EVT), forest canopy cover (CC), and forest canopy height (CH). EVC is the vertically projected percent cover of the live canopy layer; EVH is the average height of the dominant vegetation; EVT is the type of plant community present; CC is the percent cover the tree canopy in a stand; CH is only provided for forested areas and is the average height of the top of a vegetated canopy (LANDFIRE 2013). We used GME to calculate the proportion of vegetation cover within 250 meters of the survey location (Beyer 2015). From these layers we extracted geospatial habitat information for a total of 167 variables that were then used to build resource selection functions (RSF).

We evaluated relative habitat use with resource selection functions calibrated using general linear mixed models (GLMM) with a logistic link function and binomial error distribution using the lme4 package in program R (Bates et al. 2015). We developed a set of approximately 1600 candidate models, including a null (intercept only model), representing our expectations regarding the relationships between our response variable (detected = 1, not detected = 0) and our habitat factors (independent variables). We included a random intercept term for unique IMBCR survey routes to account for potential spatial autocorrelation in the data because survey points are clustered along routes (Zuur et al. 2009).

We hypothesized that behavioral responses of use to some habitat variables may not be linear, and we performed preliminary screenings of linear, pseudo-threshold, and quadratic functional responses using univariate models. Habitat variables, such as proportion of conifer forest or proportion of Douglas fir may exhibit a threshold pattern so we tested pseudo-threshold models by evaluating the natural log of the explanatory variables (ln[x + 0.001; Franklin et al. 2000, McNew et al. 2015). We evaluated support for non-linear relations by comparing GLMMs with linear and non-linear terms using Akaike’s Information Criterion corrected for finite sample size (AICc). Each univariate model of the different functional responses for a habitat variable was compared to the null model, and if a model had a lower AICc value, then the variable with that behavioral response was kept. If a habitat variable had more than one functional response that resulted in a model ranked above the null model via AICc, then the functional response that had the lowest AICc value was kept.

After preliminary screenings of the function responses, we tested for multicollinearity in the remaining 109 habitat predictor variables using Spearman-rank correlations; if correlations were (|r| > 0.7), we deemed the variables correlated. If variables were correlated, the variable with the lower AICc value was selected and the other variable was removed from our analysis. We evaluated relative habitat use of the remaining 63 habitat predictor variables using the dredge function in the MuMIN package in program R (Barton 2018). We screened variables in groups of eight. Each combination of six variables was then evaluated in a competing RSF model. The variables in the model with the lowest AICc value were kept, and the two variables not in the model with the lowest AICc were removed.

We evaluated and assessed support for our final sets of models representing our competing hypotheses regarding habitat suitability using AICc (Burnham and Anderson 2002). We considered models that differed in AICc values ≤2 from the best-fitting model to be parsimonious (Burnham and Anderson 2002). In the case of model uncertainty, we used multimodel inference via model averaging of standardized coefficients across parsimonious models to obtain parameter estimates (AICcmodavg package for R; Mozerolle 2016). As suggested by Arnold (2010), we evaluated effect sizes using 85% confidence intervals so that the AICc model selection and parameter evaluation criteria were consistent.

Probabilities obtained from a logistic regression model are not appropriate to describe the true probability of use in a study design based on used versus available habitats (Manly et al. 2001:100). Therefore, we estimated the relative probability that sites were used by dusky grouse using the slope coefficients (βi) using the corresponding coefficients from the logistic regression. The sampling probabilities of used and available habitat units were unknown and the intercept term of (β0) of a resource selection probability function could not be estimated (Manly et al. 2001).

We validated our resource selection function model using an independent data set gathered by the Montana Department of Fish, Wildlife, and Parks (MFWP). This dataset consisted of 132 incidental dusky grouse locations collected during 2017–2018 by MFWP personnel during April–early June. For each independent observation, we used our RSF model to calculate RSF values and categorized those values into quantile bins representing the likelihood of points being classified as a site using by dusky grouse (Boyce et al. 2000, McNew et al. 2013). We then regressed the observed proportion of grouse locations in each quantile bin with the proportions classified in each bin for the original model training set (McNew et al. 2013). A good model fit leads to a high R2 value, a slope not different from 1.0 and an intercept not different from zero when comparing training and test data sets using linear regression (Johnson et al. 2006).

The model averaged coefficients of the supported models and their corresponding variables were chosen to construct a predictive map of relative occurrence for dusky grouse in Montana. Resolution = 250 m. We calculated the total area (km2) predicted to fall within each of 5 quantile bins of increasing RSF values by summing the number of pixels predicted for each category and multiplying by the pixel size (0.0625 km2).

*Results*. – Of the top ten candidate models, four models were within 2 AICc units of the top model and were considered parsimonious (Table 1). Several habitat attributes had a significant effect on whether a dusky grouse was detected or not detected at survey sites, including proportion of rocky mountain subalpine montane mesic meadow, proportion of northern Rocky mountain dry-mesic montane mixed conifer forest, proportion of Douglas fir forest, proportion of area with shrubs 0.5–1 meter in height, average elevation, proportion of northern Rocky Mountain ponderosa pine woodland and savanna, average slope, proportion of riparian area, distance to the edge of conifer forest, proportion of total conifer forest, and proportion of total Douglas fir forest within 250 meters of the survey site. Relative use was higher in areas with higher proportions of mixed conifer forest (β = 1.86 ± 1.53) and subalpine meadows (β = 3.89 ± 1.10). Relative use was lower as the distance to conifer forest increased (β = -0.002 ± 0.006) and in areas with higher proportions of riparian area (β = -3.33 ± 5.31). Several habitat attributes exhibited non-linear relationships with relative use such as proportion of shrub coverage (woody vegetation 0.5–1 meter in height), average elevation, and proportion of conifer forest. Relative use exhibited positive non-linear relationships with the proportional coverage of the Douglas fir forest (β = 0.29 ± 0.23), in which relative use increased rapidly until about 40% of the survey area was classified as Douglas fir forest, and proportion of conifer forest (β = 0.14 ± 0.30), in which relative use increases rapidly until 40–50 % of the survey area was classified as conifer forest (Table 2). Relative use also exhibited a positive non-linear relationship with average slope (β = 0.24 ± 0.41), in which relative use increased rapidly until about 20º, and with proportion of ponderosa pine forest (β = 0.16 ± 0.22), in which relative use increased until about 20–30 % of the survey area was classified as ponderosa pine forest (Table 2). Conditional and marginal r2 for the top model were 0.75 and 0.82, respectively, indicating most of the variation in the response data was described by the fixed effects; only an additional 7% of the modeled variation was associated with unmodeled conditions associated with clustered survey routes.

Our model of relative habitat suitability correctly classified 88 out of 132 (66.7%) of the independently detected grouse locations into the two highest relative probabilities of use categories (Fig. 1). Regression validations produced a *R*2 value of 0.99, an intercept not overlapping zero (95% CI: -0.244 – -0.188), and a slope of 2.08 (SE = 0.06); indicating high predictive accuracy for our resource selection model.

Our model of relative habitat suitability classified 6,413,526 km2 of Montana into the two highest relative probability of use categories. The highest total amounts of suitable dusky grouse habitat was predicted to occur in Montana FWP administrative regions 1, 2, and 3 (Table 3).

*Goals for Next Quarter*

We will use the predictive map to stratify region 3 into areas with different relative probabilities of occurrence (0-20%, 20-40%, 40-60%, 60-80%, 80-100%). We will then generate possible transect locations for spring and summer surveys in the areas with the higher probabilities of occurrence (>60 %) stratified into the two highest strata. We will meet with MFWP biologists to select appropriate survey sites from the list of possible transect locations.

**Objective 2: Develop and evaluate unbiased survey methods that provide statewide and regional estimates of dusky grouse densities and annual trend monitoring in Montana**

**Objective 3: Develop methods that facilitate rigorous and cost-effective evaluations of grouse-habitat relationships and the effects of management (e.g. timber harvest)**

*Accomplishments*

We conducted a series of statistical simulations to evaluate the efficacy of potential survey protocols for monitoring dusky grouse populations. Based on discussions with FWP Region 3 personnel, an acceptable monitoring program would produce an unbiased index of annual population in each administrative region. In addition, the annual estimate or index should have a coefficient of variation (CV) of less than 15% in order to be adequately precise for management. Our simulation approach was to use the same model to build and analyze simulated observational data sets representing varying scenarios of survey effort. We simulated sixteen data sets and analyses of dusky grouse abundance across various survey protocols, including 2–3 replicated surveys within a period of population closure at 50, 100, 200, and 500 independent survey sites (Table 4). Each simulation was parameterized with a unique combination of number of survey sites and number of replicate surveys (2 or 3), under two specifications of mean local abundance per site (λ = 0.625 grouse per survey site and 1.25 grouse per survey site). Preliminary work in northeastern Utah has indicated that average dusky grouse abundance in good to excellent habitat ranges from 0.625 to 1.25 grouse per survey site (Dahlgren et al. 2018). All simulations assumed that detection probability of dusky grouse during a survey was similar across sites and averaged 0.5 (D. Dahlgren, Utah State University, personal communication). Stochasticity in local abundance was included by sampling abundance from a Poisson distribution; site specific abundance was determined by and for scenarios designed to represent medium and high grouse densities. Observations of grouse at each site *i* during survey *j* was simulated by drawing randomly from a binomial distribution where the probability of detecting a grouse (*p*) = 0.5.

We analyzed our sixteen simulated datasets using the same single-season N-mixture model:

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where the ecological process underlying the true abundance at site *i* is distributed as a Poisson random variable. The observation process was assumed to be a binomial random variable where ( is the observed counts at site *i* during replicate survey *j* and *p* is the probability of detecting a grouse during a survey (Royle 2004). We used WinBUGS to analyze the N-mixture model in a Bayesian framework (Lunn et al. 2000) and used vague priors for all hyper-parameters that provided little or no information about the estimated parameters (see Appendix A for a description of the simulations and model in the BUGS language). We estimated the total number of individuals across all sites by summing the estimated number of individuals at each survey site. We ran three chains of length 40,000 after a burn-in period of 10,000 and thinned the posterior chains by 100 to ensure independence. We assessed convergence using the Gelman-Rubin () statistic, which examines the variance ratio of the Markov chain Monte Carlo (MCMC) algorithm within and between chains across iterations (Gelman and Rubin 1992). We accepted parameter estimates when they came from Markov chains with between 1.0 and 1.01. All simulations and analyses were conducted in R computing software (R Core Team 2017).

To quantify bias of estimates for each survey protocol scenario, we ran 400 iterations of each data simulation and subsequent analysis and calculated the difference between the estimated local abundance () and the true abundance known for the simulated site (*Ni*). Similarly, we quantified bias in the total estimated population size by calculating the difference between Total estimated as and the true known total abundance for all sites (. We compared the posterior distributions of the mean differences between each estimate and the true values across all 400 simulations to evaluate the bias of each estimate. We considered an estimate to be clearly biased in the 95% credible interval (CrI) of the differences did not include 0. In addition, at each of the 400 iterations, we estimated the precision of each estimate by calculating the coefficient of variation . We evaluated the posterior distributions of the 400 derived CV estimates to determine whether survey protocols yielded acceptable levels of precision for average local abundance and total population size. We estimated probability that the average coefficient of variation would meet the manager-determined threshold of 15% by calculating the proportion of the total posterior distribution density greater than 0.15.

Results of our simulations revealed that 3 replicate surveys at each of 100 independent survey sites yielded unbiased and relatively precise (≤15% CV) indices of regional population abundance when site-specific abundance was at least 0.625 grouse (Table 4). For example, the mean difference between true and estimated local abundance was 0.02 (95% CrI: -0.13 – 0.19) when 100 independent sites were each surveyed 3 times and the average local abundance was 0.625 grouse. The N-mixture model yielded unbiased estimates of total abundance for all other scenarios as well (Table 4). Precision associated with estimates of local abundance and total population size (summed site-specific estimated abundance;) increased with the number of sites surveyed as well as the number of replicate visits per site (Table 4). For example, the CV from 400 simulation runs averaged 0.09 (95% CrI: 0.6–0.14) when 100 sites were each surveyed 3 times (when λ = 1.25, *p* = 0.5); the probability that the CV ≥ 0.15 was 0.02. When average local abundance was half as high (λ = 0.625), the average CV of the total population size estimate was 0.13 (95%CrI: 0.07–0.16) and the probability that CV ≥ 0.15 was 0.09 under the same survey protocols (100 sites, 3 visits). As expected, reducing the number of replicate survey visits per site from 3 to 2 reduced precision. An average CV ≤ 0.15 was only achieved when the number of survey sites was increased from 100 to 500 (Table 4). Overall, our results suggest that a survey design where 100 sites are each surveyed 3 times during a period of population closure is the most efficient protocol for meeting management objectives relative to annual monitoring region-specific dusky grouse populations.

A secondary objective is that our survey protocol and analytical framework can be used with little modification to evaluate the associations between dusky grouse abundance and habitat conditions or management actions (e.g., effects of beetle-kill or timber harvest). We therefore developed four additional simulated datasets to evaluate the effects of a hypothetical habitat condition on dusky grouse local abundance. An acceptable sampling protocol would yield unbiased and precise estimates of 1) the true regional population size, 2) the effect of the habitat covariate on local dusky grouse abundance (βcovariateX). Based on results of our previously-described simulations, we limited simulation scenarios to include 3 replicate surveys per site and evaluated the ability of surveying 100 and 200 sites in producing unbiased indices of regional population size and effects of the habitat covariate. We did not consider a protocol with more than 200 survey sites due to practical limitations of FWP staff time. The simulated site habitat covariate (X) was distributed as a uniform random variable ranging from -1 to 1. The first scenarios included a relatively strong effect of the habitat covariate (X) on site-specific abundance (λ = exp(0.5 - 1(X)), reflecting a 50% decrease in local abundance for 50% increase in the habitat covariate (e.g., proportion beetle killed forest). We evaluated a weaker, but still negative, effect of the habitat covariate on local abundance in a second scenario (λ = exp(0.5 – 0.5(X)) where site-specific abundance is distributed as random Poisson(λ). The mean expected abundance of per site (λ) was ~ 0.63 and 1.68 grouse per site, emulating population sizes occurring in good and excellent habitat on average (Dahlgren et al. 2018). Although abundance was modeled uniquely for each simulation, we simulated all datasets to have similar probabilities of detection (*p*) that randomly distributed according to a binomial distribution and averaged 0.5 across sites. We evaluated bias and the CV of modeled estimates of total population size () as described above. In addition we estimated bias in model parameters related to the habitat covariate by calculating the difference between the true intercepts (α) and slope coefficients (β) and the intercept and slope coefficients estimated by our model. Data were simulated and analyzed using a modified N-mixture model (Appendix B) 400 times and estimated bias calculated at each iteration. We considered a sampling protocol to provide unbiased estimates of α and β if the 95% CrI of the posterior distribution of estimated bias overlapped 0.

A scenario where 100 sites are surveyed three times yielded unbiased estimates of regional population size and unbiased estimates of effect size of the site covariate regardless of whether the effect of the covariate was strong or weak (Table 4). However, the sampling protocol did not always yield acceptable levels of precision for total population size estimates; for example, the CV of total population size averaged 0.15 (95%CrI: 0.08 –0.27) under a scenario where site-specific abundance declined strongly with the site covariate (Table 4; Sim 17). There was a 34% probability that the CV of the total population size estimate would exceed the threshold value of 0.15 under scenario 17. We found similar results when the effect of the site covariate was relatively weak; the probability that the CV of total population size would be ≤ 0.15 was 0.24. That is, managers can expect that estimates of total population size to have adequate precision 76% of the time. Increasing the number of surveys sites to 200 resulted in unbiased estimates with high probabilities of suitable precision (Table 4).

*Overall, results of our simulations indicate that a survey protocol in which at least 100 independent sites are surveyed three times per year will usually yield unbiased and acceptably precise estimates of regional dusky grouse populations and allow for evaluation of associations between local grouse abundance and a habitat covariate or management action. Evaluation of relationships between local abundance and a continuous habitat covariates may require additional survey sites ≤ 200.*

*Goals for Next Quarter*

During February­–March, we will work with MFWP and USFS personnel to select sites for dusky grouse survey transects based on the results of our habitat suitability model. We expect Spring surveys of breeding grouse to occur during April–May. Surveys routes (n= 20) will likely consist of 5 survey sites occurring along a hexagonal (or circular) transects. Additional surveys will occur during the summer brood-rearing period and employ a call-back protocol similar to that described by Dahlgren et al. (2018). At least two four-minute point counts would occur at each point with female calls being used during the later point count to maximize detections. Summer surveys will likely occur during June–July.

Table 1. Support for candidate models predicting dusky grouse occurrence. Model set consists of the top ten models and the null model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | K\* | AICc | Δ AICc | AICc Wt |
| Subalpine meadow + mixed conifer + shrub medium height + shrub medium height2 + ln(all Douglas fir + 0.001) + elevMN | 8 | 784.55 | 0.00 | 0.31 |
| Subalpine meadow + mixed conifer + shrub medium height + shrub medium height 2 + ln(SlopeMN + 0.001) + ln(all douglas fir + 0.001) | 8 | 784.90 | 0.35 | 0.26 |
| ln(Ponderosa pine + 0.001) + riparian + subalpine meadow + elevMN + elevMN2 + ln(conifer + 0.001) | 8 | 785.53 | 0.98 | 0.19 |
| Dist. to conifer + subalpine meadow + ln(ponderosa pine + 0.001) + riparian + elevMN + elevMN2 | 8 | 786.17 | 1.62 | 0.14 |
| ln(Ponderosa pine + 0.001) + riparian + subalpine meadow + xeric Douglas fir + xeric Douglas fir + ln(conifer + 0.001) | 8 | 787.35 | 2.80 | 0.08 |
| Dist. to conifer + shrub medium height + shrub medium height 2 + subalpine meadow + ln(ponderosa pine + 0.001) + riparian | 8 | 790.18 | 5.63 | 0.02 |
| Dist. to conifer + shrub medium height + shrub medium height 2 + subalpine meadow + ln(ponderosa pine + 0.001) + Rocky Mt. Douglas fir | 8 | 798.42 | 13.87 | 0.00 |
| subalpine meadow + mixed conifer + shrub medium height + shrub medium height 2 + ln(conifer + 0.001) + elevMN | 8 | 799.90 | 15.35 | 0.00 |
| elevMN + I(elevMN^2) + shrub medium height + shrub medium height 2 + shrubland + mixed conifer | 8 | 812.65 | 28.10 | 0.00 |
| elevMN + I(elevMN^2) + shrub medium height + shrub medium height 2 + shrubland + riparian | 8 | 816.18 | 31.63 | 0.00 |
| Null | 2 | 869.27 | 84.71 | 0.00 |

\* K = number of fixed parameters

Table 2. Effect sizes for model averaged estimates for all terms in any of the supported models.

|  |  |  |  |
| --- | --- | --- | --- |
| Variable | Estimated slope (βi) | Lower 85% Confidence Interval | Upper 85% Confidence Interval |
| Subalpine meadow | 3.89 | -6.67 | 1.24 |
| Mixed conifer | 2.92 | 1.84 | 4.00 |
| Shrub medium height | 24.06 | 10.87 | 37.25 |
| shrub medium height^2 | -116.80 | -192.80 | -40.80 |
| ln(all Douglas fir + 0.001) | 0.46 | 0.35 | 0.56 |
| elevMN | 0.002 | 0.001 | 0.004 |
| elevMN^2 | -3.55e-07 | -5.39e-07 | -1.70e-07 |
| ln(SlopeMN + 0.001) | 0.83 | 0.42 | 1.24 |
| ln(ponderosa pine + 0.001) | 0.44 | 0.31 | 0.58 |
| Riparian | -9.13 | -16.26 | -2.00 |
| ln(conifer + 0.001) | 0.68 | 0.32 | 1.03 |
| Dist. to conifer | -0.01 | -0.02 | -0.01 |

Table 3. Area (km2) of predicted dusky grouse habitat as quantified by relative use bins for Montana FWP administrative regions.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| FWP Region | Low | Low-Med | Med | Med-High | High |
| 1 | 45030 | 198331 | 625433 | 1084422 | 732706 |
| 2 | 5758 | 114516 | 316777 | 682195 | 745029 |
| 3 | 202321 | 688443 | 752492 | 954207 | 907808 |
| 4 | 2035204 | 1325958 | 701864 | 475709 | 405993 |
| 5 | 568173 | 1168275 | 1020742 | 236898 | 144630 |
| 6 | 2724384 | 1037035 | 323208 | 28093 | 194 |
| 7 | 2142763 | 2303362 | 1288016 | 15550 | 94 |



\*Table printed as image here to fit the page; a spreadsheet of this table is available in provided supplemental materials.

Table 5. Definitions for all variables in any of the supported models for predicting dusky grouse occurrence.

|  |  |
| --- | --- |
| Variable | Description |
| Subalpine meadow | Proportion of Rocky Mountain subalpine-montane mesic meadow within a 250 x 250 meter grid cell (from Landfire data) |
| Mixed Conifer | Proportion of northern rocky mountain dry-mesic montane mixed conifer forest within a 250 x 250 meter grid cell (from Landfire data) |
| Shrub medium height | Proportion of area with shrub between 0.5-1 meter tall within a 250 x 250 meter grid cell (from Landfire data) |
| Ponderosa pine | Proportion of northern Rocky Mountain ponderosa pine woodland and savanna within a 250 x 250 meter grid cell (from Landfire data) |
| ElevMN | Average elevation in a 250 x 250 meter grid cell |
| SlopeMN | Average slope in a 250 x 250 meter grid cell |
| conifer | Proportion of conifer forest within a 250 x 250 meter grid cell. Vegetation types (from Landfire dataset) classified as conifer forest: northern Rocky Mountain dry-mesic montane mixed conifer forest, northern Rocky Mountain subalpine woodland and parkland, northern rocky Mountain mesic montane mixed conifer forest, northwestern great plains highland white spruce woodland, rocky mountain foothill limber pine-juniper woodland, rocky mountain lodgepole pine forest, southern Rocky Mountain dry-mesic montane mixed conifer forest and woodland, Southern Rocky Mountain mesic montane mixed conifer forest and woodland, northern Rocky Mountain ponderosa pine woodland and savanna, southern Rocky Mountain ponderosa pine woodland, Rocky Mountain subalpine dry-mesic spruce-fir forest and woodland, Rocky Mountain subalpine mesic-wet spruce-fir forest and woodland, rocky mountain subalpine-montane limber bristlecone pine woodland, inter-mountain basins montane riparian forest and woodland, Rocky Mountain montane riparian forest and woodland, northern Rocky Mountain foothill conifer wooded steppe, middle Rocky Mountain montane Douglas-fir forest and woodland, Rocky Mountain poor-site lodgepole pine forest, northwestern great plains- Black Hills ponderosa pine woodland and savanna, dry-mesic montane western larch forest, abies grandis forest, subalpine Douglas-fir forest, mesic montane Douglas-fir forest, xeric montane Douglas-fir forest, subalpine western larch forest, mesic montane western larch forest, western cool temperate urban evergreen forest, western cool temperate urban mixed forest |
| All Douglas fir | Proportion of all Douglas fir forest vegetation types within a 250 x 250 meter grid cell. Vegetation types from (Landfire dataset) classified as Douglas fir forest: middle Rocky mountain montane Douglas-fir forest and woodland, dry-mesic montane Douglas fir forest, subalpine Douglas-fir forest, mesic montane Douglas-fir forest, xeric montane Douglas-fir forest |
| riparian | Proportion of riparian area within a 250 x 250 meter grid cell (from Landfire data set) |
| Dist. to conifer | Average distance to the edge of conifer forest within a 250 x 250 meter grid cell |

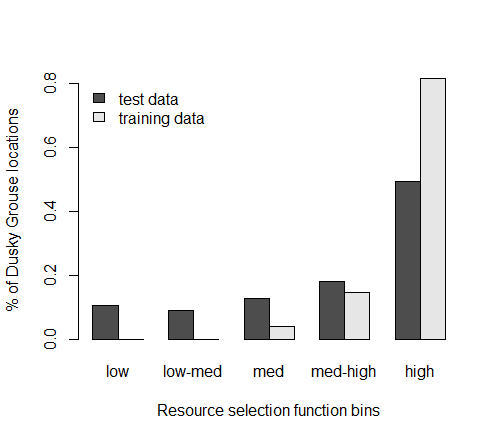


Figure 1. Proportion of dusky grouse locations in five bins of increasing resource selection function values that we used to train (n=102) and test (n=132) our model of habitat suitability. A good predictive model will assign most of the training and test dusky grouse locations to med-high and high categories of predicted use.

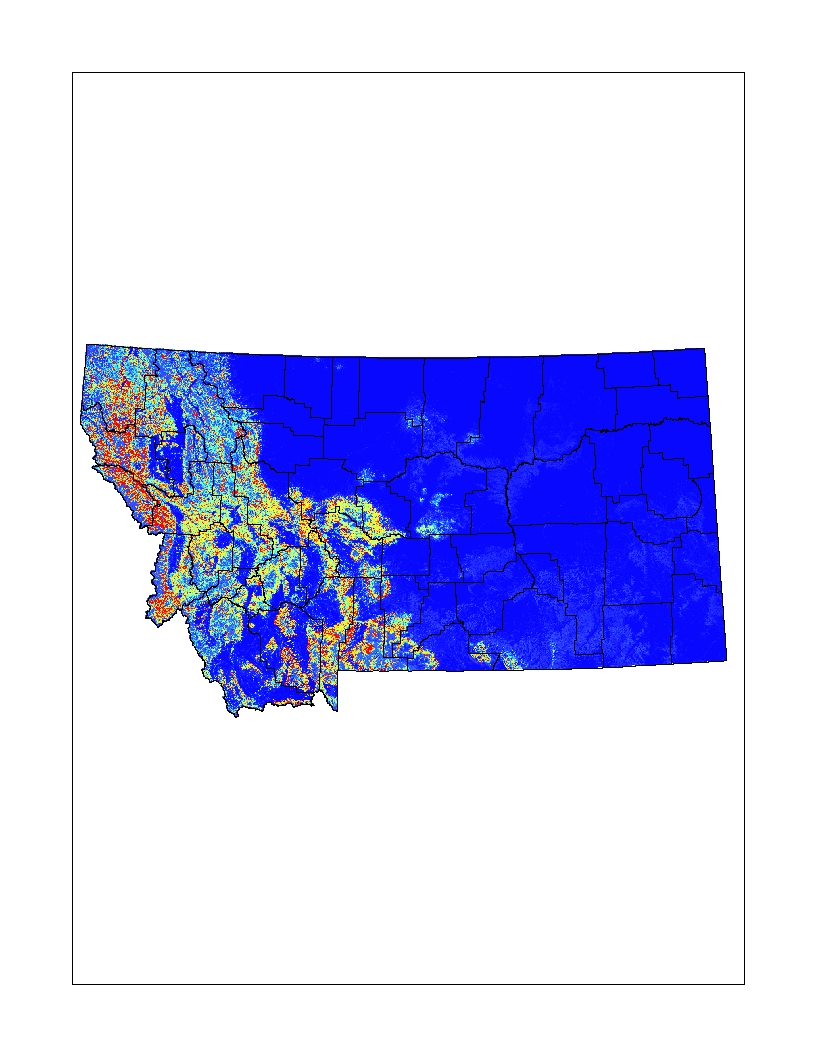


Figure 2. Predictive map of habitat suitability for dusky grouse for central and western Montana. Warmer colors (green – red) represent higher areas of relative use.

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APPENDIX A. Complete Bayesian model specification and simulation code in R language for one of 16 simulations evaluating dusky grouse survey protocols for a population in which local abundance was similar across all sites and averaged 1.25 and individual detection probability averaged 0.5.

# Define model

sink("model.c.txt")

cat("

model {

# Priors

lambda ~ dgamma(0.005, 0.005) # Standard vague prior for lambda

# or lambda ~ dunif(0, 10)

p ~ dunif(0, 1)

# Likelihood

# Biological model for true abundance

for (i in 1:R) {

N[i] ~ dpois(lambda)

# Observation model for replicated counts

for (j in 1:T) {

C[i,j] ~ dbin(p, N[i])

} # j

} # i

#Derived parameters

Ntotal <- sum(N[]) # Total population size at M sites combined

}

",fill = TRUE)

sink()

##LOOP FOR REPLICATING DATASETS AND ASSESSING BIAS ##################################

nsim <- 400 # how many times to simulate dataset and run model

# Create a bunch of empty vectors to store results from replicated datasets

m.bias.Nsite <- vector("list",nsim)

sd.bias.Nsite <- vector("list",nsim)

baye.p.Nsite <- vector("list",nsim)

m.bias.p <- vector("list",nsim)

sd.bias.p <- vector("list",nsim)

baye.p.p <- vector("list",nsim)

m.bias.Ntot <- vector("list",nsim)

sd.bias.Ntot <- vector("list",nsim)

baye.p.Ntot <- vector("list",nsim)

m.bias.lam <- vector("list",nsim)

sd.bias.lam <- vector("list",nsim)

baye.p.lam <- vector("list",nsim)

m.CV.lam <- vector("list",nsim)

sd.CV.lam <- vector("list",nsim)

prop.CV.lam <- vector("list", nsim)

m.CV.Ntot <- vector("list",nsim)

sd.CV.Ntot <- vector("list",nsim)

prop.CV.Ntot <- vector("list", nsim)

system.time(for (k in 1:nsim){ # Stick the simulations in a for loop and replicate them nsim times

##INPUT DATA FOR SIMULATIONS

##Simulate truth and count data

R = 100 #100 survey points located along 20 transects (5 pts / transect)

T = 3

lambda = 1.25

p = 0.5

# Create structure to contain counts

C <- matrix(nrow = R, ncol = T)

# Sample abundance from a Poisson(lambda=2)

N <- rpois(n = R, lambda = lambda)

# Sample counts from a Binomial(N, p=0.5)

for (j in 1:T){

C[,j] <- rbinom(n = R, size = N, prob = p)

}

# Bundle data for WinBUGS

win.data <- list(C = C, R = nrow(C), T = ncol(C))

# initial values

Nst <- apply(C, 1, max) + 1 # This line is vital

inits <- function() list(N = Nst)

# Define parameters to be monitored

params <- c("lambda", "p", "N","Ntotal")

# MCMC settings

ni <- 40000

nt <- 100

nb <- 10000

nc <- 3

# Call WinBUGS from R and time the run

start.time = Sys.time() # Set timer

out <- bugs(win.data, inits, params, "model.c.txt", n.chains = nc,

n.thin = nt, n.iter = ni, n.burnin = nb, debug = FALSE, bugs.directory = "C:\\Users\\p73v837\\Documents\\WinBUGS14", working.directory = getwd())

end.time = Sys.time()

elapsed.time = round(difftime(end.time, start.time, units='mins'), dig = 2)

cat('Posterior computed in ', elapsed.time, ' minutes\n\n', sep='')

####Evaluate bias ########################

##Bias in site specific abundance

bias.Nsite <- out$mean$N - N

m.bias.Nsite[k] <- mean(bias.Nsite)

sd.bias.Nsite[k] <- sd(bias.Nsite)

baye.p.Nsite[k] <-mean(N > out$mean$N) #Baysian P-value (proportion of simulations where the true abundance

#was greater than the estimated abundance - values close to 0 or 1 indicate signficant bias)

##Bias in average local abundance (lambda)

bias.lam <- out$mean$lambda - lambda

m.bias.lam[k] <- mean(bias.lam)

sd.bias.lam[k] <- sd(bias.lam)

baye.p.lam[k] <- mean(lambda > out$mean$lambda)

##Bias in p

bias.p <- out$mean$p - p

m.bias.p[k] <- mean(bias.p)

sd.bias.p[k] <- sd(bias.p)

baye.p.p[k] <- mean(p > out$mean$p)

##Bias in Ntotal

bias.Ntot <- out$mean$Ntotal - sum(N)

m.bias.Ntot[k] <- mean(bias.Ntot)

sd.bias.Ntot[k] <- sd(bias.Ntot)

baye.p.Ntot[k] <- mean(sum(N) > out$mean$Ntotal)

##Coefficient of Variation in Ntotal

CV.Ntot <- out$sd$Ntotal/out$mean$Ntotal

m.CV.Ntot[k] <- mean(CV.Ntot)

sd.CV.Ntot[k] <- sd(CV.Ntot)

prop.CV.Ntot[k] <- mean(CV.Ntot < 0.15)

#Coefficient of Variation in local abundance (lambda)

CV.lam <- out$sd$lambda/out$mean$lambda

m.CV.lam[k] <- mean(CV.lam)

sd.CV.lam[k] <- sd(CV.lam)

prop.CV.lam[k] <- mean(CV.lam < 0.15)

} ) #This will be the end of the simulations

APPENDIX B. Complete Bayesian model specification and simulation code in R language for one of 4 simulations evaluating dusky grouse survey protocols for a population in which local abundance declined strongly (B = -1) with a standardized hypothetical site covariate. Individual detection probability was constant and averaged 0.5.

# Define model

sink("model.txt")

cat("

model {

# Priors

alpha.lam ~ dunif(-10, 10)

beta.lam ~ dunif(-10, 10)

alpha.p ~ dunif(-10, 10)

beta.p ~ dunif(-10, 10)

# Likelihood

# Ecological model for true abundance

for (i in 1:R) {

N[i] ~ dpois(lambda[i])

log(lambda[i]) <- alpha.lam + beta.lam \* X[i]

# Observation model for replicated counts

for (j in 1:T) {

y[i,j] ~ dbin(p[i,j], N[i])

p[i,j] <- exp(lp[i,j])/(1+exp(lp[i,j]))

lp[i,j] <- alpha.p + beta.p \* X[i]

} #j

} #i

# Derived quantities

totalN <- sum(N[])

}

",fill = TRUE)

sink()

#################################### LOOP FOR REPLICATING DATASETS AND ASSESSING BIAS ##################################

nsim <- 400 # how many times to simulate dataset and run model

# Create a bunch of empty vectors to store results from replicated datasets

m.bias.Nsite <- vector("list",nsim)

sd.bias.Nsite <- vector("list",nsim)

baye.p.Nsite <- vector("list",nsim)

m.bias.p <- vector("list",nsim)

sd.bias.p <- vector("list",nsim)

baye.p.p <- vector("list",nsim)

m.bias.Ntot <- vector("list",nsim)

sd.bias.Ntot <- vector("list",nsim)

baye.p.Ntot <- vector("list",nsim)

m.CV.Ntot <- vector("list",nsim)

sd.CV.Ntot <- vector("list",nsim)

prop.CV.Ntot <- vector("list", nsim)

m.bias.alpha.lam <- vector("list",nsim)

sd.bias.alpha.lam <- vector("list",nsim)

m.bias.beta.lam <- vector("list",nsim)

sd.bias.beta.lam <- vector("list",nsim)

m.CV.alphalam <- vector("list",nsim)

sd.CV.alphalam <- vector("list",nsim)

prop.CV.alphalam <- vector("list", nsim)

m.CV.betalam <- vector("list",nsim)

sd.CV.betalam <- vector("list",nsim)

prop.CV.betalam <- vector("list", nsim)

system.time(for (k in 1:nsim){ # Stick the simulations in a for loop and replicate them nsim times

##############INPUT DATA FOR SIMULATIONS

##With a covariate that affects both lambda and p

R = 200 #100 survey points located along 20 transects (5 pts / transect)

T = 3

xmin = -1

xmax = 1

alpha.lam = 0.5

beta.lam = -1

p = 0.5

y <- array(dim = c(R, T)) # Array for counts

# Ecological process

# Covariate values

X <- sort(runif(n = R, min = xmin, max = xmax))

# Relationship expected abundance ? covariate

lam <- exp(alpha.lam + beta.lam \* X)

# Add Poisson noise: draw N from Poisson(lambda)

N <- rpois(n = R, lambda = lam)

table(N) # Distribution of abundances across sites

sum(N > 0) / R # Empirical occupancy

totalN <- sum(N) ; totalN

# Make a ?census? (i.e., go out and count things)

for (i in 1:T){

y[,i] <- rbinom(n = R, size = N, prob = p)

}

# Naive regression

naive.pred <- exp(predict(glm(apply(y, 1, max) ~ X + I(X^2), family = poisson)))

win.data <- list(y = y, R = nrow(y), T = ncol(y), X = X)

# initial values

Nst <- apply(y, 1, max) + 1 # This line is vital

inits <- function() list(N = Nst, alpha.lam = runif(1, -1, 1), beta.lam = runif(1, -1, 1), alpha.p = runif(1, -1, 1), beta.p = runif(1, -1, 1))

# Define parameters to be monitored

params <- c("N","totalN", "alpha.lam", "beta.lam", "p") #monitor abundance at each site

# MCMC settings

ni <- 50000

nt <- 100

nb <- 2000

nc <- 3

# Call WinBUGS from R and time the run

start.time = Sys.time() # Set timer

out <- bugs(win.data, inits, params, "model.txt", n.chains = nc,

n.thin = nt, n.iter = ni, n.burnin = nb, debug = FALSE, bugs.directory = "C:\\Users\\p73v837\\Documents\\WinBUGS14", working.directory = getwd())

end.time = Sys.time()

elapsed.time = round(difftime(end.time, start.time, units='mins'), dig = 2)

cat('Posterior computed in ', elapsed.time, ' minutes\n\n', sep='')

####EValuate bias ########################

##Bias in site specific abundance

bias.Nsite <- out$mean$N - N

m.bias.Nsite[k] <- mean(bias.Nsite)

sd.bias.Nsite[k] <- sd(bias.Nsite)

baye.p.Nsite[k] <-mean(N > out$mean$N) #Baysian P-value (proportion of simulations where the true abundance

#was greater than the estimated abundance - values close to 0 or 1 indicate signficant bias)

##Bias in model intercept for abundance (alpha.lam)

bias.alpha.lam <- out$mean$alpha.lam - alpha.lam

m.bias.alpha.lam[k] <- mean(bias.alpha.lam)

#sd.bias.alpha.lam[k] <- sd(bias.alpha.lam)

#baye.p.alpha.lam[k] <-mean(alpha.lam > out$mean$alpha.lam) #Baysian P-value (proportion of simulations where the true alpha.lam

#was greater than the estimated alpha.lam - values close to 0 or 1 indicate signficant bias)

##Bias in model slope coefficient (beta.lam)

bias.beta.lam <- out$mean$beta.lam - beta.lam

m.bias.beta.lam[k] <- mean(bias.beta.lam)

#sd.bias.beta.lam[k] <- sd(bias.beta.lam)

#baye.p.beta.lam[k] <-mean(N > out$mean$beta.lam) #Baysian P-value (proportion of simulations where the true abundance

#was greater than the estimated abundance - values close to 0 or 1 indicate signficant bias)

##Bias in p

bias.p <- out$mean$p - p

m.bias.p[k] <- mean(bias.p)

sd.bias.p[k] <- sd(bias.p)

baye.p.p[k] <- mean(p > out$mean$p)

##Bias in Ntotal

bias.Ntot <- out$mean$totalN - sum(N)

m.bias.Ntot[k] <- mean(bias.Ntot)

sd.bias.Ntot[k] <- sd(bias.Ntot)

baye.p.Ntot[k] <- mean(sum(N) > out$mean$Ntotal)

##Coefficient of Variation in Ntotal

CV.Ntot <- out$sd$totalN/out$mean$totalN

m.CV.Ntot[k] <- mean(CV.Ntot)

sd.CV.Ntot[k] <- sd(CV.Ntot)

prop.CV.Ntot[k] <- mean(CV.Ntot < 0.15)

#Coefficient of Variation in alpha.lam

CV.alphalam <- out$sd$alpha.lam/out$mean$alpha.lam

m.CV.alphalam[k] <- mean(CV.alphalam)

sd.CV.alphalam[k] <- sd(CV.alphalam)

prop.CV.alphalam[k] <- mean(CV.alphalam < 0.15)

#Coefficient of Variation in beta.lam

CV.betalam <- abs(out$sd$beta.lam/out$mean$beta.lam)

m.CV.betalam[k] <- mean(CV.betalam)

sd.CV.betalam[k] <- sd(CV.betalam)

prop.CV.betalam[k] <- mean(CV.betalam < 0.15)

} ) #This will be the end of the simulations