Golden Eagle Modeling Approach, Summary Document

Here, we summarize the modeling approach and general interpretation of model results for the Golden Eagle Decision Support Tool (DST) (www.raptormapper.com). This summary was created for the average DST user, and we do not assume readers have a strong background in ecological modeling. We begin by describing the creation and testing of four Golden Eagle life history models that represent: 1) breeding areas, 2) non-breeding season areas (excluding migration), 3) fall migration, and 4) spring migration. Nesting area models were developed based on known nest locations, and represent habitat used by adult eagles and their pre-dispersal young during the breeding season. The non-breeding season model was created for both residents and migrants that spend part of the year in Wyoming, but it excluded locations within breeding areas and locations used during migration. Fall and spring migration models were developed for adult and non-adult migrants, and only used locations during migration.

We also present the results of testing how well the models predicted variation in Golden Eagle density during other life history phases. For example, we evaluated how well the breeding area model and non-breeding model accounted for variation in adult non-breeding Golden Eagle habitat use during the breeding season. Similarly, we evaluated how those same models accounted for variation in non-breeding non-adult Golden Eagle habitat use during the breeding season. Essentially, we evaluated whether the four "base models" adequately accounted for a variety of Golden Eagle age classes, behaviors, and seasons that were not included in the base models.

What was modeled and what did we estimate?

We created models of Golden Eagle nesting area density, density of non-breeding season locations, density of fall migration locations, and density spring migration locations. Our nesting area density model was built using nest locations and estimates the relative density of individual nesting areas (territories), *not total nests* (several of which can occur within a single territory). Non-breeding and migration models were built using GPS relocation data from individual eagles during those periods. Non-breeding season density of locations refers to daytime use locations during the non-breeding season but excluded locations that occurred within breeding territories (regardless of when they were used) or during migration. Density of use of non-breeding locations represents the *density of eagle locations*, and should not be interpreted as equivalent to density of *individual* Golden Eagles. Similarly, for both fall and spring migration models, we modeled the density of use during migration, not the density of individual eagles.

Analytical Approach

Our goal was to make accurate predictions to support conservation planning, rather than to test hypotheses about Golden Eagle ecology (Tredennick et al. 2021). Accordingly, we developed models using a flexible, multi-stage process that emphasized prediction. We selected from a large set of candidate predictors, fitted models with a machine learning algorithm (MaxEnt; Phillips et al. 2006), used a tuning process to minimize the risk of over- or under-fitting, then conducted an extensive set of evaluations to quantify the predictive performance of the models overall and among various geographic regions in the study area. The purpose of the geographic evaluation of the models was to understand whether the models worked well, in general, while making accurate predictions in some geographic regions and inaccurate predictions in other regions versus working well, in general, and working well in most/all geographic regions.

We compiled a library of environmental variables we hypothesized would affect Golden Eagle habitat selection, consisting of >100 base variables from the categories of climate indices, developed areas, land cover, topographic indices and landforms, vegetation indices, wind and uplift indices, and ecoregions. We summarized these variables at ≤6 spatial extents (120 m to 6.4 km) relevant to scales of habitat selection by Golden Eagles using a moving window approach and estimated four focal statistics (mean, standard deviation, minimum, and maximum) appropriate to each variable (Dunk et al. 2019, Wallace et al. in review, Woodbridge et al. in prep).

We used three methods to assess the performance of models:

1) We compared relative density *predicted* by the model to those *observed*, using cross-validation, withheld data, and/or independent data. We used each model to predict the number of locations in each of 10 geometric bins of relative density following the methods of Dunk et al. (2019). We then calculated the coefficient of determination (R^2) between the observed and predicted number of locations for all groups, and interpreted higher values to indicate better fit.

2) We evaluated the extent to which the distribution of locations differed from random expectation under the model's predictions using the Boyce Index (Boyce 2002, Hirzel 2006). We estimated the area adjusted frequencies (AAF, defined as the proportion of locations divided by the proportion of area) of the cross-validated/withheld data locations in each of 10 geometric bins of relative density, then calculated the Boyce Index as the rank correlation between the AAF of the bins and the bin ranks.

3) We estimated the magnitude of the difference between the values of the highest and lowest AAF bins as an indicator of maximum difference in relative density among bins.

Nesting Area Model (Nest-based models):

For the nesting area model, we began with a dataset of Golden Eagle nest locations compiled by the USFWS through an extensive outreach effort to Federal, State, Tribal, and non-governmental organizations (Dunk et al. 2019). We added new nest records for areas where we were aware of recent nest inventories, but we did not conduct an exhaustive outreach because the dataset already included numerous records distributed across the study area. The dataset included nest location records with spatial precision <120 m and status indicating occupancy by breeding eagles (Dunk et al. 2019). To reduce spatial redundancy, we thinned locations within 3 km using an algorithm (Tack and Fedy 2015) that retained more recent records with higher levels of nesting status (i.e., records of direct observations of eggs or behavior indicative of a nest containing eggs were preferred over records with presence of an adult pair or sign of recent nest repair or use). We followed the modeling procedures of Dunk et al. (2019), except for the fact that they subdivided the Western U.S. into discrete modeling regions and modeled each region separately, whereas we created a single model for our study area, and used modeling region as a categorical variable in the model. One issue with creating individual MaxEnt models for different geographic areas is that the models' predictions cannot be directly compared region-by-region. For example a predicted value of 0.5 could have a different meaning among three modeling regions. Creating a single model for a larger area had the *potential* drawback of being overly general, compared to region-specific models. One of the benefits, however, is that model interpretation is identical throughout the modeling area, so predicted values have the same meaning throughout.

Non-nesting Area and Migration Models (Telemetry-based models):

For the telemetry-based models, we compiled satellite-derived location data for Golden Eagles from across western North America. The dataset included locations from Golden Eagles instrumented primarily with Global Positioning System (GPS) or (rarely) Argos Doppler satellite geolocators as part of 12 studies by collaborators from Federal, State, Tribal, non-governmental, and other organizations. We processed raw telemetry location data to remove erroneous locations following the methods of Woodbridge et al. (in prep.), then subsampled to a maximum of one location per hour (see Wallace et al. (in review), and Bedrosian et al. (in prep.) for more details).

Results

Nesting Area Model:

The nesting area model was trained with 2,642 nests. Moderate-high and high nest density areas represented 10% and 8.1% of Wyoming, respectively (Table 1, Figure 1). In contrast, moderate low and low density nesting areas were estimated to be quite common in Wyoming, representing 55% of the state (Table 1, Figure 1). In summary, areas with relatively few nest sites are quite common in Wyoming, but areas with many nest sites are relatively rare.

The nesting area model was extremely accurate in predicting spatial variation in nesting densities of Golden Eagles (Figure 2), based on cross-validation. The model is an excellent predictor of spatial variation in nesting density within and among ecological regions (r^2=0.98, Figure 3a) and subregions (r^2=0.88, Figure 3b) and performs nearly equally well throughout the study area, with no appreciable differences in predictive ability among various ecological regions or subregions (Figures 3a and 3b). Overall, the nesting model was an excellent predictor of spatial variation in nesting areas throughout Wyoming.

Table 1. Proportion of Wyoming in various density of use classes, by model.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.265	0.113	0.305	0.158
Moderate-low	0.285	0.160	0.239	0.222
Neutral	0.270	0.371	0.263	0.395
Moderate-high	0.100	0.237	0.108	0.163
High	0.081	0.120	0.085	0.062

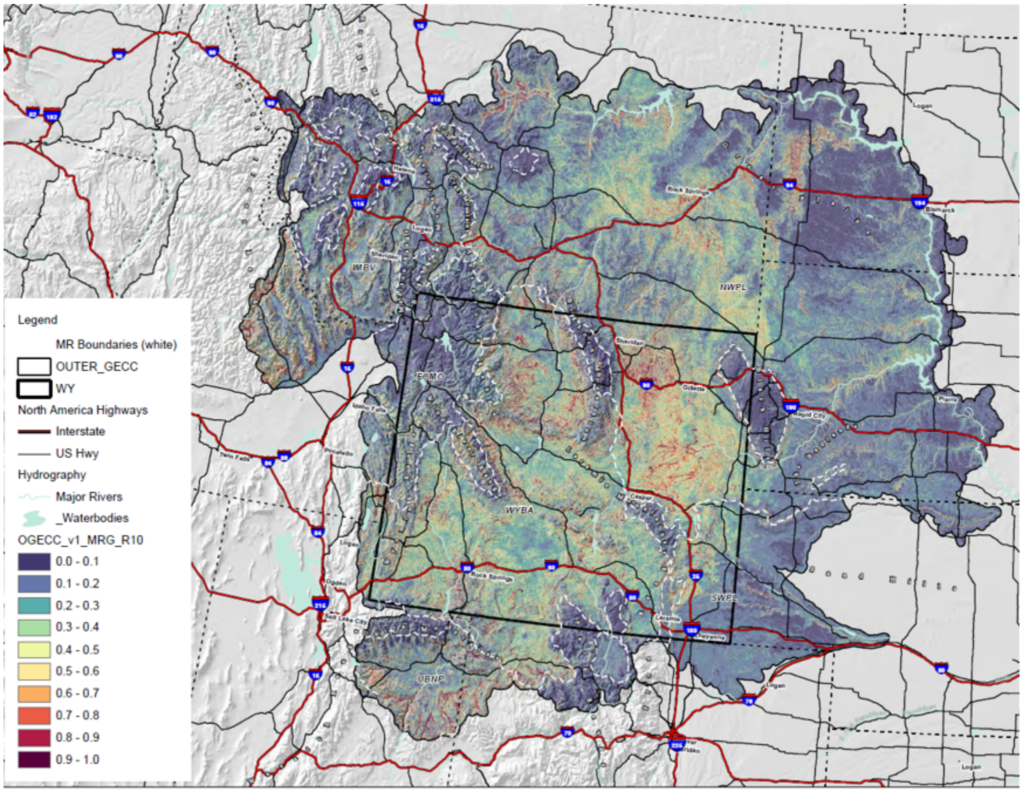


Figure 1. Map depicting spatial variation in nest density across Wyoming and adjacent states.

Area adjusted frequency values for the nesting area model varied dramatically among the five density classes (Table 2). Area adjusted frequency values are estimated by dividing the proportion of locations within a density class by the proportion of the modeling area within that class (see Dunk et al. 2019 and Wallace et al. in review). Therefore, the high density class AAF value of 6.704 means that areas of Wyoming classified into the high density nesting area bin had ~6.7 times more nesting areas than would be expected based on the area encompassed by that bin; or, put simply, ~8 percent of the area of Wyoming contains >50% of the nests. Areas in the high and medium high categories have higher AAF values (Table 2) and have disproportionately more nesting areas than would be expected based on their extent. In contrast, areas in the low and moderate-low categories have lower AAF values (Table 2), and have disproportionately fewer nesting areas than would be expected based on their extent.

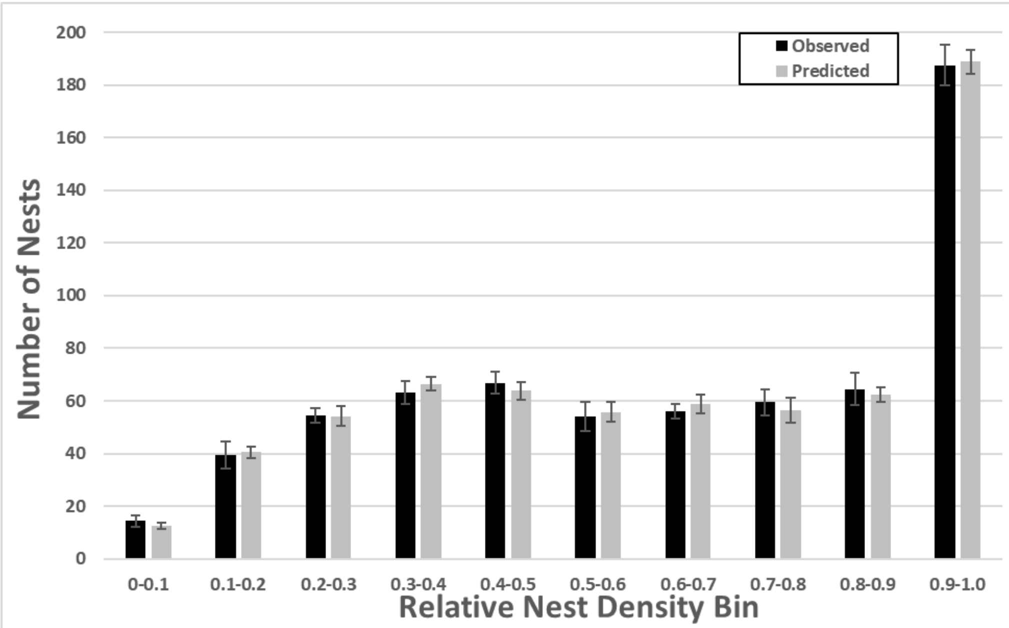
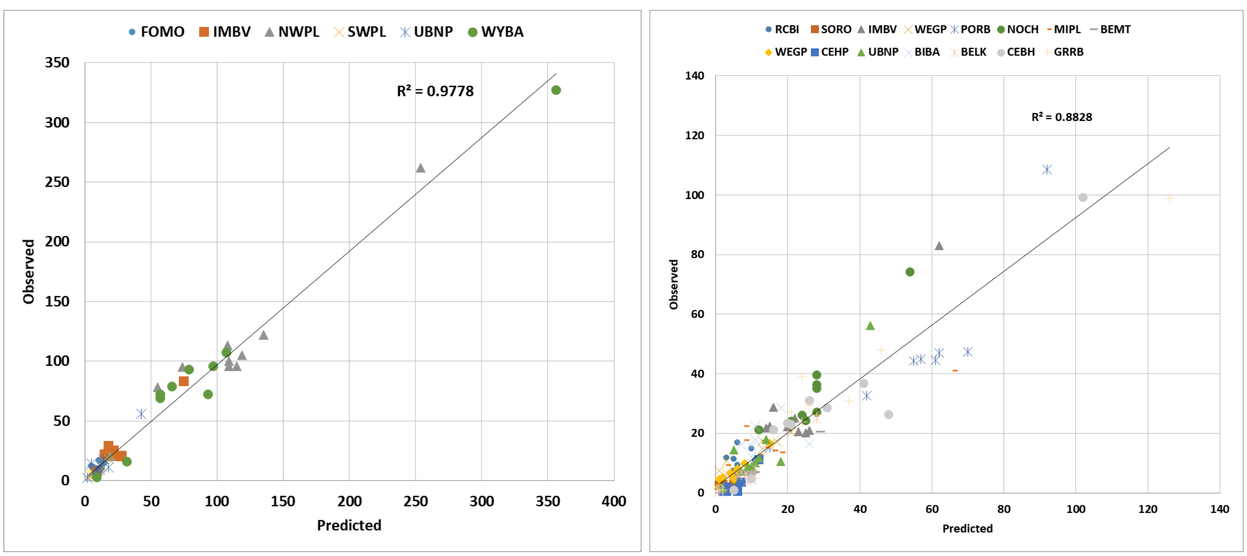


Figure 2. Mean (±2 SE) number of nests predicted by the nesting area model compared to the observed (actual) number among 10 Relative Nest Density bins. Predicted and observed nests were from 10 replicates of cross-validation, and for the 25% of nests that were withheld for testing during each replicate.



Figures 3a (left) and b (right). Relationship of predicted to observed nests among 10 RND bins within each of six ecological regions (3a) and fifteen sub-regions for which the nesting area model was created. The ecological regions and sub-regions included all of Wyoming, but also parts of Montana, Utah, Colorado, Idaho, North Dakota, and South Dakota.

Table 2. Area Adjusted Frequencies by model and relative density of use class within Wyoming.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.198	0.216	0.231	0.207
Moderate-low	0.482	0.500	0.495	0.508
Moderate	1.041	1.110	0.952	1.046
Moderate high	2.161	2.176	2.137	1.991
High	6.704	4.805	5.871	4.234

Area adjusted frequency values represent the magnitude of difference between the proportion of locations and proportion of area within each density class. They also allow for a quick and easy method of estimating the magnitude of difference in density of locations among density classes. For example, for the nesting area model the high and low density classes have AAF values of 6.704 and 0.198, respectively. Dividing 6.704 by 0.198 estimates the magnitude of difference in density between those density classes. Hence, the high density nesting areas have ~ 33.9 times higher density of nesting areas compared to the low density nesting areas. Dividing any two density classes provides such estimates. For example, the high density class nesting area has a 2.75 times higher nesting area density than the moderate-high density class (=6.704/2.161). This means that if we had two equal-sized areas, one composed only of high density nesting area and the other composed only of moderate-high density nesting areas, the high density nesting area is predicted to have 2.75 times more nesting areas than the moderate-high area.

Winter (Non-nesting) Model:

The winter/non-nesting area model was trained with 26,490 daytime locations from 203 Golden Eagles, and tested using 8,829 daytime locations. Moderate-high and high density of use areas were relatively abundant, compared to the same classes of nesting areas, and represented 23.7% and 12.0% of Wyoming, respectively (Table 3, Figure 4). In contrast, moderate-low and low density of use wintering areas were relatively rare (compared to the same categories of nesting areas), and were estimated to represent just over one quarter (27.3%) of the state (Table 3, Figure 4). Areas in the neutral winter density of use category were the most abundant, representing an estimated 37.1% of Wyoming. In summary, Wyoming has relatively large amounts of neutral to high density of use wintering habitats, whereas low and moderately low density of use areas are relatively rare.

The winter/non-nesting model was extremely accurate in predicting spatial variation in density of locations (Figure 5), based on predicting distribution of the test data. The model is an excellent predictor of spatial variation in density of locations within and among ecological regions (r^2=0.98, Figure 6a) and subregions (r^2=0.91, Figure 6b) and performs nearly equally well throughout the study area, with no appreciable differences in predictive ability among various ecological regions or subregions (Figures 6a and 6b). Overall, the winter/non-nesting model was an excellent predictor of spatial variation in density of locations throughout Wyoming.

Table 3. Proportion of Wyoming in various density of use classes, by model. Note, Table 3 is identical to Table 1 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.265	0.113	0.305	0.158
Moderate-low	0.285	0.160	0.239	0.222
Neutral	0.270	0.371	0.263	0.395
Moderate-high	0.100	0.237	0.108	0.163
High	0.081	0.120	0.085	0.062

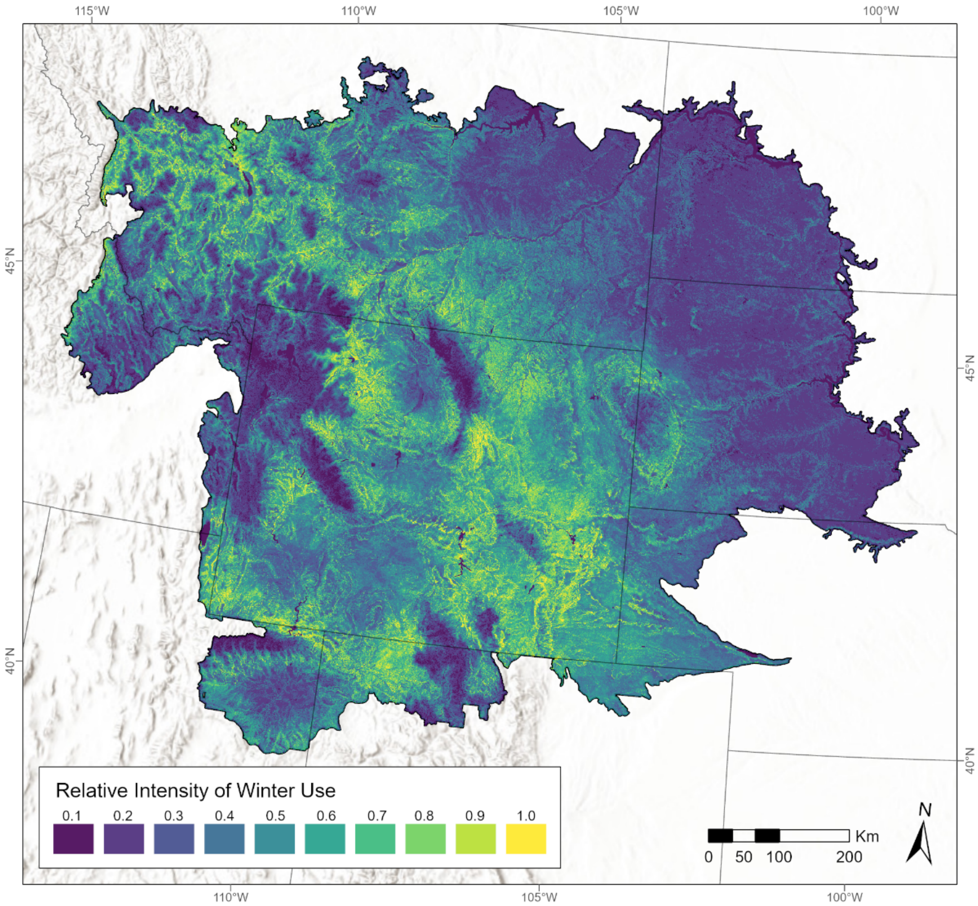


Figure 4. Map depicting spatial variation in winter/non-nesting density of Golden Eagle locations across Wyoming and adjacent states (from Wallace et al. in review).

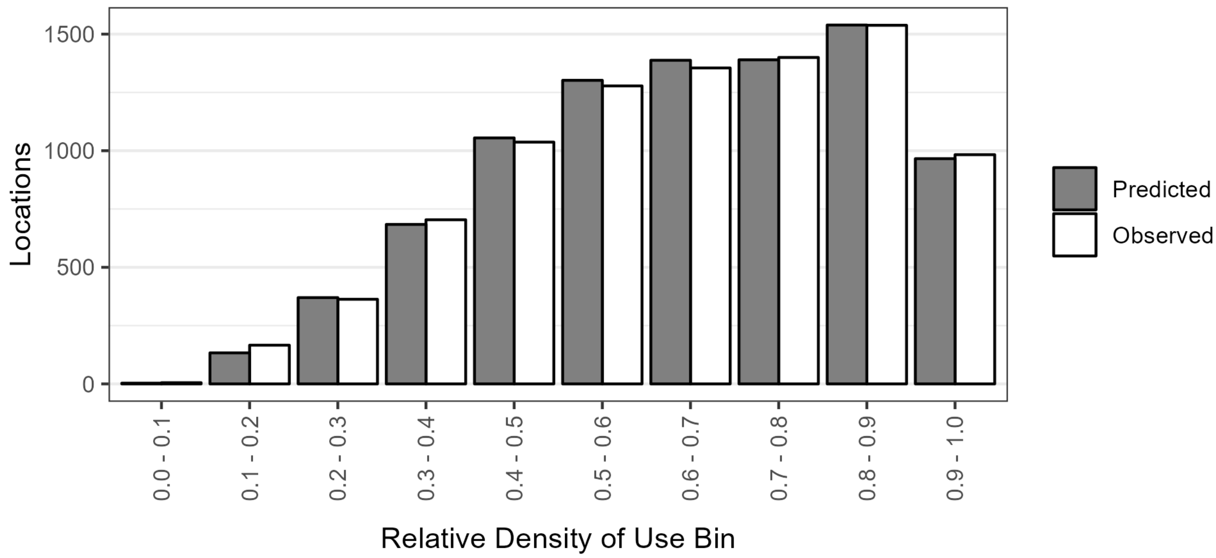
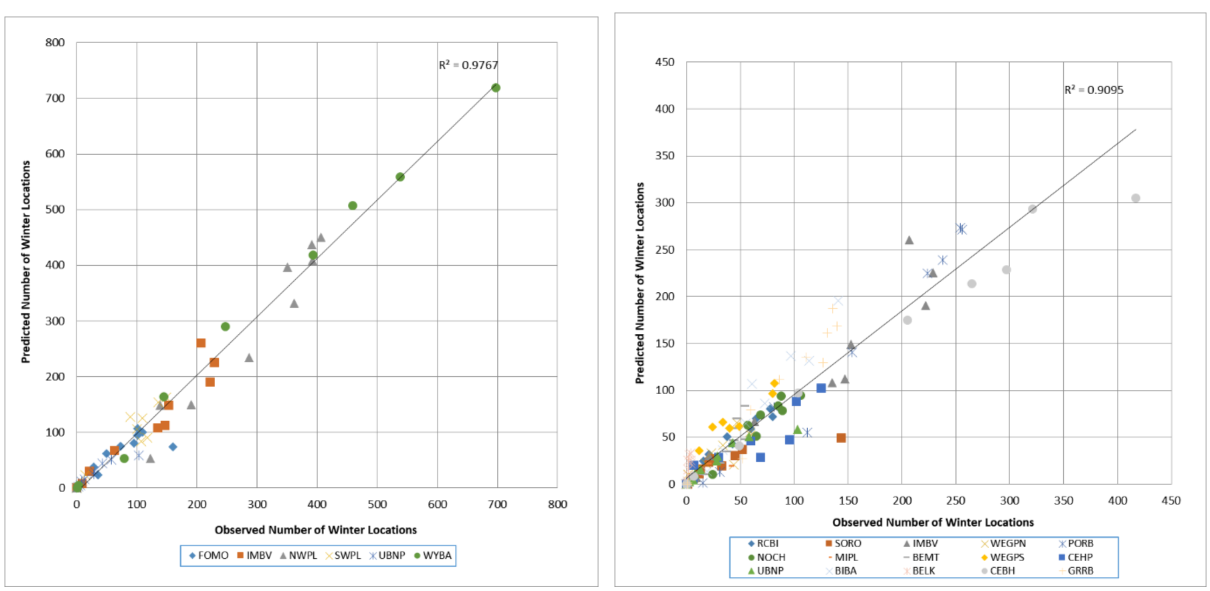


Figure 5. Number of test (n=8,829) Golden Eagle winter locations predicted by our model versus the number observed among 10 density of use bins. This includes data for Wyoming and surrounding states (see Figure 4).



Figures 6a (left) and b (right). Relationship of model-predicted to observed winter Golden Eagle locations among 10 density of use bins within each of six ecological regions (6a) and fifteen sub-regions (6b) for which the model was created. The ecological regions and sub-regions included all of Wyoming, but also parts of Montana, Utah, Colorado, Idaho, North Dakota, and South Dakota.

Area adjusted frequency values for the winter/non-nesting model varied dramatically among the five density classes (Table 4). Area adjusted values are estimated by dividing the proportion of locations within a density class by the proportion of the modeling area within that class (see Dunk et al. 2019 and Wallace et al. in review). Therefore, the high density class AAF value of 4.805 means that areas of Wyoming classified into the high density nesting area bin had ~4.8 times more winter/non-nesting daytime locations than would be expected based on the area encompassed by that bin; or, put simply, ~12 percent of the area of Wyoming contains >50% of the winter/non-nesting daytime use locations. Areas in the high and medium high categories have higher AAF values (Table 4) and have disproportionately more winter/non-nesting daytime use locations than would be expected based on their extent. In contrast, areas in the low and moderate-low categories have lower AAF values (Table 4), and have disproportionately fewer winter/non-nesting daytime use locations than would be expected based on their extent.

Table 4. Area Adjusted Frequencies by model and relative density of use class within Wyoming. Note, Table 4 is identical to Table 2 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.198	0.216	0.231	0.207
Moderate-low	0.482	0.500	0.495	0.508
Moderate	1.041	1.110	0.952	1.046
Moderate high	2.161	2.176	2.137	1.991
High	6.704	4.805	5.871	4.234

As noted above, AAF values represent the magnitude of difference between the proportion of locations and proportion of area within each density of use class. They also allow for a quick and easy method of estimating the magnitude of difference in density of use locations among density classes. For example, for the winter/non-nesting model the high and low density classes have AAF values of 4.805 and 0.216, respectively. Dividing 4.805 by 0.216 estimates the magnitude of difference between those classes. Hence, the high density of use areas have ~22 times higher density of use compared to the low density of use areas. Dividing any two density classes provides such estimates.

Fall Migration Model:

The fall migration model was trained with 3,204 daytime locations from 107 Golden Eagles, and tested using 1,068 daytime locations. Moderate-high and high location density areas were relatively rare, representing 10.8% and 8.5% of Wyoming, respectively (Table 5, Figure 7). In contrast, moderate-low and low density areas were estimated to represent just over one half of the state (Table 5, Figure 7). Areas in the neutral density category were estimated to represent 26.3% of Wyoming. In summary, Wyoming has relatively small amounts of moderate-high to high density of fall migration areas, whereas low, moderate-low, and neutral density of use areas are common.

The fall migration model was extremely accurate in predicting spatial variation in density of fall migration locations (Figure 8), based on predicting distribution of the test data. The model is an excellent predictor of spatial variation in density of fall migration locations within and among ecological regions (r^2=0.944, Figure 9a) and subregions (r^2=0.934, Figure 9b) and performs nearly equally well throughout the study area, with no appreciable differences in predictive ability among various ecological regions or subregions (Figures 9a and 9b). Overall, the fall migration model was an excellent predictor of spatial variation in density of fall migration locations throughout Wyoming.

Table 5. Proportion of Wyoming in various density of use classes, by model. Note, Table 5 is identical to Tables 1 and 3 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.265	0.113	0.305	0.158
Moderate-low	0.285	0.160	0.239	0.222
Neutral	0.270	0.371	0.263	0.395
Moderate-high	0.100	0.237	0.108	0.163
High	0.081	0.120	0.085	0.062

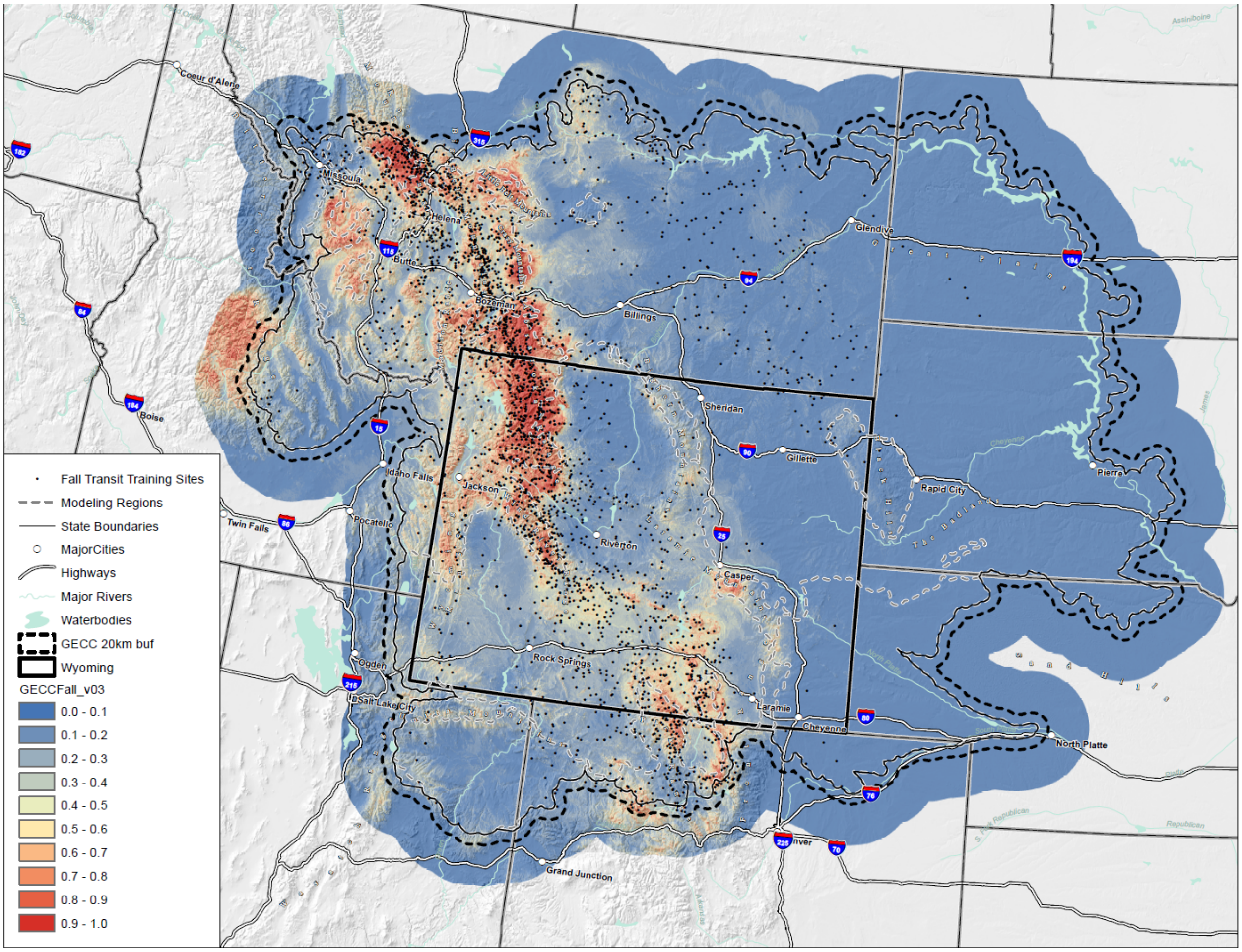


Figure 7. Map depicting spatial variation in Golden Eagle density of fall migration locations across Wyoming and adjacent states (from Bedrosian et al. in prep.).

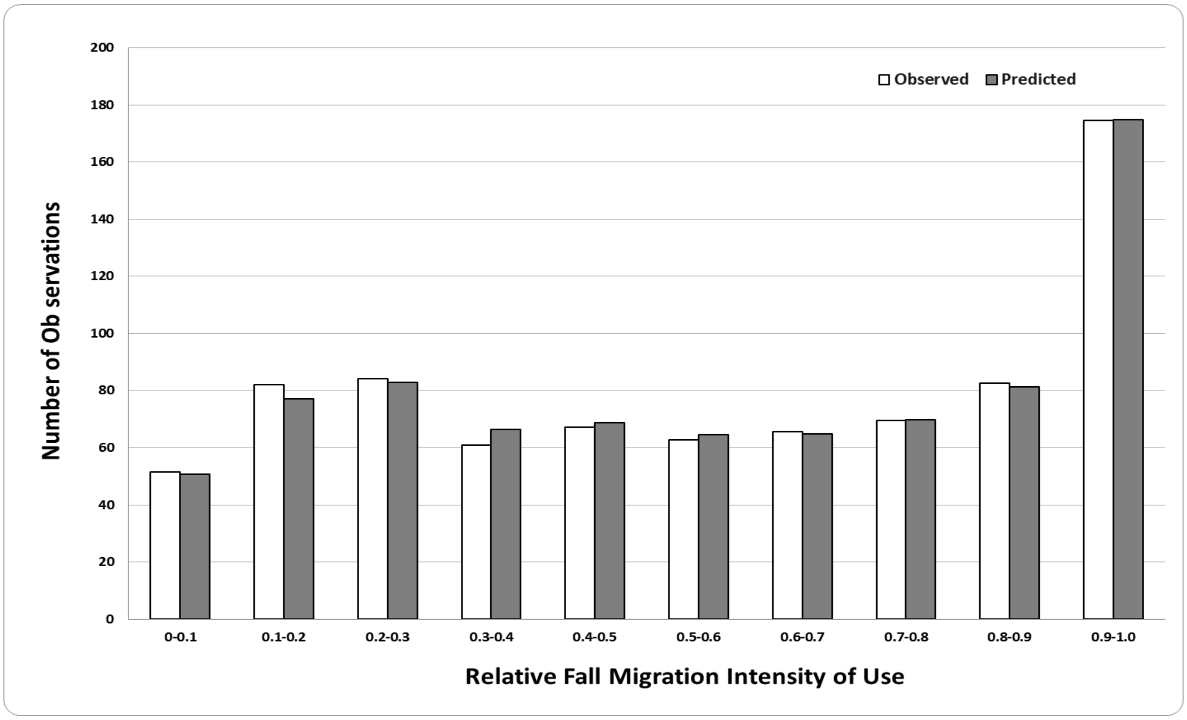
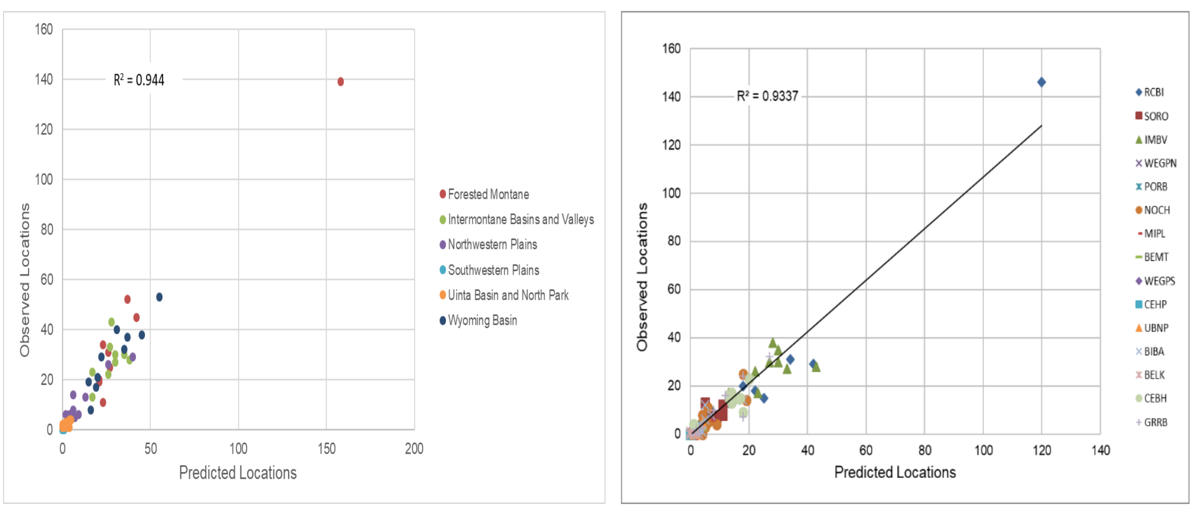


Figure 8. Number of test (n=1,068) Golden Eagle fall migration locations predicted by our model versus the number observed among 10 density of use bins. This includes data for Wyoming and surrounding states (see Figure 7).



Figures 9a (left) and b (right). Relationship of model-predicted versus observed Golden Eagle fall migration locations among 10 density of use bins within each of six ecological regions (9a) and fifteen sub-regions (9b) for which the model was created. The ecological regions and sub-regions included all of Wyoming and parts of Montana, Utah, Colorado, Idaho, North Dakota, and South Dakota.

Area adjusted frequency values for the fall migration model varied dramatically among the five density classes (Table 6). Area adjusted values are estimated by dividing the proportion of locations within a density class by the proportion of the modeling area within that class (see Dunk et al. 2019 and Wallace et al. in review). Therefore, the high density of use class AAF value of 5.871 means that areas of Wyoming classified into the high density of use area bin had ~5.9 times more fall migration locations than would be expected based on the area encompassed by that bin; or, put simply, ~8.5 percent of the area of Wyoming contains ~50% of the fall migration locations. Areas in the high and moderate high categories have higher AAF values (Table 6) and have disproportionately more fall migration locations than would be expected based on their extent. In contrast, areas in the low and moderate-low categories have lower AAF values (Table 6), and have disproportionately fewer fall migration locations than would be expected based on their extent.

Table 6. Area Adjusted Frequencies by model and relative density of use class within Wyoming. Note, Table 6 is identical to Tables 2 and 4 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.198	0.216	0.231	0.207
Moderate-low	0.482	0.500	0.495	0.508
Moderate	1.041	1.110	0.952	1.046
Moderate high	2.161	2.176	2.137	1.991
High	6.704	4.805	5.871	4.234

As noted above, AAF values represent the magnitude of difference between the proportion of locations and proportion of area within each density of use class. They also allow for a quick and easy method of estimating the magnitude of difference in density of use locations among density classes. For example, for the fall migration model the high and low density classes have AAF values of 5.871 and 0.231, respectively. Dividing 5.871 by 0.231 estimates the magnitude of difference between those classes. Hence, the high density of use areas have ~25 times higher density of locations compared to the low density of use areas. Dividing any two density classes provides such estimates.

Spring Migration Model:

The spring migration model was trained with 3,286 daytime locations from 101 Golden Eagles, and tested using 1,095 daytime locations. Moderate-high and high location density areas were relatively rare, and represented 16.3% and 6.2% of Wyoming, respectively (Table 7, Figure 10). Low location density spring migration areas were estimated to represent 15.8% of the state (Table 7, Figure 9), whereas moderate-low and neutral spring migration location density categories were estimated to represent 22.2% and 39.5% of Wyoming, respectively. In summary, Wyoming has very small amounts of high density spring migration location areas, whereas moderate-low and neutral location density areas are fairly common.

The spring migration model was extremely accurate in predicting spatial variation in density of spring migration locations (Figure 11), based on predicting distribution of the test data. The model is an excellent predictor of spatial variation in spring migration location density within and among ecological regions (r^2=0.951, Figure 12a) and subregions (r^2=0.953, Figure 12b) and performs nearly equally well throughout the study area, with no appreciable differences in predictive ability among various ecological regions or subregions (Figures 12a and 12b). Overall, the spring migration model was an excellent predictor of spatial variation in density of spring migration locations throughout Wyoming.

Table 7. Proportion of Wyoming in various density of use classes, by model. Note, Table 7 is identical to Tables 1, 3, and 5 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.265	0.113	0.305	0.158
Moderate-low	0.285	0.160	0.239	0.222
Neutral	0.270	0.371	0.263	0.395
Moderate-high	0.100	0.237	0.108	0.163
High	0.081	0.120	0.085	0.062

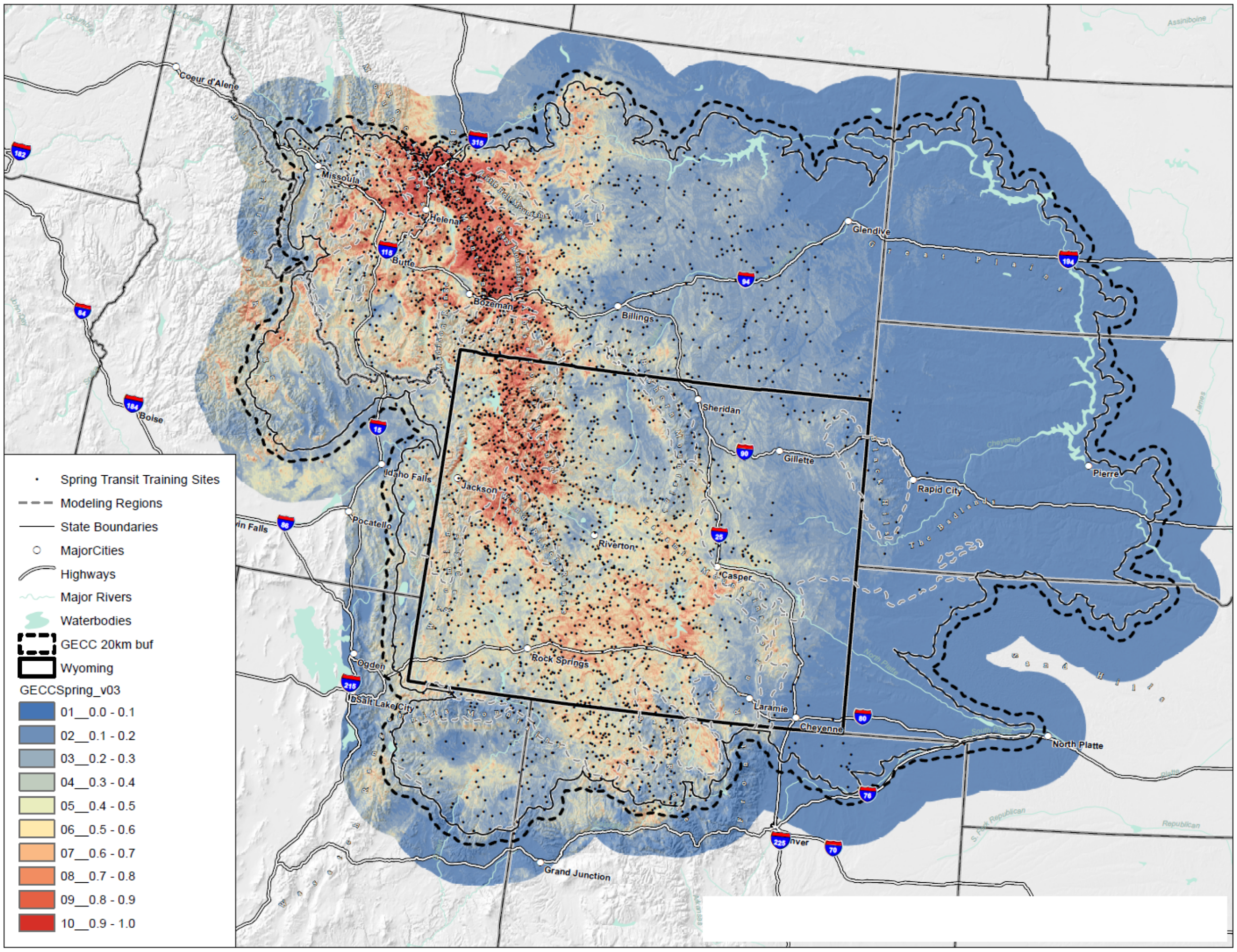


Figure 10. Map depicting spatial variation in Golden Eagle spring migration location density across Wyoming and adjacent states (from Bedrosian et al. in prep.).

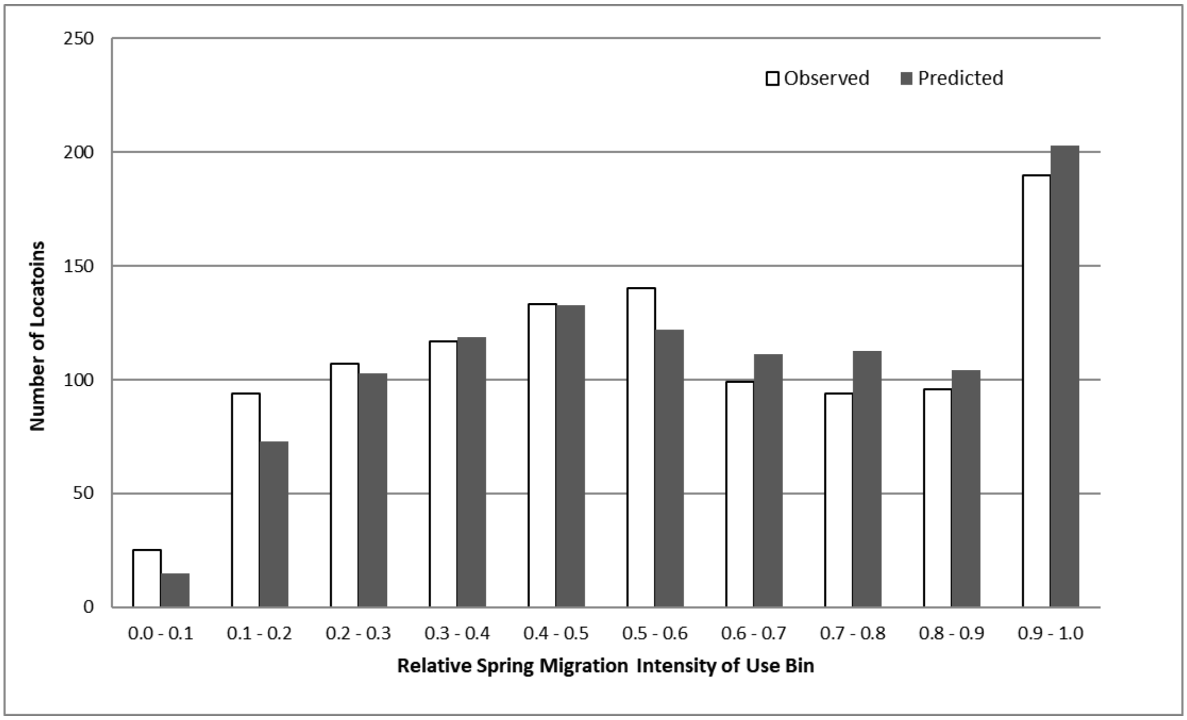
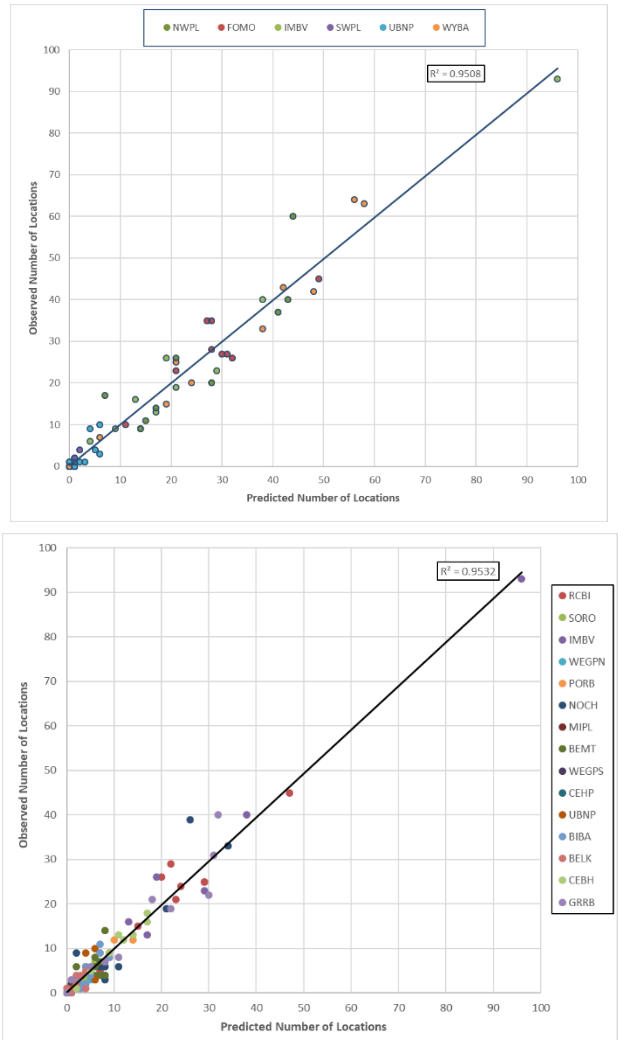


Figure 11. Number of test (n=1,095) Golden Eagle spring migration locations predicted by our model versus the number observed among 10 density of use bins. This includes data for Wyoming and surrounding states (see Figure 7).



Figures 12a (left) and b (right). Relationship of model-predicted versus observed Golden Eagle spring migration locations among 10 density of use bins within each of six ecological regions (12a) and fifteen sub-regions (12b) for which the model was created. The ecological regions and sub-regions included all of Wyoming and also parts of Montana, Utah, Colorado, Idaho, North Dakota, and South Dakota.

Area adjusted frequency values for the spring migration model varied dramatically among the five density classes (Table 8). Area adjusted values are estimated by dividing the proportion of locations within a density class by the proportion of the modeling area within that class (see Dunk et al. 2019 and Wallace et al. in review). Therefore, the high density class AAF value of 4.234 means that areas of Wyoming classified into the high location density bin had ~4.2 times more spring migration locations than would be expected based on the area encompassed by that bin; or, put simply, ~6.2% of the area of Wyoming contains ~25% of the spring migration locations. Areas in the high and moderate high categories have higher AAF values (Table 8) and have disproportionately more spring migration locations than would be expected based on their extent. In contrast, areas in the low and moderate-low categories have lower AAF values (Table 8), and have disproportionately fewer spring migration locations than would be expected based on their extent.

Table 8. Area Adjusted Frequencies by model and relative location density class within Wyoming. Note, Table 8 is identical to Tables 2, 4, and 6 but is replicated here for ease of reference.

Density Class	Nesting	Winter	Fall Migration	Spring Migration
Low	0.198	0.216	0.231	0.207
Moderate-low	0.482	0.500	0.495	0.508
Moderate	1.041	1.110	0.952	1.046
Moderate high	2.161	2.176	2.137	1.991
High	6.704	4.805	5.871	4.234

As noted above, AAF values represent the magnitude of difference between the proportion of locations and proportion of area within each density of use class. They also allow for a quick and easy method of estimating the magnitude of difference in density of locations among density classes. For example, for the spring migration model the high and low density classes have AAF values of 4.234 and 0.207, respectively. Dividing 4.234 by 0.207 estimates the magnitude of difference between those classes. Hence, the high density of use areas have ~20 times higher density of locations compared to the low density location areas. Dividing any two density classes provides such estimates.