Chapter 8: Occurrence of Large and Medium-Sized Mammals: Occurrence But Not Count Models Predict Pronghorn Distribution

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Abstract. Management of medium to large-sized terrestrial mammals (Antilocapridae, Canidae, Cervidae, Leporidae, Mustelidae, Ochotonidae) in the western United States is multifaceted and complex. Species in this group generally are charismatic and provide economic opportunities, although others are considered a nuisance at one extreme or are listed as species of conservation concern at the other. Understanding the relative influence of land cover, habitat fragmentation, and human land use on their distribution during the breeding season is imperative to inform management decisions on land use and conservation planning for these species. We surveyed medium to large-sized sagebrush (Artemisia spp.)-associated mammal species in 2005 and 2006 on 141 random transects (mean length = 1.1 km) in the Wyoming Basins, an area undergoing rapid land cover transformation due to human actions including energy development. Overall, we observed 10 species but only obtained enough observations of pronghorn (Antilocapra americana) to develop spatially explicit distribution models. For pronghorn, occurrence related positively to proportion of sagebrush land cover within 0.27 km, mixed shrubland land cover within 3 km, riparian land cover within 5 km, Normalized Difference Vegetation Index (NDVI) within 0.27 km, road density within 5 km, and decay distance to power line corridors at 1 km, but negatively to salt-desert shrubland cover within 18 km and an interaction between sagebrush and NDVI within 0.27 km. We found excellent predictive capability of this model when

evaluated with independent test data. The model provides a basis for assessing the effects of proposed development on pronghorn and can aid planning efforts to avoid or mitigate adverse effects on pronghorn.

Key words: abundance, anthropogenic disturbance, *Antilocapra americana*, count-based regression models, habitat, logistic regression, occurrence, pronghorn.

The Wyoming Basins are called the Serengeti of North America because this region contains a rich diversity of medium to large-sized mammals, particularly ungulates (Sawyer et al. 2005), and supports ungulate migrations between breeding and wintering ranges over distances equal to or exceeding those of well-publicized African ungulate migrations (Berger 2004). Mammalian diversity in the Wyoming Basins is imperiled as many medium- to large-sized species have experienced severe population declines. Wyoming's list of species of special concern includes 50 mammal species, of which six (black-tailed prairie dog [Cynomys ludovicianus], white-tailed prairie dog [C. leucurus], least weasel [Mustela nivalis], pygmy rabbit [Brachylagus idahoensis], and spotted ground squirrel [Xerospermophilus spilosoma]) overlap with sagebrush (Arte*misia* spp.) steppe habitat (Wyoming Game and Fish Department 2005).

The Wyoming Basins and adjacent areas within Colorado, Utah, and Wyoming have experienced recent rapid expansion in energy development (Braun et al. 2002, Weller 2002, Walker et al. 2007, Doherty et al. 2008, Copeland et al. 2009, Ch. 3). Many studies have reported negative effects of energy development and other human stressors on mammalian game species. Indirect effects of energy development include habitat avoidance within 2.7 to 3.7 km from well pads by mule deer (Odocoileus hemionus) (Sawyer et al. 2006). Pronghorn (Antilocapra ameri*cana*) populations have declined owing to changes in habitat quality and habitat loss from human activities, including urban expansion and energy development (Sawyer et al. 2002). Moreover, oil and gas developments, fences, housing, and highways in the Wyoming Basins disrupt the historic migration route of pronghorn between summering grounds in the Grand Teton National Park and wintering grounds in the Green River Basin of Wyoming; about 75% of this migration corridor has been converted or lost (Berger 2003, Berger 2004). Pronghorn are also sensitive to vehicular traffic, which influences foraging efficiency (Berger et al. 1983, Gavin and Komers 2006). However, little is known how other medium to large-sized terrestrial non-game mammal species respond to energy development and other human stressors. White-tailed prairie dogs occupy roughly 5% of their historic range. Agricultural development, shooting, poisoning, and plague (Yersinia pestis) are significant factors contributing to these declines (Miller et al. 1994, Miller et al. 2000, Miller and Cully 2001). Similarly, pygmy rabbits show severe population declines across their range (Flinders 1999, Janson 2002), with loss of sagebrush habitat considered to be the most important factor contributing to population declines (Heady and Laundré 2005). There is a need to identify factors influencing the distribution of medium and large-sized mammal species in relation to human stressors and land cover.

Our objectives were to survey mediumand large-sized sagebrush-associated mammals on randomly walked transects placed along human land use and sagebrush productivity gradients within the Wyoming Basin Ecoregional Assessment (WBEA) area and to develop species distribution models for those species with sufficient sample sizes. These species distribution models are important for assessing effects of additional proposed development across the WBEA area on sagebrush-associated species and in crafting management practices to avoid and/or mitigate potential human stressors.

METHODS

Field Surveys

We surveyed medium to large-sized mammals on 141 randomly placed transects of variable length (Koenen 2002) during May and June of 2005 (n = 90) or 2006 (n = 51). Transect end points overlapped with the center of randomly selected nearroad (n = 40) and far-road (n = 101) survey blocks (Ch. 4). We delineated transects using a least-cost path analysis in Arc-Map 9.2 (ESRI 2006) based on minimal change in elevation, between far-road and on-road survey blocks, and between nearroad survey blocks and a point on nearest road. Transects were uploaded on Global Positioning System (GPS; Garmin eTrex) units (Ch. 4). Average transect length was 1.1 km (SD = 0.84 km; median = 1.06 km, range = 0.11 - 6.97 km).

Observers geo-referenced locations of individual medium to large-sized mammals or centers of herds (Buckland et al. 2001) while slowly following predetermined transects by recording location of observer (latitude and longitude) using a GPS, measuring azimuth using a compass, and estimating distance between observer and an individual using a rangefinder (Bushnell Yardage Pro Legend). We plotted individual sightings in ArcMap 9.2 (ESRI 2006) and selected only those sightings within a rectangular-shaped inference space centered on transects.

Abundance Categories

We used Program DISTANCE (Thomas et al. 2009) to calculate detection probabilities and transect-specific densities. We included cluster size (number of individuals detected in a herd) when estimating detection probability because of expected increased detection of larger clusters. In addition, we adjusted detection probabilities by year to account for observer bias, and time of year (May vs. June) to account for seasonal effects.

Model Development

We *a priori* excluded predictor variables from the candidate set of predictor data (Table 4.2) deemed biologically irrelevant for medium to large-sized mammal species based on a literature review. We derived predictor variable values for each transect using a slightly different, but equivalent, method than outlined in Chapter 4. Due to the variable length and shape of transects, we used six different sized buffers (0.27, 0.54, 1, 3, 5, and 18 km) around each transect. Within buffers we calculated land cover, vegetation productivity as measured by Normalized Vegetation Difference Index (NDVI), and terrain-derived variables using zonal statistics in ArcMap 9.2 (ESRI 2006). We derived landscape metrics within three buffer distances (1, 3, and 5 km) in FRAGSTATS (McGarigal et al. 2002). We calculated descriptive statistics for all predictor variables within presence/absence or abundance classes for each species modeled. We also determined the number of transects with predictor variable values > 0within each abundance class and excluded from model development all variables/extents with <20 survey blocks in a class. We excluded correlated predictor variables $(r_s \ge 0.70)$ from potential analyses prior to model development (Ch. 4).

We used a hierarchical multi-stage modeling approach (Ch. 4) because little is known about how anthropogenic disturbance and landscape composition and configuration influence the distribution of medium to large-sized mammal species (O'Brien et al. 2005). We based our analyses either on presence/absence data using logistic regression models or on countbased models using either negative binomial or Poisson regression models depending on distribution of data. For count-based models, we first checked if count data were zero-inflated using a Vuong test (Vuong 1989) based on intercept models. We used an offset term in the general linear model (GLM) of observed counts while incorporating transect-specific detection probabilities (Buckland et al. 2009). We used scatterplots and histograms to initially scan for non-linearities and interactions. If visual inspection indicated a potential non-linearity or interaction we included these functions in subsequent modeling steps. We employed Akaike Information Criterion, corrected for small sample sizes (AIC_c), for model selection (Burnham and Anderson 2002).

We first evaluated each sagebrush and NDVI variable and identified spatial extent and the combination of the sagebrush and NDVI variables that best represented habitat use. We used these selected sagebrush/NDVI variables as our base model to test all spatial extents for each variable in the vegetation, abiotic, and disturbance submodels. We limited the number of variables in all competing models to the smaller of 10% of either occurrence or absence transects (Hosmer and Lemeshow 2000). After identifying the AIC_c-best model within vegetation, abiotic, and disturbance submodels, we allowed variables within these models to compete both within and across submodels to develop the best overall model. We incorporated model uncertainty by averaging coefficients from models within a cumulative AIC_c weight of just ≥ 0.9 (Burnham and Anderson 2002) while setting coefficients to zero for those variables not contained within a model. To assess model fit for logistic regression models, we used receiver operating characteristic (ROC) plots to estimate area under the curve (AUC, Metz 1978). We determined an optimal cutoff threshold for predicting presence-absence of each

TABLE 8.1. Uncorrected total counts and number of transects on which a species occurred (i.e., includes observations that extended beyond transect) for 10 media large-sized mammal species surveyed on 141 transects during May and June of 2005 (n = 90) or 2006 (n = 51) in the Wyoming Basins Ecoregional Assessment area.

				Sighting	S				Transects		
	1	20	05	20	90		20	005	200	9(
Species	Scientific name	May	June	May	June	Total	May	June	May	June	Total
Cottontail	Sylvilagus spp.	7	34	4	5	50	9	18	2	5	25
Coyote	Canis latrans	1	0	2	Ζ	10	1	0	7	3	8
EIK	Cervus canadensis	0	13	42	2	57	0	2	4	2	6
Moose	Alces alces	0	0	0	1	1	0	0	0	1	2
Mule deer	Odocoileus hemionus	4	4	25	9	39	7	ю	9	4	15
Prairie dog	Cynomys leucurus or C. ludovicianus	42	79	5	22	148	5	Г	7	4	15
Pronghorn	Antilocapra americana	449	364	124	87	1,024	45	54	20	23	117
Red fox	Vulpes vulpes	0	0	0	7	2	0	0	0	1	2
White-tailed jackrabbit	Lepus townsendii	1	6	8	7	20	1	8	∞	2	18
Wyoming ground squirrel	Spermophilus elegans	0	2	2	ю	L	0	2	1	1	4
Wyoming ground squirrel	Spermophilus elegans	0	5	7	n	L	0		5	2 1	2 1 1

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species (habitat or non-habitat) using a sensitivity-specificity equality approach (Liu et al. 2005) and applied this threshold to assess predictive capacity for each model (Nielsen et al. 2004). All statistical analyses were conducted using STATA 10.1 (STATA Corporation, College Station Texas, USA).

Spatial Application and Dose Response

We predicted species densities in a Geographical Information System (GIS) at a 90-m cell size using the final model coefficients in ArcMap 9.2 raster calculator (ESRI 2006) and binned final model predictions, depending on modeling approach, either into 10% probability classes for logistic regression models or 10 equalarea density classes for count-based regression analyses for summary and display. We masked non-sagebrush habitats (areas with <3% sagebrush habitat in a 5-km moving window) and areas outside the known range of each mammal of interest.

We plotted predicted densities or probability of occurrence of medium to large-sized mammals relative to changes in sagebrush quantity or vegetation productivity in order to assess critical levels of sagebrush habitat or habitat productivity. We calculated these values across one percent intervals of the sagebrush predictor or 0.01 intervals of the NDVI predictor using the Dose Response Calculator tool for ArcGIS (Hanser et al. 2011). We used the optimal cutoff threshold to identify the sagebrush or productivity threshold value, above which each mammalian species was likely to occur.

Model Evaluation

We evaluated model fit for species for which independent data were available by comparing observed proportion of independent locations in each probability bin against expected proportion of locations from the model using regression analysis (Johnson et al. 2006). A model with good fit should have a high R² value, a slope not different from 1.0, and an intercept not different from zero (Johnson et al. 2006).

RESULTS

Field Surveys

We detected 1,358 individuals of 10 different species of medium to large-sized mammals on 141 transects (Table 8.1) when using uncorrected counts (i.e., observations beyond transect included). Pronghorn were the most commonly detected species, followed by prairie dog (blacktailed and white-tailed combined), elk (Cervus canadensis), cottontail (Sylvilagus spp.), and mule deer. Pronghorn were the only species that occurred on >50 transects (Fig. 8.1), the minimum number of transects required to adequately model species distributions (Ch. 4). Given insufficient samples sizes to develop species distribution models for the other medium to largesize mammals, we focus on pronghorn in this chapter.

For the pronghorn analyses, we removed all detections that extended beyond the end points of transects; this reduced total number of detected pronghorn on transects from 1,024 to 344. We detected pronghorn on 62 (44.0%) of 141 transects; 42 transects (46.7%, n = 90) in 2005 and 20 transects (39.2%, n = 51) in 2006. Herd size ranged from 1-30 individuals. We accumulated 157 detections with the majority of sightings consisting of singletons (57.3%); the rest of sightings were small herds consisting of doubles (15.9%), triples (8.3%), and quadruples (2.5%).

Abundance Categories

The detection model with observer as a covariate had the lowest AIC value. However, model fit was poor, with observed detections different from expected (goodness-of-fit test, $\chi^2_{10} = 19.45$, p = 0.04). Consequently, we used the second best model selected by ΔAIC_c (0.89). This model was based on a half-normal cosine function with distances truncated at 362 m (10% reduc-



FIG. 8.1. Distribution of transects (n = 141) surveyed for pronghorn in the Wyoming Basins Ecoregional Assessment area. Transects were designated as present (black) and absent (grey) for model development.

tion) and was robust with a non-significant Kolmogorov–Smirnov test (K-S = 0.06, p = 0.57) and goodness-of-fit test (χ^2_{14} = 19.81, p = 0.14). Herd size did not significantly influence detection probability (Student's t = -0.65, df = 139, p = 0.26). Overall detection probability was 0.77 (95% CI = 0.70–0.84) with variance in detection probability explained by detection probability (7.2%), encounter rate (73.0%), and herd size (19.8%). All other models had ΔAIC_c values ranging from 1.67 to 3.96 (observer and

sampling May vs. June [round 1 vs. round 2] $\Delta AIC_c = 1.67$, non-covariate model ΔAIC_c = 1.98; sampling May vs. June [round 1 vs. round 2] $\Delta AIC_c = 3.01$; time of day ΔAIC_c = 3.87; year and Julian date $\Delta AIC_c = 3.96$). Overall density was 0.04 pronghorn/ha (95% CI = 0.03–0.05) and ranged between 0-0.33 pronghorn/ha on transects.

Model Development

We excluded three sagebrush variables at the subspecies level (ABIGSAGE ([A. tridentata], BIGSAGE [A. t. ssp. tridentata, A. t. ssp. wyomingensis], and MTNSAGE [A. t. ssp. vaseyana]) from the analyses (all spatial extents; n = 18) because pronghorn show no preference for one sagebrush type over another (Kilgore and Fairbanks 1997, MacKenzie 2006). In addition, we excluded eight soil variables (acidity, available water capacity, bulk density, clay content, depth, salinity, sand content, and silt content). We excluded several predictor variables from the candidate set, including sagebrush mean patch size (PATCH_{1km}, PATCH_{3km}, $PATCH_{5km}$) and compound topographic index (CTI) that were correlated with all sagebrush (ALLSAGE); mean annual maximum temperature (T_{max}) was correlated with elevation (ELEV); and precipitation (PRECIP), terrain roughness index (TRI) and slope (SLOPE) were correlated with Normalized Difference Vegetation Index (NDVI). We also excluded predictor variables with values > 0 on <20 transects, including coniferous forest (CFRST₂₇₀ and $CFRST_{540}$) and mixed shrubland (MIX₂₇₀) and MIX₅₄₀). Overall, we excluded 31 variables leaving 91 predictor variables for the pronghorn model.

Our first step was to model pronghorn density using count-based regression models with transect-level detection probability included as an offset (Buckland et al. 2009). We used a three-tiered approach to determine appropriate error structure (negative-binomial, Poisson, zero-inflated negative-binomial, or zero-inflated Poisson) of the pronghorn count data in general linear models. First, Vuong tests (Vuong 1989) of intercept models without the offset term indicated superior fit of the negative-binomial over the zero-inflated negative binomial, zero-inflated Poisson, and Poisson regression models. Second, we plotted count vs. predicted/observed and found that the negative binomial showed the best data fit. Last, we regressed count against all sagebrush within 0.27 km (ALL- $SAGE_{270}$) including the offset term. The Vuong test was non-significant (z = 0.1, p =

0.46), indicating that the negative binomial error structure was appropriate. We then ran all submodels and developed a model-averaged composite model from eight models with cumulative AIC_c weights of just \geq 0.9. The final negative binomial regression model is below.

We spatially applied the composite model and evaluated model prediction with pronghorn aerial counts conducted by the Wyoming Fish and Game Department during May and June of 2005 in the Worland Basin. We found no correlation between predicted density (estimated density from model) and independent counts $(r_s = -0.003, p = 0.96, n = 350)$, indicating that the negative binomial regression model performed poorly. We therefore re-analyzed the presence/absence pronghorn data using logistic regression analyses. After removing observations >362 m, the truncation distance determined by removing 10% of the farthest observations in Program DISTANCE (Thomas et al. 2009), all transects with ≥ 1 pronghorn were coded as presence.

Logistic regression model

The AIC_c-selected top sagebrush/NDVI model consisted of all sagebrush within 0.27 km (ALLSAGE₂₇₀), NDVI within 0.27 km (NDVI₂₇₀), and an interaction (ALL-SAGE₂₇₀ * NDVI₂₇₀) (Table 8.2). The other 3 models with AIC_c \leq 2 consisted of all sagebrush and NDVI at larger extents with quadratic terms. Within a 0.27-km radius, there was on average 13.3% more all sagebrush land cover at occupied transects (80.6%, SE = 0.03) compared to absence transects (67.3%, SE = 0.03) (Appendix 8.1).

TABLE 8.2. Results of AIC_c-based model selection for pronghorn occurrence in relation to multi-scale sagebrush and NDVI variables in the Wyoming Basins Ecorgional Assessment area; the table also shows log-likelihood (LL), number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AIC_c), change in AIC_c value from the top model (Δ AIC_c), and Akaike weight (w_i). Only models with Δ AIC_c \leq 2 are shown.

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Number	Model ^a	LL	К	AIC _c	ΔAIC_{c}	Wi
1	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270}$	-86.06	4	180.12	0.00	0.13
2	$ALLSAGE_{540} + NDVI_{270} + ALLSAGE_{540} * NDVI_{270}$	-86.16	4	180.33	0.21	0.12
3	$ALLSAGE_{1km} + NDVI_{270} + ALLSAGE_{1km} * NDVI_{270}$	-86.73	4	181.45	1.33	0.07
4	$ALLSAGE_{270} + NDVI_{540} + ALLSAGE_{270} * NDVI_{540}$	-86.92	4	181.84	1.72	0.06

None of the AIC_c-selected univariate models included a non-linear quadratic term and the moving window radius of selected land cover variables ranged from 1-18 km (Table 8.3). The top vegetation, abiotic and disturbance submodels consisted of one to three variables in addition to the sagebrush/NDVI base model. The top vegetation submodel consisted of mixed shrubland land cover within 3 km (MIX_{3km}) , riparian land cover within 5 km (RIP_{5km}), and salt-desert shrubland within $18 \text{ km} (\text{SALT}_{18\text{km}})$; the top abiotic submodel consisted of elevation (ELEV); and the top disturbance model consisted of density of all roads within 5 km (RDdens_{5km}) and 1-km distance decay from power lines (POWER $_{1km}$) (Table 8.4).

Pronghorn occurrence during the breeding season was influenced primarily by land cover and to a lesser degree by abiotic and disturbance factors (Table 8.5). Pronghorn occurrence was positively associated with increased land cover of all sagebrush within 0.27 km, riparian land cover within 5 km, mixed shrubland within 3 km, NDVI within 0.27 km, elevation, 1-km distance decay from power lines, and higher road densities within 5 km. Pronghorn occurrence was negatively associated with increased salt desert shrubland within 18 km and an interaction between all sagebrush and NDVI within 0.27 km. The final model was a composite of 15 models, with the top AIC_c model having a low weight of evidence (wi = 0.25). The final composite probability of occurrence model is below.

(8.2)

$$\begin{aligned} &\text{Prob} = 1/\left(1 + (\exp\left(-(-7.98 + 8.75 * \\ \text{ALLSAGE}_{270} + 14.10 * \text{NDVI}_{270} - 19.87 * \\ \text{ALLSAGE}_{270} * \text{NDVI}_{270} - 6.88 * \\ \text{SALT}_{18km} + 2.76 * \text{RIP}_{5km} + 7.81 * \\ \text{MIX}_{3km} + 0.00047 * \text{ELEV} + 1.42 * \\ \text{POWER}_{1km} + 0.3 * \text{RDdens}_{5km})))) \end{aligned}$$

The composite model of pronghorn occurrence had good accuracy (ROC AUC = 0.83) and was a slight improvement over the AIC_c-selected top model (ROC AUC = 0.82). This model had an optimal sensitivity-specificity equality threshold of 0.46 with 74.1% of transects correctly classified.

Spatial Application and Dose Response

Pronghorn occurrence was predicted throughout the WBEA area (Fig. 8.2). Based on our optimal cutoff point and a binary presence/absence classification, 9,439 km² (13.3%) of suitable pronghorn habitat was predicted within the WBEA study area (Fig. 8.3). Pronghorn were more likely to occur in areas with either <7% or >76% of the landscape containing all sagebrush land cover within a 0.27km radius (Fig. 8.4) and in areas of medium to high above-ground productivity (NDVI values > 0.26) within a 0.27-km radius (Fig. 8.5).

TABLE 8.3. Evaluation statistics from AIC_c-based univariate model selection for pronghorn occurrence in the Wyoming Basins Ecorgional Assessment area in relation to multi-scale vegetation, abiotic, and disturbance predictor variables (log-likelihood [LL], number of parameters [K], Akaike's Information Criterion corrected for small sample sizes [AIC_c], change in AIC_c value from the top model [Δ AIC_c], and Akaike weight [w_i]). All logistic regression models included all sagebrush within a 0.27-km radius, NDVI within a 0.27-km radius, and an interaction term. We used AIC_c to sort models for each variable in ascending order to identify the extent at which pronghorn respond to individual variables.

Category	Variable ^a	LL	К	AIC _c	ΔAIC_{c}	Wi
Vegetation	CFRST _{18km}	-85.88	5	182.57	0.00	0.27
	CFRST _{3km}	-85.89	5	182.60	0.03	0.26
	CFRST _{1km}	-85.97	5	182.75	0.17	0.24
	CFRST _{5km}	-86.03	5	182.88	0.31	0.23
	GRASS _{18km}	-85.48	5	181.77	0.00	0.27
	GRASS _{1km}	-85.99	5	182.80	1.03	0.20
	GRASS ₂₇₀	-86.02	5	182.86	1.09	0.20
	GRASS ₅₄₀	-86.01	5	182.83	1.06	0.20
	GRASS _{5km}	-86.01	5	182.83	1.06	0.20
	GRASS _{3km}	-86.05	5	182.92	1.15	0.19
	MIX _{3km}	-85.19	5	181.19	0.00	0.17
	MIX_{1km}	-85.21	5	181.23	0.03	0.17
	MIX _{18km}	-85.21	5	181.24	0.05	0.16
	MIX _{5km}	-85.50	5	181.81	0.61	0.12
	RIP _{5km}	-83.00	5	176.82	0.00	0.17
	RIP _{3km}	-83.54	5	177.90	1.08	0.10
	RIP _{18km}	-83.91	5	178.64	1.82	0.07
	RIP ₅₄₀	-85.20	5	181.21	4.39	0.02
	RIP_{1km}	-85.39	5	181.60	4.78	0.02
	RIP ₂₇₀	-85.74	5	182.30	5.48	0.01
	SALT _{18km}	-81.12	5	173.06	0.00	0.94
	SALT _{5km}	-84.77	5	180.35	7.29	0.02
	SALT _{3km}	-85.19	5	181.18	8.13	0.02
	SALT _{1km}	-85.95	5	182.71	9.65	0.01
	SALT ₂₇₀	-86.04	5	182.89	9.83	0.01
	SALT ₅₄₀	-86.05	5	182.91	9.85	0.01
	CONTAG _{5km}	-85.26	5	181.34	0.00	0.39
	CONTAG _{1km}	-85.44	5	181.70	0.36	0.33
	CONTAG _{3km}	-85.62	5	182.06	0.71	0.28
	EDGE _{1km}	-85.75	5	182.32	0.00	0.37
	EDGE _{5km}	-85.84	5	182.49	0.17	0.34
	EDGE _{3km}	-85.98	5	182.77	0.45	0.29

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Category	Variable ^a	LL	Κ	AIC _c	ΔAIC_{c}	Wi
Abiotic	CTI	-86.02	5	182.85	0.00	0.75
	CTI ^b	-86.01	6	184.84	2.18	0.25
	ELEV	-82.51	5	175.83	0.00	0.71
	ELEV ^b	-82.30	6	177.42	1.77	0.29
	SOLAR	-85.66	5	182.14	0.00	0.58
	SOLAR ^b	-84.91	6	182.64	0.68	0.42
	TRI 1km	-85.25	5	181.32	0.00	0.14
	TRI 18km	-85.37	5	181.56	0.25	0.13
	TRI _{5km}	-85.44	5	181.69	0.37	0.12
	TRI _{18km} ^b	-84.64	6	182.09	0.96	0.09
	TRI	-85.86	5	182.54	1.23	0.08
	TRI ^b	-85.96	5	182.74	1.42	0.07
	TRI _{3km}	-85.96	5	182.74	1.43	0.07
	TRI 540	-86.04	5	182.89	1.57	0.07
	TRI 270	-86.05	5	182.92	1.60	0.06
	TRI 1km ^b	-85.10	6	183.02	1.88	0.06
	TRI 5km ^b	-85.38	6	183.57	2.44	0.04
	TRI _{3km} ^b	-85.69	6	184.20	3.06	0.03
	TRI 270 ^b	-85.93	6	184.68	3.55	0.02
	TRI 540 ^b	-85.96	6	184.72	3.59	0.02
	Tmin	-84.40	5	179.62	0.00	0.50
	Tmin ^b	-84.40	5	179.62	0.00	0.50
	iH2Od _{1km} ^c	-86.03	5	182.88	0.00	0.34
	iH2Od ₅₀₀ ^c	-86.05	5	182.91	0.03	0.33
	iH2Od ₂₅₀ ^c	-86.06	5	182.93	0.05	0.33
	pH2Od ₂₅₀ ^c	-85.91	5	182.64	0.00	0.36
	pH2Od ₅₀₀ ^c	-85.99	5	182.80	0.16	0.33
	pH2Od _{1km} ^c	-86.06	5	182.93	0.29	0.31
Disturbance	AG_{250}^{c}	-85.69	5	182.20	0.00	0.42
	$\mathrm{AG}_{500}^{\mathrm{c}}$	-86.05	5	182.91	0.71	0.29
	AG_{1km}^{c}	-86.06	5	182.93	0.73	0.29
	MjRD _{1km} ^c	-85.45	5	181.72	0.00	0.37
	MjRD ₅₀₀ ^c	-85.54	5	181.90	0.19	0.33
	MjRD ₂₅₀ ^c	-85.65	5	182.11	0.40	0.30
	PIPE ₂₅₀ ^c	-85.99	5	182.80	0.00	0.34
	PIPE ₅₀₀ ^c	-86.00	5	182.81	0.01	0.34
	PIPE _{1km} ^c	-86.03	5	182.88	0.08	0.33

TABLE 8.3. Continued

Category	Variable ^a	LL	К	AIC _c	ΔAIC_{c}	Wi
	POWER _{1km} ^c	-83.14	5	177.09	0.00	0.42
	POWER ₅₀₀ ^c	-83.45	5	177.71	0.62	0.31
	POWER ₂₅₀ ^c	-83.61	5	178.03	0.94	0.27
	$2RD_{1km}^{c}$	-86.00	5	182.82	0.00	0.34
	2RD ₂₅₀ ^c	-86.02	5	182.86	0.04	0.33
	2RD ₅₀₀ ^c	-86.06	5	182.93	0.11	0.32
	WELL ₅₀₀ ^c	-86.03	5	182.88	0.00	0.34
	WELL ₂₅₀ ^c	-86.04	5	182.90	0.02	0.33
	WELL _{1km} ^c	-86.06	5	182.93	0.06	0.33
	RDdens _{5km}	-83.27	5	177.35	0.00	0.68
	RDdens _{3km}	-85.16	5	181.13	3.78	0.10
	RDdens ₂₇₀	-85.40	5	181.61	4.25	0.08
	RDdens _{18km}	-85.89	5	182.60	5.24	0.05
	RDdens ₅₄₀	-86.04	5	182.89	5.54	0.04
	B Ddens	-86.05	5	182 92	5 57	0.04

TABLE 8.3.	Continued
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^b Quadratic function (variable + variable²)

^c Distance decay function (e^(Euclidean distance from feature/-distance parameter))

Model Evaluation

We evaluated model predictions with pronghorn aerial counts conducted by the Wyoming Fish and Game Department during May and June of 2005 in the Worland Basin. Each observation was spatially geo-referenced and attributed with a herd count (range = 1-16 pronghorn).

We found strong corroboration of the test data with model predictions. Regressing observed probability of occurrence against predicted probability of occurrence resulted in a slope close to 1.0 but significantly different from zero, and an intercept close to zero with a high R² (slope = 0.99, SE = 0.20; intercept = 0.00083, SE = 0.02; R² = 0.75; F_{1.8} = 24.53, p = 0.001).

DISCUSSION

We identified three land cover types at three different extents that related positively to pronghorn occurrence during the breeding season. In order of increasing extent, pronghorn were more likely to occur in areas where proportion of sagebrush land cover was either high (>76%) or low (<7%) within 0.27 km, in areas with greater proportions of mixed shrubland (i.e., rubber [Ericameria spp.] and yellow [Chrysothamnus spp.] rabbitbrush and winterfat [Krascheninnikovia lanata]) within 3 km, and in areas with greater proportions of riparian land cover within 5 km. Our findings corroborate other studies that identified the importance of shrubs in pronghorn diet, particularly winterfat (Stephenson et al. 1985), typically found in mixed shrubland, and pronghorn habitat use (Dirschl 1963, Martinka 1967, Bayless 1969, Beale and Smith 1970, Clary and Beale 1983, MacKenzie 2006). Shrub cover was the most important variable predicting pronghorn winter density and fawn:doe ratios (Irwin and Cook 1985).

TABLE 8.4. Re (LL) , number of weight (w_i) . Only	ssults of A. parameter y models w	C_c -based submodel selection for pronghorn occurrence in the Wyoming Basins Ecorgional Assess s (K), Akaike's Information Criterion corrected for small sample sizes (AIC _c), change in AIC _c varith $\Delta AIC_c \leq 2$ are shown.	nent area; lue from th	the tal	ole also sho model (∆A	ws log-lik JC _c), and	elihood Akaike
Category	Rank	Model ^a	TL	К	AIC_c	$\Delta \text{AIC}_{\rm c}$	$w_{\rm i}$
Vegetation	1	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + MIX_{3km} + RIP_{3km} + SALT_{18km}$	-77.77	7	171.22	0.00	0.32
	2	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + MIX_{3km} + SALT_{13km}$	-79.39	9	172.02	0.81	0.22
	3	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + CFRST_{18km} + SALT_{18km}$	-79.49	9	172.23	1.01	0.20
	4	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + RIP_{3km} + SALT_{18km}$	-79.81	9	172.88	1.66	0.14
	5	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + SALT_{18km}$	-81.12	5	173.13	1.91	0.12
Abiotic	1	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + ELEV$	-82.51	S	175.91	0.00	0.13
	2	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + ELEV + TRI_{1km}$	-81.65	9	176.55	0.65	0.10
	ю	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + ELEV + SOLAR$	-81.72	9	176.70	0.79	0.09
	4	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + ELEV + SOLAR + TRI_{1km}$	-80.82	7	177.33	1.43	0.07
Disturbance	1	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + RDdenS_{8tm} + POWER_{1km}$	-80.43	9	173.49	0.00	0.18
	2	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + PIPE_{250} + RDdens_{54m} + POWER_{14m}$	-79.39	7	173.63	0.14	0.17
	ю	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + AG_{250} + RDdens_{8km} + POWER_{1km}$	-79.63	7	174.11	0.62	0.13
	4	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + WELL_{500} + RDdens_{Skm} + POWER_{1km}$	-79.87	٢	174.59	1.10	0.10
	5	$ALLSAGE_{270} + NDVI_{270} + ALLSAGE_{270} * NDVI_{270} + 2RD_{1km} + RDdens_{3km} + POWER_{1km}$	-80.32	7	175.48	1.99	0.07

Our study also corroborates other studies that show riparian land cover is important to pronghorn occurrence. Availability of water is a critical component of pronghorn ranges (Ryder 1983), especially during summer and fall (Einarsen 1948). Drought conditions during midsummer decreased doe survival in the southwestern United States, which was a more important correlative of population trend than winter-rain influence on fawn survival (Brown et al. 2006). Habitats that maintain high pronghorn densities had water available within 1.6 km (Yoakum 1974, Ockenfels et al. 1994). In Wyoming, 95% of over 12,000 pronghorn detections were observed within 6.4 km of water (Sundstrom 1968).

Pronghorn occurrence in the WBEA study area was related negatively to an interaction between all sagebrush and NDVI within 0.27 km, and salt-desert shrubland within 18 km. The interaction between all sagebrush and NDVI indicates that not all sagebrush can be treated equally; our study suggests that pronghorn used sagebrush habitat only in areas with higher aboveground productivity. As above-ground productivity varies spatially and temporally (Bradley and Mustard 2008), it is to be expected that habitat use by pronghorn may shift annually within sagebrush and mixed shrubland. Future studies should investigate how annual variation in aboveground productivity, particularly grass biomass that forms the major component of pronghorn diet (McInnis and Vavra 1986), relates to pronghorn occurrence. In regard to salt-desert shrubland, extensive patches of this ecological system that lack extensive herbaceous cover may offer little forage for pronghorn (West 1983). Shadscale saltbush (Atriplex confertifolia), a dominant shrub species, is nearly absent in the pronghorn diet (McInnis and Vara 1987).

For abiotic variables, NDVI within 0.27 km and elevation related positively to pronghorn occurrence in the WBEA area. Selection of sagebrush at higher elevations in areas with higher above-ground bio-

mass, as indicated by higher NDVI values, may maximize caloric intake. Pronghorn consume a higher percentage of forbs during summer (Stephenson et al. 1985), and selection for higher elevations in our study likely captured increases in forb abundance at higher elevations in sagebrush ecosystems (Franklin and Dyrness 1988).

Two anthropogenic features, 1-km distance decay from power lines and road density within 5 km, were positively associated with pronghorn occurrence. This was unexpected because several studies found negative effects of anthropogenic factors on pronghorn occupancy or behavior, including human disturbance (Berger et al. 1983, Easterly and Guenzel 1992, Sawyer et al. 2005), oil and gas extraction (Easterly et al. 1991, Easterly and Guenzel 1992), vehicular traffic volume (Berger et al. 1983, Gavin and Komers 2006, Harrington and Conover 2006), and recreation, such as hiking and mountain biking (Fairbanks and Tullous 2002, Taylor and Knight 2003). We used a stratified sampling design based on sagebrush habitat productivity and cumulative effects of human land use (Ch. 4). Consequently, we may have under-sampled responses by pronghorn to specific anthropogenic stressors, such as high-volume traffic roads. In our study, only 12% of randomly selected transects started on high-traffic interstates/state and federal highways. Alternatively, it is also possible that the two anthropogenic features are surrogate variables for flat areas, in the case of power lines, and food availability, in the case of road density, as road verges may contain higher grass and forb cover, particularly of exotic species, compared to sagebrush habitat adjacent to roads (Gelbard and Belnap 2003, Ch. 10).

Our study indicates that walking-transect sampling works well for large but not for medium-sized mammals. Why the transect method resulted in few medium-sized mammal sightings is perplexing because other studies have successfully employed similar survey methods to study lagomorph

TABLE 8.5. Results of AIC_c-based model selection for the combined pronghorn occurrence models^a in the Wyoming Basins Ecoregional Assessment area; the table also shows parameter estimates (Beta [SE]) and evaluation statistics (Log-likelihood [LL], number of parameters [K], Akaike's Information Criterion corrected for small sample sizes [AIC_c], change in AIC_c value from the top model [Δ AIC_c], and cumulative Akaike weight [Σw_i]). Models shown with cumulative Akaike weight (w_i) of just ≥ 0.9 .

Rank	Constant	ALLSAGE ₂₇₀	NDVI ₂₇₀	ALLSAGE ₂₇₀ * NDVI ₂₇₀	SALT _{18km}	POWER _{1km}
1	-8.33 (2.80)	10.14 (3.42)	17.01 (7.16)	-23.59 (9.29)	-11.00 (4.06)	1.97 (0.78)
2	-8.35 (2.81)	10.79 (3.44)	17.24 (7.03)	-24.19 (9.14)	-10.40 (4.24)	2.05 (0.78)
3	-7.20 (2.62)	9.92 (3.31)	15.87 (7.00)	-22.23 (9.07)	-12.13 (4.16)	2.04 (0.78)
4	-12.24 (2.87)	9.92 (3.20)	14.37 (6.95)	-21.61 (8.92)		
5	-12.30 (2.98)	9.90 (3.30)	15.86 (7.24)	-22.44 (9.29)		1.68 (0.75)
6	-11.86 (2.91)	9.24 (3.18)	14.45 (7.14)	-20.27 (9.18)		1.89 (0.76)
7	-12.67 (3.02)	9.71 (3.26)	15.46 (7.28)	-22.50 (9.36)		
8	-8.08 (2.78)	10.30 (3.41)	16.86 (7.26)	-24.23 (9.41)	-9.29 (3.61)	
9	-7.81 (2.74)	10.31 (3.38)	16.43 (6.97)	-23.51 (9.05)	-9.62 (3.87)	
10	-10.34 (2.80)	11.73 (3.42)	20.20 (6.94)	-26.91 (8.96)		1.95 (0.76)
11	-10.93 (2.91)	12.08 (3.52)	20.86 (7.16)	-28.09 (9.24)		1.82 (0.75)
12	-6.68 (2.57)	9.51 (3.26)	15.16 (6.96)	-21.72 (9.03)	-11.28 (3.84)	
13	-8.86 (3.02)	9.22 (3.23)	13.98 (7.17)	-20.61 (9.27)	-8.34 (4.30)	
14	-8.69 (2.88)	10.88 (3.50)	17.61 (7.27)	-25.34 (9.42)	-8.29 (3.68)	
15	-11.54 (2.85)	10.54 (3.25)	15.09 (7.05)	-22.81 (9.03)		

^b Values are multiplied by 10²

(Gross et al. 1974, Daniel et al. 1993, Bartel et al. 2008) and ground squirrel ecology (Greene et al. 2009) in the sagebrush ecosystem. Low detection rates could be attributed to low population densities during 2005 and 2006 when we sampled these species. This may apply to the Wyoming ground squirrel because both transect and survey block surveys resulted in insufficient sample sizes to develop species distribution models (Ch. 7). In contrast, we detected cottontails and white-tailed jackrabbits in sufficient sample sizes using area searches within 7.29-ha survey blocks, but not on transects (Ch. 7). The serpentine sampling pattern on survey blocks may have resulted in higher flushing rates compared to the straight-line walking pattern

on transects. In contrast, transect sampling appeared well suited to survey pronghorn, the most commonly observed mammal in this study. Most pronghorn were detected close to transects (mean detection distance = 225 m, SD = 201 m, range = 4-1,041 m,n = 169) with a high detection probability (0.77). Walking transects coupled with distance sampling may be a cost effective alternative to expensive aerial pronghorn surveys (Rabe et al. 2002). In addition, walking transects are well suited for use in citizen science programs, which could be implemented to help evaluate long-term pronghorn population trends. For medium-sized mammals, we recommend the area-search method, which was more effective in achieving minimum sample sizes

TABLE 8.5. Extended

RDdens.	RIP.	MIX.	ELEV ^b	LL	К	AIC	AAIC	$\Sigma_{W_{i}}$
0.86 (0.49)	Skm	3km		-75.42	7	166.52	0.00	0.25
	9.43 (5.88)			-75.93	7	167.54	1.02	0.41
				-77.28	6	167.82	1.30	0.54
	14.93 (5.79)	46.14 (23.53)	0.20 (0.07)	-76.70	7	169.08	2.56	0.61
1.06 (0.51)			0.17 (0.07)	-76.88	7	169.44	2.92	0.67
		44.45 (22.62)	0.21 (0.07)	-77.03	7	169.74	3.22	0.72
1.11 (0.51)		41.16 (22.45)	0.20 (0.07)	-77.33	7	170.35	3.83	0.76
0.94 (0.50)				-78.97	6	171.18	4.66	0.78
	9.96 (5.67)	39.91 (23.58)		-77.77	7	171.22	4.70	0.81
	15.66 (5.82)	33.71 (19.68)		-77.96	7	171.59	5.07	0.83
0.74 (0.44)	11.95 (5.79)			-78.13	7	171.95	5.43	0.84
		36.90 (23.31)		-79.39	6	172.02	5.50	0.86
		42.85 (24.55)	0.11 (0.07)	-78.20	7	172.09	5.57	0.88
0.78 (0.49)	6.72 (5.79)			-78.28	7	172.24	5.72	0.89
	13.17 (5.66)		0.17 (0.06)	-79.52	6	172.29	5.77	0.90

required for species distribution models (Ch. 7). We further suggest multiple visits to each survey block such that species distribution models can be based on occupancy modeling, which adjusts naïve occupancy estimates by detection probabilities (MacKenzie et al. 2006).

Predictive performance of the simple logistic regression model was superior over the more complex count-based negative binomial regression model when evaluated with independent aerial pronghorn survey data (Wyoming Fish and Game Department). Why did the performance between the models differ so profoundly? First, we may have identified the incorrect link function which could have led to invalid model structure and therefore poor model performance (Potts and Elith 2006). Potts and Elith (2006) found that when keeping model structure fixed, the negative binomial regression model performed worst when compared to Poisson, quasi-Poisson, zero-inflated Poisson, and hurdle models. This seems to be less likely as the Vuong test (Vuong 1989) clearly identified the negative binomial regression model as appropriate for the pronghorn density data. Second, it is possible that the set of predictor variables in our study were not a valid index to pronghorn abundance patterns. In our study, 43% of observations consisted of pronghorn herds ranging in size from two to 30 individuals. Herd composition differed among observations because we sampled a mixture of bachelor



FIG. 8.2. Pronghorn probability of occurrence in the Wyoming Basins Ecoregional Assessment area. Black areas are outside the inference of our models (<3% sagebrush within 5 km or within a body of water). Pronghorn are likely to occur in areas with probability > 0.46.

herds, doe-fawn pairs, and herds consisting of multiple doe-fawn pairs and territorial males (Kitchen 1974). Therefore, differences in social interaction and herd composition within high-density pronghorn areas could have led to an invalid model structure as different social structures conceivably overlapped with a different suite of environmental factors not included in our predictor variables (Nielsen et al. 2005) or included only as surrogate variables (Vanreusel et al. 2007). Model structure incongruence between occurrence and abundance models has been shown for bracken fern (*Pteridium aquilinum*) and high-density moose (*Alcer alcer*) areas (Nielsen et al. 2005).

Model structure differed between negative binomial and logistic regression models with transect-level detection probabilities included as offsets (Buckland et al. 2009) in the negative binomial regression model. Some predictor variables were included in both models at the same extent



FIG. 8.3. Distribution of pronghorn in the Wyoming Basins Ecoregional Assessment area based on optimum probability cutoff threshold of 0.46. Black areas are outside the inference of our models (<3% sagebrush within 5 km or within a body of water).

(RIP_{5km} and SALT_{18km}), while others were unique to one model but not the other (negative binomial regression only: SOLAR and Tmin; logistic regression only: MIX_{3km}, ELEV and POWER_{1km}), or were the same type but differed in extent (negative binomial regression vs. logistic regression: ALLSAGE_{5km} vs. ALLSAGE₂₇₀; NDVI vs. NDVI₂₇₀; RDdens₅₄₀ vs. RDdens_{5km}). Not including detection probabilities in modeling resource selection could lead to misleading selection of predictor variables; predictor variables can be correlated with detecting individuals rather than habitat use (MacKenzie 2006). For example, MacKenzie (2006) found that the variable "distance to water" was in the top AICselected logistic regression models when detection probabilities were not included, but when he included detection probabilities the variable "distance to water" was not in the top AIC-selected logistic regression models. Although we found the predictive capability of the simple lo-



FIG. 8.4. The distribution of pronghorn probability of occurrence within the Wyoming Basins Ecoregional Assessment area in relation to proportion of all sagebrush (*Artemisia* spp.) within a 0.27-km radius. Mean probability of occurrence (black line) and standard deviation (dashed lines) values were calculated in each one percent increment of all sagebrush within a 0.27-km radius moving window. Range of predictions relate to the observed range of sagebrush at study site locations. The dashed horizontal line represents the optimal cutoff threshold (0.46), above which pronghorn occurrence is predicted. Histogram values represent the proportion of the total study area in each 10% segment of all sagebrush within 0.27 km.



FIG. 8.5. The distribution of pronghorn probability of occurrence within the Wyoming Basins Ecoregional Assessment area in relation to NDVI (Normalized Difference Vegetation Index) within a 0.27-km radius. Mean probability of occurrence (black line) and standard deviation (dashed lines) values were calculated in each 0.01 increment of NDVI within a 0.27-km radius moving window. Range of predictions relate to the observed range of NDVI at study site locations. The dashed horizontal line represents the optimal cutoff threshold (0.46), above which pronghorn occurrence is predicted. Histogram values represent the proportion of the total study area in each 0.01 segment of NDVI within 0.27 km.

gistic regression model to be excellent, the structure of this model needs to be further evaluated against a model developed in an occupancy modeling framework where detection probability is included in the model structure (MacKenzie et al. 2006).

Conclusion

Pronghorn occurrence in the WBEA area was best predicted by the distribution and extent of various land cover types, but current levels of anthropogenic disturbances did not appear to affect occurrence of pronghorn during the breeding season. However, anthropogenic stressors may influence different components of fitness that were not assessed in this study. We were unable to incorporate additional anthropogenic stressors into our analyses, as spatial data for these stressors did not exist at the time of our study. For example, fences restrict daily and seasonal pronghorn movement and may result in injury and mortality (Spillet et al. 1967, Ryder et al. 1984, Yoakum and O'Gara 2000, Harrington and Conover 2006). Despite these limitations, we found that the pronghorn model had superior predictive capabilities and therefore can be an important tool to assess the effects of future development on pronghorn occurrence.

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APPENDIX 8.1.

This appendix contains descriptive statistics for explanatory variables used to model pronghorn occurrence. Variables are summarized by occurrence class, and statistics include mean, standard error, lower and upper 95% confidence interval, and minimum and maximum value. This appendix is archived electronically and can be downloaded at the following URL: http://sagemap.wr.usgs.gov/wbea.aspx.