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MODEL OF BREEDING HABITAT OF THE MOUNTAIN PLOVER (*CHARADRIUS MONTANUS*) IN WESTERN WYOMING

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ABSTRACT. —To aid the conservation and management of Mountain Plovers (*Charadrius montanus*), we developed a spatially explicit model of breeding habitat for the shrub-steppe of western Wyoming. Points of Mountain Plover presence and absence were determined by field surveys conducted May through June 1999. At each point we measured topographic slope and a cover type suitability index related to vegetation height and density. Logistic regression revealed a strong negative relationship between presence and slope, and a weaker and positive relationship between presence and cover index. A multiple logistic regression model using slope and cover index to predict presence successfully classified 87% of the points in an independent data set covering much of western Wyoming. The spatial expression of this model will help managers target future surveys and identify currently unsuitable habitat that could be improved via vegetation management. Patches of suitable breeding habitat of the Mountain Plover in western Wyoming are probably functions of poor soil, low precipitation, and wind scour, and thus are likely rather persistent in space and time. Combined with the relatively large proportion of publicly owned land here, this may make conservation and recovery of the Mountain Plover easier in western Wyoming than in the more dynamic and privately controlled Great Plains.

Key words: Mountain Plover, Charadrius montanus, *habitat, logistic regression, modeling, shrub-steppe, Wyoming.*

The Mountain Plover (*Charadrius montanus*) is endemic to western North America where it breeds in flat, dry, and sparsely vegetated sites in short-grass prairie and adjacent shrub-steppe (Knopf 1996). Population declines began early in the 20th century (Cooke 1915, Abbott 1940, Laun 1957) and have continued to the present (Graul and Webster 1976, Knopf 1994, 1996). Several factors may be responsible for these declines; the most significant are probably cultivation, fire-suppression, and alteration of native grazing regimes in the short-grass prairie (Knopf 1994, 1996). Cultivation can destroy nests directly (Shackford et al. 1999) and, along with altered disturbance regimes, can reduce habitat quality by producing tall and relatively dense vegetation. These factors may have converted some parts of the short-grass prairie from population sources to population sinks, though further research is needed.

On 16 February 1999 the U.S. Fish and Wildlife Service proposed listing the Mountain Plover as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1999), making the species a management priority for land and wildlife managers. Coordinating conservation efforts for Mountain Plovers in the short-grass prairie is complicated by the large proportion of privately owned land in the region. However, much of the western shrub-steppe part of the breeding range is under the jurisdiction of the USDI Bureau of Land Management, providing an opportunity to coordinate recovery efforts over a fairly large area. Furthermore, this region is not subject to as much cultivation as the short-grass prairie. The most pervasive human land use in shrub-steppe systems is open-range livestock grazing, which is not only compatible with Mountain Plover reproduction but, in some situations, can increase habitat quality (Kantrud and Kologiski 1982, Knopf 1996).

To integrate conservation of Mountain Plovers with other land uses, natural resource managers need to know the potential for Mountain Plover occurrence both locally and regionally. Such knowledge would make field surveys more efficient by identifying areas of likely occurrence and also would help identify currently unsuitable habitat that could be made suitable via management. Our objective was to model the probability of Mountain Plover occurrence across a relatively unstudied part of their range, the shrub-steppe of western Wyoming, using habitat attributes that are currently available to managers in digital form.

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We built a model with observations of Mountain Plovers we collected in the field, and then validated it with an independent set of observations from an existing database of wildlife occurrences.

STUDY AREA

This project was conducted in the Jack Morrow Hills, a region of about 2.8×10^5 ha in southwestern Wyoming east of the town of Farson and south of South Pass City (Fig. 1a). This area includes parts of the Green River, Sweetwater River, and Great Divide Basin watersheds and encompasses the site where John Kirk Townsend collected the first Mountain Plover known to science in 1832 (Knopf 1996). The study area lies completely within the Wyoming Basins ecoregion (Fig. 1b), a shrub-dominated semidesert whose current boundaries were modified from Bailey (1995) by Groves et al. (2000).

Elevation in the study area ranges from 2020 m to 2640 m; topography is variable, ranging from broad flats to steep ridges and buttes. Coarse, rocky soils alternate with stabilized sand (Munn and Arneson 1998). Annual precipitation ranges from 203 mm to 305 mm, the majority of which occurs in April and May (Martner 1986). Land cover is dominated by Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) and desert shrub assemblages (e.g., *Atriplex confertifolia, Sarcobatus vermiculatus*), with frequent patches of bare soil, rock outcrops, and vegetated and unvegetated sand dunes (Merrill et al. 1996). Small patches of aspen (*Populus tremuloides*) and juniper (*Juniperus scopulorum, J. osteosperma*) occur infrequently near seeps and springs. Over 90% of the study area is under the jurisdiction of the USDI Bureau of Land Management.

METHODS

Field Surveys and Habitat Measurement

Survey routes for Mountain Plovers were established along roads in 3 parts of the study area (Fig. 1a). Cumulative length of all survey route segments was 191 km, and variation in vegetation and topography along the routes was representative of the entire study area. Five Mountain Plover surveys were conducted on each route from 18 May to 30 June 1999. Each survey was performed from a vehicle traveling 30–40 km $\cdot$ hr^{-1} between 0600 and 1900 hours in favorable weather and involved 2 experienced observers searching for birds by eye and binocular. The same 2 observers performed all surveys. Each observation of Mountain Plovers was located to at least the nearest 16 m using vehicle odometer and 1:24,000-scale topographic maps, and entered into a digital point theme using the ArcView (version 3.1; Environmental Systems Research Institute, Redlands, CA) geographic information system. The 16-m level of precision was chosen to match the mapping precision of the points in the model data set to those in the validation data set. We termed these points "present-points" to reflect the confirmed presence of Mountain Plovers.

We then measured topographic slope and vegetation type at each present-point by overlaying the point on (1) a raster map of topographic slope and (2) a polygon map of land cover types. The first map identified percent slope ([rise/run] *100) within each 30×30-m section of Wyoming and was derived from a digital elevation model based on satellite imagery (W. Reiners and K. Driese, University of Wyoming, Laramie).

The land cover map is described in detail in Merrill et al. (1996). Briefly, it delineates polygons of unique primary and secondary land cover types (Table 1) and estimates percent coverage of each type, based on satellite imagery and computer classification. For some polygons, percent coverage of primary and secondary types did not sum to 100, and an "other" (tertiary) cover type also was identified. We calculated an index of cover suitability at each present-point by first scoring cover types 1–5 according to their suitability as Mountain Plover breeding habitat (Table 1). Those scores were based primarily on typical height and density of vegetation in each cover type, although substrate mobility and soil moisture also were considered for some types (e.g., active dunes, grass-dominated riparian). Scores were assigned following a review of published studies of Mountain Plover habitat use (e.g., Wallis and Wershler 1981, Olson and Edge 1985, Parrish 1988) and consultation with experts on Wyoming vegetation (W. Fertig and G. Jones, Wyoming Natural Diversity Database, University of Wyoming, Laramie). The cover suitability index at each present-point was calculated as:

Cover suitability index = (primary cover type score * [% coverage of primary type / 100]) + (secondary cover type score * [% coverage of secondary type / 100]) + (tertiary cover type score * [% coverage of tertiary type / 100]) (1)

The 3rd term was not necessary for some observations because percent cover of the primary and secondary types summed to 100.

Using similar methodology, we measured topographic slope and cover suitability index at each of 60 points along the survey routes at which Mountain Plovers were not observed ("absent-points"). That number, selected after our field surveys were complete, was chosen to match the ratio of present-points : absent-points in the model data set to that of the validation data set. The set of absent-points was developed by generating a point every 1000 m along each segment of the survey routes (191 points total), then eliminating points that fell within 1000 m of Mountain Plover observations. We then selected 60 of the remaining points; selection was random within the constraint that the number of points selected on a given route segment was proportional to the length of that segment. This ensured that absent-points were distributed evenly across the survey routes.

Model-Building and Validation

To ensure that our results were as robust as possible, we removed potentially biased observations from the model data set. Mountain Plovers are most often reported from flat and sparsely vegetated sites (e.g., Graul 1975, Parrish 1988); because observers are most likely to see birds in such sites, there is a strong possibility of bias when surveying across several vegetation types and topographies. To minimize that bias, we noted the position and behavior of each bird when it was first seen. The present-points used to build our statistical model included only those points where birds were initially observed on the road surface or road margin. Because visibility of birds in those positions was not a direct function of vegetation or topography, the relative frequency of those observations was a less biased estimate of the relative frequency of occurrence of Mountain Plovers in the terrain immediately adjacent to the road.

This is based on the assumption that roads hold little attraction for Mountain Plovers in our study area, and that Mountain Plover distribution here is driven primarily by the qualities of adjacent cover types and not the roads themselves. This assumption may not hold in cultivated areas where Mountain Plovers are increasingly attracted to road surfaces as crops take over the formerly bare fields that initially attracted the birds. There is no cultivation in our study area, nor is there any other substantial change in height or density of vegetation during the Mountain Plover breeding season.

To minimize spatial autocorrelation between present-points, we identified points that fell within 1000 m of each other, then eliminated one of the pair at random. Because mean internest distance has been estimated at <200 m (Graul 1973) and brood rearing areas at <91 ha (Knopf and Rupert 1996), a spacing of 1000 m increased the probability that each present-point represented an independent observation.

We used logistic regression within the program Minitab (version 11; Minitab Inc., State College, PA) to model the relationship between Mountain Plover occurrence, topographic slope, and cover suitability index. Logistic regression is a statistically robust modeling technique (Press and Wilson 1978) that defines the probability of the "true" (or, in this case, "present") condition of a binary response variable as a function of independent variables (Hosmer and Lemeshow 1989). The model included the unbiased set of present-points and all 60 randomly chosen absent-points, used Mountain Plover presence / absence as the dependent variable, and cover suitability index and percent slope as independent variables. Three separate models were constructed: 2 using each of the independent variables separately, and 1 using both independent variables simultaneously.

Accuracy of the latter model was evaluated as its ability to predict Mountain Plover presence and absence for points in the modeling data set and in an independent validation data set. The validation data set consisted of 455 points distributed throughout the Wyoming portion of the Wyoming Basins ecoregion (Fig.

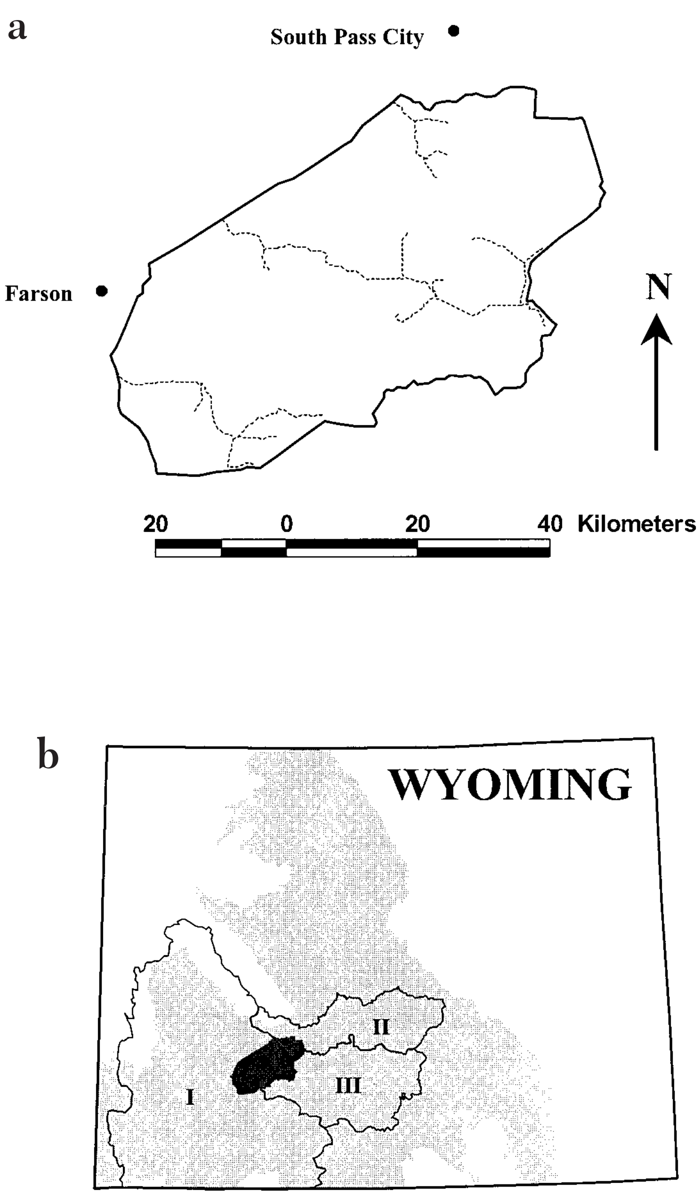

Fig. 1. (a) Detail of the Jack Morrow Hills study area, showing the 3 Mountain Plover survey routes (dotted lines). (b) The Jack Morrow Hills study area (small, dark polygon) in the context of the Wyoming portion of the Wyoming Basins ecoregion (larger, lighter polygon). I = Green River watershed; II = Sweetwater River watershed; III = Great Divide Basin watershed.

1b). Sixty-five of those were confirmed observations of Mountain Plovers that were made during the breeding season and mapped to ≤16 m of their actual location, as documented in the Biological and Conservation Database at the Wyoming Natural Diversity Database (University of Wyoming, Laramie). The remaining 390 points were located randomly and thus represented available rather than unoccupied habitat. Because intensity and distribution of survey effort for Mountain Plovers were unknown for the entire validation region, we could not reliably identify absent-points to include in the validation data set. All points in

TABLE 1. Mountain Plover habitat suitability scores for Wyoming land cover types identified by Merrill et al. (1996). Scores were assigned following a literature review of Mountain Plover habitat use and discussions with experts on Wyoming vegetation types, and were based primarily on the height and density of vegetation within each land cover type; 1= least suitable; 5 = most suitable.

Land cover type	Habitat suitability score
All forested types	1
Open water	1
Permanent snow	1
Subalpine meadow	2
Shrub-dominated riparian	2
Meadow tundra	2
Alpine exposed rock and soil	2
Human settlements	2
Surface-mining operations	2
Grass-dominated wetland	2
Grass-dominated riparian	2
Mesic upland shrub	2
Xeric upland shrub	2
Basin big sagebrush	2
Irrigated crops	3
Bitterbrush shrub steppe	3
Mountain big sagebrush	3
Wyoming big sagebrush	3
Desert shrub	3
Greasewood fans and flats	3
Vegetated dunes	3
Active sand dunes	3
Black sagebrush steppe	4
Saltbush fans and flats	4
Dryland crops	4
Unvegetated playa	4
Basin exposed soil	5
Great Basin foothills grassland	5
Mixed-grass prairie	5
Short-grass prairie	5

the validation data set were separated by at least 1000 m.

To estimate classification success of the multiple logistic regression model, it was necessary to select a cutoff probability such that a predicted probability greater than the cutoff indicated presence, and a predicted probability less than the cutoff indicated absence. Following Fielding and Haworth (1995), we defined the cutoff probability as the midpoint between mean probabilities for the present- and absent-points.

RESULTS

We recorded 23 observations of Mountain Plovers during the surveys. This included 16 observations of single birds and 7 observations of ≥2 birds (observations of ≥2 birds were treated as single present-points in the modeling procedure). Although we observed no nests or hatchlings, we saw vigorous broken-wing displays from adults on both the first and last surveys of the project, suggesting that birds were in breeding condition during the entire survey period and that nests were in the vicinity.

Eleven of the 23 observations were of walking or motionless birds >20 m from the road center in low and open vegetation; we eliminated these from the model data set. Two of the remaining 12 observations were within 1000 m of similar observations; we randomly eliminated 1 observation from each pair. One of the remaining 10 observations was of a single bird that flushed from the road margin about 3 m from the road center and 50 m in front of the survey vehicle. Although we did not initially observe that bird on the ground, we included the observation in the model data set on the assumption that we would have seen the bird even if it had not flushed. Therefore, the final model data set consisted of 10 present-points and 60 absent-points, all separated by ≥1000 m. The ratio of present-points to absent-points in the model data set (10/60 = 0.17) is equal to the ratio of present-points to available-points in the validation data set (65/390 = 0.17).

The logistic relationship between probability of Mountain Plover presence and percent slope was strongly negative, with an essentially zero probability of presence at slope values >8% (Fig. 2a). The null hypothesis that all slopes in the model were zero was rejected ($G = 6.764$, df = 1, $P = 0.009$), and the model had good fit to the data (deviance chi square = 20.524, df = 33, $P = 0.956$). The relationship between probability of Mountain Plover presence and cover suitability index was positive, with probability increasing sharply at suitability indices >3.3 (Fig. 2b). This model was only weakly significant ($G = 1.877$, df = 1, $P = 0.171$), and goodness-of-fit was rather low (deviance chi square = 13.901, df = 6, $P = 0.031$). Note that the model data set contained a relatively small range (2.30–4.10) of cover suitability indices.

Multiple logistic regression of probability of Mountain Plover presence on percent slope and cover suitability index yielded a significant ($G = 8.799$, df = 2, $P = 0.012$) model with good fit (deviance chi square = 37.527, df = 56, $P = 0.973$). Percent slope was a

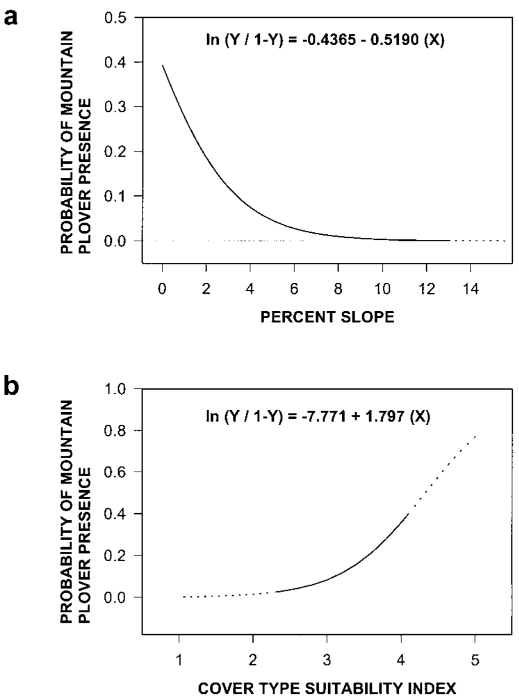

Fig. 2. Logistic relationship between probability of Mountain Plover presence and (a) percent slope, and (b) cover type suitability index. Percent slope = [rise / run] * 100, and was derived from a digital elevation model with 30-m resolution. Cover type suitability index is outlined in equation 1 (in text) and Table 1. Solid-line segments indicate ranges of data from which the models were estimated; dotted segments are extrapolations beyond those ranges. Y = probability of Mountain Plover presence.

strong predictor ($Z = -2.25$, $P = 0.024$), whereas cover suitability index was weaker ($Z = 1.42$, $P = 0.156$). The multiple logistic regression equation was:

$$\ln (Y / 1 - Y) = -7.824 + 2.241 \text{ (cover suitability index)} - 0.5661 \text{ (percent slope)}, \tag{2}$$

where Y = probability of Mountain Plover presence.

This model successfully classified 8 of 10 (80%) present-points and 43 of 60 (72%) absent-points in the modeling data set. Overall classification success for the modeling data set was 73%. The model also predicted presence at 39 of 65 (60%) present-points in the validation data set and predicted absence at 356 of 390 (91%) available-points in the validation data set, for an overall validation success of 87%.

DISCUSSION

Model Success

As has been documented elsewhere in their range (e.g., Graul 1975, Parrish 1988, Knopf and Miller 1994), we found Mountain Plover occurrence in our study area to be a function of topographic slope and vegetation stature. Percent slope was a strong predictor of Mountain Plover presence when used either as a sole predictor (Fig. 2a) or in combination with the cover suitability index (equation 2).

Although the cover suitability index was a statistically weaker predictor in both single- (Fig. 2b) and double-variable (equation 2) models, it is important to note that the model data set contained a rather narrow range of cover suitability indices (Fig. 2b). The predictive power of this variable is likely most apparent at extreme values, because animal presence and absence are more predictable in very suitable and very unsuitable cover types, respectively. To investigate this further, we compared the classification success of the multiple logistic regression model to that of a model using slope alone as a predictor, using only those points in the validation data set with cover suitability indices ≤2.0 or ≥4.0 ($N = 82$). The double-variable model predicted presence at 15 of 15 (100%) present-points and absence at 54 of 67 (81%) available-points (overall classification success = 84%). The single-variable model predicted presence at 11 of 15 (73%) present-points and absence at 56 of 67 (84%) available-points (overall classification success = 82%). Because of the relatively high success rate of the double-variable model, and because the cover suitability index increased success predicting presence in very suitable cover types, we selected the double-variable model as the best tool to map suitable Mountain Plover habitat in the shrub-steppe of western Wyoming. This model predicted 66% of our study area to have ≤1% probability of Mountain Plover presence, and 1% of our study area to have ≥70% probability of Mountain Plover presence.

There are likely other habitat factors to which Mountain Plovers are responding when selecting breeding areas, and the inclusion of such variables in the model may significantly improve its classification success. For example, amount of soil moisture, coverage of bare ground (Knopf and Miller 1994), and availability of small patches of shade (Shackford 1996) are all thought to be important. Also, note that the vegetation map used in this study was based on a minimum mapping unit of 100 ha (Merrill et al. 1996), and there is much variation in vegetation type and structure within this scale. A model of Mountain Plover occurrence based on finer-scale vegetation information may have higher classification success.

Additionally, Mountain Plovers may be using non-physical factors to select breeding sites. Mountain Plovers tend to nest in clusters in seemingly homogenous habitat (Graul 1973, Knopf 1996), suggesting a preference for close proximity to conspecifics; the 23 Mountain Plover observations recorded in this study formed 2 rather loose clusters separated by about 13 km. Also, Graul (1973, 1975) noted that on native prairie adults often nested within previous year's breeding territories, and chicks often returned to their hatching territory to nest. Even Mountain Plovers nesting on cultivated fields show inter-year site fidelity, although it is weaker than among those nesting on native prairie (Shackford and Leslie 2000). Thus, strong site fidelity may cause some birds to return to territories that have changed substantially since they were first selected; i.e., some individuals may be responding to past, rather than current, territory conditions. This behavior would weaken models such as ours that relate bird positions to current vegetative structure.

Habitat Selection

The preference of Mountain Plovers for flat and sparsely vegetated sites documented in this study is completely consistent with results of studies conducted elsewhere (e.g., Graul 1975, Parrish 1988, Knopf and Miller 1994). This preference ultimately may be a predator-avoidance strategy (but see Sordahl 1991). Predators take a significant proportion of Mountain Plover eggs (Graul 1975, Miller and Knopf 1993, Knopf and Rupert 1996) and chicks (Miller and Knopf 1993, Knopf and Rupert 1996), suggesting strong pressure to develop anti-predator behaviors. Flat areas devoid of tall vegetation afford maximum sight distance to nesting and foraging birds, and Mountain Plovers observed in this study were constantly alert and scanning their surroundings.

We observed Mountain Plovers only on 2 general landforms: rims of broad ridges and flats far from superior topographic features. This suggests that avoidance of aerial predators may be especially important. Even low-flying ambush raptors such as Prairie Falcons (*Falco mexicanus*), Short-eared Owls (*Asio flammeus*), and Northern Harriers (*Circus cyaneus*) would be forced to silhouette themselves against the sky when approaching these landforms. We observed all 3 of these raptor species on our study area, with the latter being the most common.

It is likely that patches of suitable Mountain Plover habitat are more stable in size and position in western Wyoming than in short-grass prairie. In short-grass prairie, low and sparse vegetation is largely due to episodic drought, fire, and intense grazing. The spatio-temporal distribution of these processes is highly variable, and prairie vegetation can recover from such disturbances on a relatively short time scale. Thus, distribution of high-quality habitat probably shifted rapidly across the prairie historically and likely continues to do so within the constraints of cultivation, fire-suppression, and artificial grazing regimes.

In contrast, patches of low and sparse vegetation in the shrub-steppe of western Wyoming are largely due to poor soil quality, chronically low precipitation, and constant wind scour (especially during winter). These factors are relatively static in time and space, leading to persistent bare patches. Thus, distribution of high-quality Mountain Plover habitat was likely very stable historically and, because human actions have not substantially changed the causative factors, may be much the same now as in presettlement times.

Because patches of high-quality habitat may be primarily controlled by abiotic factors in shrub-steppe systems, the association between Mountain Plovers and prairie dogs (*Cynomys* spp.) may be weaker here than in short-grass prairie. In short-grass prairie, Mountain Plovers prefer colonies of black-tailed prairie dogs (*C. ludovicianus*) to areas without prairie dogs (Tyler 1968, Campbell and Clark 1981, Knowles et al. 1982, Knowles and Knowles 1984, Olson and Edge 1985, Olson-Edge and Edge 1987). Black-tailed prairie dogs typically form large and dense colonies. Intense herbivory by black-tailed prairie dogs in and around such colonies maintains short vegetation. In contrast, white-tailed prairie dogs (*C. leucurus*) in western Wyoming form more diffuse colonies in areas with substantial shrub cover and topographical variation. Although Mountain Plovers do nest on colonies of white-tailed prairie dogs (Campbell and Clark 1981), studies comparing density or frequency of occurrence between sites on and off colonies of white-tailed prairie dogs have not yet been performed.

Model Applications

As with output from all predictive models, our model results are best viewed as hypotheses on Mountain Plover distribution. Although the model was generally successful at predicting Mountain Plover occurrence over a large area, there is some error associated with its predictions. This is especially true in the prediction of Mountain Plover presence (60% success) at any given site. Therefore, the most appropriate use of this model is to identify areas of probable occurrence on which to focus future surveys. Mountain Plover conservation will be best served by confirming presence of breeding birds through such surveys, then designing management actions to minimally impact areas of known occupation.

A second appropriate use of our model is to identify currently unsuitable habitat that could become suitable via vegetation management. In the shrub-steppe of western Wyoming, there are several sites of low topographic slope currently dominated by shrubs or other tall vegetation but with the potential to support short-grass or cushion plant communities following fire, grazing, or other manipulations. Pursuing such manipulations on appropriate sites might allow managers to facilitate population recovery by not only protecting currently suitable habitat but also by increasing habitat area.

Because suitable habitat occurs as relatively rare, small, well-bounded, and persistent patches in western Wyoming, land and wildlife managers should be able to efficiently survey for Mountain Plovers here. Furthermore, maintaining and enhancing habitat quality across most of this region should be relatively easy due to the high proportion of land under federal jurisdiction. This contrasts with the situation in short-grass prairie, where flat and sparsely vegetated areas are larger, more diffuse and ephemeral, and typically under private ownership.

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