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RESEARCH ARTICLE

Predicting pup-rearing habitat for Mexican wolves

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Abstract

Population monitoring is essential to document recovery efforts for threatened and endangered species. Mexican wolves (*Canis lupus baileyi*) are an endangered subspecies of gray wolves that historically occupied large portions of the American Southwest and Mexico. Recently, the Mexican wolf population in the United States has been growing rapidly and traditional approaches for population monitoring (e.g., capture and radio collaring) are becoming difficult and expensive as wolves expand into new areas. We developed predictive models of pup-rearing habitat (i.e., den and rendezvous sites) that could help guide future population monitoring efforts. We located 255 den sites and 129 rendezvous sites in Arizona and New Mexico, USA (1998–2023) using tracking collars and site visits. We sampled habitat conditions in wolf-occupied regions of Arizona and New Mexico and fit logistic regressions to these data following a use–available study design to estimate resource selection functions (RSF) for den and rendezvous sites. We hypothesized wolves would select areas that offered greater physical protection, lower human-disturbance, and access to reliable water sources for pup-rearing but that the relative importance of these features would differ between the denning and rendezvous site seasons. Mexican wolves selected den sites at higher elevations in steeper and rougher terrain that were closer to permanent waterbodies but farther from rural roads. Selection of rendezvous sites was also associated with higher elevations and proximity to waterbodies but varied with availability of green leaf biomass on the landscape. While still highly predictive, our rendezvous site model was less predictive than our den model (Spearman's correlation averaged 0.81 [SE = 0.05] vs. 0.90 [SE = 0.03], respectively), possibly because water and green leaf biomass are more spatially diffuse and variable because of monsoonal rains during the rendezvous site season. Our results suggest that terrain features associated with physical protection and access to reliable water were most important in characterizing suitable pup-rearing habitat for Mexican wolves. By predicting suitable den and rendezvous site habitat across portions of the Mexican Wolf Experimental Population Area, our models can help guide future population monitoring by reducing the total search area when surveying for wolves and increase the probability of detecting all members of a pack.

KEYWORDS

Arizona, *Canis lupus baileyi*, den, habitat selection, Mexican wolf, New Mexico, rendezvous site, reproduction, resource selection function

Population monitoring is essential and legally required for documenting the recovery of federally listed species under the Endangered Species Act (ESA). The United States Fish and Wildlife Service (USFWS) implements the tenets of the ESA and generally requires population estimates meeting a specified threshold and a minimum 5-year post-delisting monitoring period for a species to be deemed fully recovered and management authority returned to states with a population (USFWS 2009). Often, ESA-listed species exist at low densities and traditional population monitoring techniques (e.g., capture and marking) may not be feasible. Thus, such population monitoring programs are often time-intensive and costly, requiring coordination among federal, state, tribal, and private partners to be successful (e.g., USFWS et al. 2012, USFWS 2023).

Mexican wolves (*Canis lupus baileyi*) are an endangered species that historically occupied large portions of the American Southwest and Mexico (Oakleaf et al. 2023). Predator control programs, loss of habitat, and settlement of the North American West led to Mexican wolf extirpation in the wild in the United States with only a few individuals remaining in Mexico by the 1980s (Oakleaf et al. 2023). The Mexican wolf was listed as endangered under the ESA in 1976 and efforts began to capture the last remaining known individuals in Mexico between 1977–1980 (Hedrick and Fredrickson 2008). These efforts resulted in the capture of 5 wolves, 3 of which were genetically distinct lineages. There were an additional 4 wolves in captivity composed of 2 additional genetic lineages (2 founders in each lineage). The wild-caught and captive wolves were used as a founding population to start a captive breeding program and supply individuals for subsequent reintroductions to Arizona and New Mexico, USA, and Mexico (Hedrick et al. 1997).

The Mexican wolf population in the United States has been growing, totaling a minimum count of 257 wolves at the end of 2023 (USFWS 2024). This population has been monitored largely through capture and radio-collaring of individuals and then obtaining pack counts and documenting reproduction from ground and aerial surveys (USFWS 2023), requiring extensive collaboration and coordination among stakeholders. Capturing and radio-collaring new and unmarked packs, however, has become increasingly challenging. It is difficult to locate wolves in new areas as they recolonize portions of their former range, and it is expensive to maintain radio-collars on a large portion of the population as it continues to grow. Camera trapping was recently tested as an alternative for monitoring this population and although it is significantly less expensive than capture and radio-collaring, cameras tended to underestimate abundance when compared to the known minimum count (Russo et al. 2023) and provide limited information about pack structure and dispersal.

One way to make survey efforts for gray wolves (*Canis lupus*) more efficient is to locate pup-rearing sites (i.e., dens, where pups are born, or rendezvous sites, where pups are moved to after the denning period) while wolf packs contain relatively immobile pups. Pup-rearing season (~April–September) is the time of year when wolves are relatively localized as adults travel to and from pup-rearing sites to provision and guard pups (Packard 2003, Theuerkauf et al. 2003). Focusing on pup-rearing habitat can reduce the area that needs to be surveyed to detect and sample wolves by 90% (Ausband et al. 2010). Pup-rearing sites have been used to guide howling and track surveys, noninvasive genetic sampling surveys, and camera surveys for wolves (Stenglein et al. 2011; Ausband et al. 2010, 2022). Pup-rearing sites are also critical components and sources of data for wolf population monitoring programs around the world (Bassi et al. 2015, Nowak and Mysłajek 2016, Gable et al. 2018, Fernández-Gil et al. 2020).

Although pup-rearing habitat for wolves consists of den and rendezvous sites, they can be characterized by different habitat features. Den sites are commonly associated with access to water and habitat features that offer protection from predators and environmental stressors (e.g., human disturbance; Trapp et al. 2008), but they are challenging to predict owing to diverse site characteristics and broad areas of potential denning habitat across the landscape (Trapp et al. 2008, Person and Russell 2009). Rendezvous site habitat is often more predictable. For many gray wolf populations (e.g., wolves in midwestern North America; Idaho, USA; and Poland), rendezvous sites are associated with wetlands or wet meadows (Joslin 1967, Theuerkauf et al. 2003, Unger et al. 2009, Ausband et al. 2010). Such areas offer access to quiet, slow moving water and are usually vegetated by dense grasses and non-woody plants with little overstory vegetation (Joslin 1967, Benson et al. 2015). These habitat features are important for young pups who cannot travel far but require ample water to excrete large amounts of nitrogenous waste due to their high protein diets; they also provide protection from predators (including real or perceived threats from humans) and good acoustic communication with adults (Unger et al. 2009, Ausband et al. 2010).

Den sites may be more predictable for Mexican wolves than gray wolves in the Rocky Mountains owing to the water-limited habitat and more rugged terrain of Arizona and New Mexico. If denning habitat is constrained to a predictable set of landscape features, it may be possible to predict potential den sites of Mexican wolves. Conversely, seasonal monsoons may make predicting potential Mexican wolf rendezvous site habitat more challenging than those of their Rocky Mountain counterparts. Monsoons often occur during the rendezvous season (1 July–15 September; Nolin and Hall-McKim 2006) and large storms followed by hot, arid weather may make wet meadows more ephemeral and therefore less predictable on the landscape. In addition, human settlements and roads have been shown to affect selection of pup-rearing sites in many wolf populations (Sazatornil et al. 2016). Human disturbance may be a particularly important predictor of den selection when pups are most vulnerable and relatively immobile (Benson et al. 2015) compared to rendezvous site selection when pups are more mobile.

Our objective was to develop predictive models of potential den and rendezvous habitat for Mexican wolves that could help guide future population monitoring efforts. We hypothesized that during the pup-rearing season, Mexican wolves would select for landscape attributes that provide reliable water and protection for pups, similar to other gray wolf subspecies, but that specific landscape attributes associated with reliable water and protection may look different in the American Southwest compared to those in northern Rocky Mountains of the United States. Specifically, we predicted denning habitat would be associated with higher elevations, steep slopes and rougher terrain, forest cover, longer distances from human disturbance, and shorter distances to reliable water sources (e.g., stock tanks and ponds maintained for watering livestock), whereas rendezvous habitat would be associated with areas that collect and hold water (e.g., wet meadows, gentle slopes and concave surface curvature), close to reliable water sources, and farther from human disturbance. We expected denning habitat would be more predictable than rendezvous site habitat given the need for more specific denning structures (e.g., steep slopes) and greater water availability during the monsoon season that overlaps when wolves rendezvous (i.e., water availability is less limiting).

STUDY AREA

Our study area overlapped portions of the Mexican Wolf Experimental Population Area (MWEPA) Zones 1 and 2 where Mexican wolf dens and rendezvous sites have been documented by the Mexican Wolf Recovery Team (Figure 1). This area encompassed parts of the Apache-Sitgreaves National Forest in east-central Arizona and the Gila and Cibola National Forests in west-central New Mexico (109.89° N, 33.60° E). Elevation ranged from 664–3,450 m and changed from desert and semi-desert lowlands (<1,500 m) to high elevation spruce (*Picea* spp.)-fir (*Abies* spp.)-Douglas-fir (*Pseudotsuga menziesii*) forests that contained small stands of aspen (*Populus tremuloides*). Intermediate areas transitioned from oaks (*Quercus* spp.) or piñon (*Pinus edulis*) and juniper (*Juniperus* spp.) to ponderosa pine (*Pinus ponderosa*) forests (Brown 1983). Wolves consistently used areas with some level of tree cover and rarely used areas <1,800 m in elevation (Brown 1983). The average minimum temperature in Alpine, Arizona (near the center of the study area, at 2,454 m elevation) was −2°C and the average maximum temperature

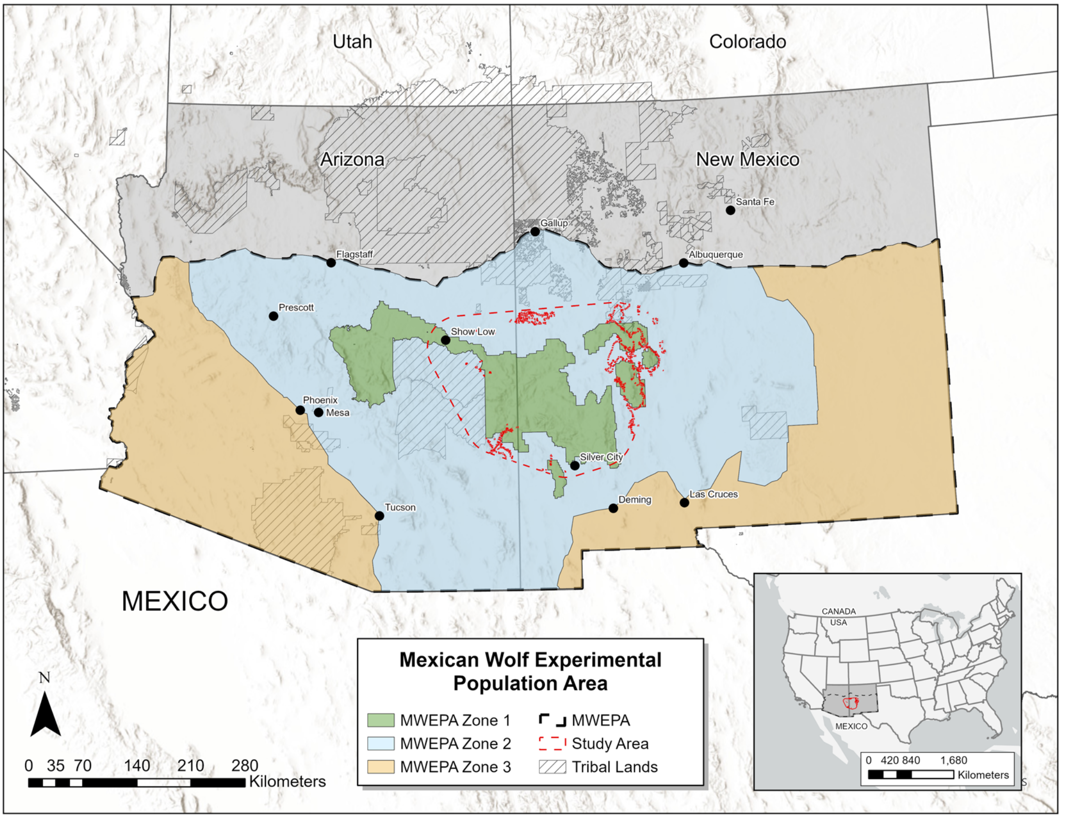

FIGURE 1 The Mexican Wolf Experimental Population Area (MWEPA) in Arizona and New Mexico, USA. We developed resource selection functions (RSF) based on data collected from 1998–2023 to predict habitat associated with Mexican wolf den and rendezvous sites within a study area (red dashed line) overlapping portions of the MWEPA Zone 1 and Zone 2.

was 15°C (Smith et al. 2023). Annual precipitation averaged 53 cm (ranging 18–94 cm depending on the region) and most precipitation occurred during the summer monsoon season (July–August), although high elevations received snowfall in winter (Smith et al. 2023). Elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*O. virginianus couesi*) were the dominant wild ungulate species throughout the study area (Smith et al. 2023). Human density averaged 1.92 people/km^2 (SE = 0.12) in MWEPA Zone 1 (Figure 1; Center for International Earth Science Information Network 2018). Small towns were widely dispersed across the recovery area and roads were typically low-use and unpaved, especially as distances increased from towns.

METHODS

Den and rendezvous site identification

Mexican wolf den and rendezvous sites were located during field surveys as part of ongoing population monitoring activities conducted by the Mexican Wolf Interagency Field Team (IFT), consisting of staff from state, federal, and tribal agencies (Clement et al. 2024). The IFT attempted to maintain at least 2 very high frequency (VHF)- or global positioning system (GPS)-collars in every documented pack and has maintained collars on a high proportion (~50%) of the counted population (USFWS 2023). The IFT determined den and rendezvous sites from 1998–2014 primarily via clusters of VHF-collar locations from aerial or ground-based radio-telemetry surveys with subsequent visual confirmation (e.g., observations of pups, active den holes, or other evidence of rendezvous site activity) in some circumstances (Oakleaf 2022). If the breeding female was radio-collared, observers used the muted or muffled VHF signal (i.e., because she was in a den hole) to confirm denning in a specific location. The IFT performed telemetry surveys to locate VHF-collared wolves weekly via aerial flights and conducted additional telemetry surveys from the ground to supplement the weekly flights. The IFT classified a cluster of telemetry locations as the initial den site based on where telemetry locations of VHF-collared wolves in the same pack localized over a period of 2 weeks during April or May. Crews rarely visited den and rendezvous sites until telemetry locations indicated wolves had left the area to minimize disturbance. Wolves generally move pups to their first rendezvous site when pups are weaned at roughly 8 weeks old, typically in June or July (Ausband et al. 2010, Boyd et al. 2023). The IFT therefore classified movement of the cluster from the initial den site to a subsequent site as either a den move (if pups were ≤10 weeks, based on when the initial den cluster was established) or a rendezvous site.

As the population grew (2014 – present), the IFT prioritized the use of GPS-collars, rather than VHF-collars, as the primary method for monitoring wolf movements. Like the VHF-collar-based clusters, the team classified a cluster of GPS-collar locations as a den when multiple GPS locations of collared wolves in the same pack localized over a 2-week period during April or May. If a breeding female was GPS-collared, the collar would stop transmitting points (i.e., the collar did not have a clear view of the sky because she was in a den hole) until she came out of the den hole, and the cessation of transmissions indicated the start of denning. Clusters would often form regularly at the suspected den once she emerged, along with other collared wolves clustering in the same location. A cluster was classified as a rendezvous site if the cluster of GPS-collar locations moved from the initial (or secondary) den cluster and pups were >10 weeks old. The IFT visited the GPS-collar clusters more frequently than the VHF-collar clusters to obtain early pup counts and to conduct foster operations (i.e., placing captive-born pups in wild wolf dens) and scat sampling (Oakleaf et al. 2023). We were more confident in the accuracy of these den and rendezvous site locations because of the limited error associated with GPS locations relative to VHF locations. The use of weekly aerial VHF locations followed by ground locations, however, adequately identified den and rendezvous sites based on subsequent visual confirmation. Approximately 35% (*n* = 91) of den sites were confirmed by on-the-ground investigation of the VHF- and GPS-based clusters. We used the middle of the cluster of VHF- or GPS-collar locations as a starting point and searched a relatively small area (<200 m) to find the den site and validate the use of clusters for other unvisited den sites. The IFT did not record whether rendezvous sites were visited but generally did not visit these areas because there was not a defined goal for visitation until scat collection from rendezvous sites was initiated in 2022. However, the IFT used clusters to identify rendezvous sites to trap near and routinely captured pups of the year to collar. We used the den and rendezvous sites identified by the IFT from 1998–2023 for subsequent analyses.

Used and available locations

Wolf packs often exhibit high fidelity to dens and rendezvous sites over time (Mech and Boitani 2003, Apollonio et al. 2004, Capitani et al. 2006). If ≥2 known den locations were within 250 m of one another and used by the same pack within or across years, we retained only one location to reduce non-independence among known den sites (Ausband et al. 2010). We used a 250-m buffer because this is the average radius of a rendezvous site for gray wolves in the northern Rocky Mountains (Stenglein et al. 2011) and most Mexican wolf dens used by the same pack were within approximately 200 m of each other. We ranked dens by the accuracy of their location and retained the den with the most accurate location if it was within 250 m of other dens used by the same pack. Den locations identified by the IFT during site visits were ranked highest, den locations identified by GPS cluster that were not visited were ranked second highest, and den locations identified by triangulation from VHF collars and not visited were ranked lowest. We repeated a similar rarefication process for known rendezvous site locations within 250 m of each other if used by the same pack. Rendezvous site locations identified by the IFT during site visits and visual observation were ranked highest, rendezvous sites identified by GPS cluster without site visits were ranked second highest, and rendezvous site locations identified by VHF triangulation without site visits were ranked lowest. We considered the reduced set of known pup-rearing sites as used locations in subsequent analyses.

We defined the spatial extent of den and rendezvous site habitat available to the Mexican wolf population (Martínez-Meyer et al. 2021) by creating a 100% minimum convex polygon (MCP) around all used pup-rearing sites and then buffered this MCP by its approximate radius using the adehabitatHR package (Calenge 2006) in Program R (R Core Team 2022). We then masked out large waterbodies (>1 km^2) and regions identified as unsuitable for Mexican wolves by superimposing a habitat suitability layer created by Martinez-Meyer et al. (2021) and excluding all areas within the MCP that did not overlap this layer (e.g., low elevation desert, areas of high human density; Martínez-Meyer et al. 2021). We considered the remaining area within the buffered MCP as available to the Mexican wolf population throughout our study (1998–2023; Figure 1). We did not use pack-specific territories to define availability for individual packs because we had insufficient data to define individual territories for all packs and years and we wanted our methods to be consistent with those described by Ausband et al. (2010). As a result, we compared the relative frequency of resources used by packs to those available throughout the study area, following a Design 2 resource selection study design (Manly et al. 2002; Thomas and Taylor 1990, 2006). We sampled 100 random locations within the buffered MCP for every 1 used location. We chose a 1:100 used:available ratio after preliminary analysis indicated coefficient estimates stabilized at this sampling intensity (Figure S1; Fieberg et al. 2021, Street et al. 2021).

Habitat predictors

We included a suite of terrain, habitat, and anthropogenic characteristics that we hypothesized influenced the selection of den and rendezvous sites (Figures S2, S3, and S4). Surface roughness and curvature can indicate the capacity of terrain to gather and hold water in areas like wet meadows (Ausband et al. 2010) and steep, rough, terrain may offer protection from predation risk for pups when they are constrained to the den. We therefore used the Shuttle Radar Topography Mission (SRTM; Farr et al. 2007) digital elevation data to extract elevation and calculate vector ruggedness measure (VRM), curvature, and slope at the 30-m resolution. We used VRM to represent surface roughness because it is more independent of slope than other commonly used indices of local terrain variability (e.g., terrain ruggedness index [TRI]; Riley et al. 1999), allowing roughness and slope to represent different characteristics of the terrain (Sappington et al. 2005). We calculated VRM from the SRTM elevation data in program R version 4.2.1 (R Core Team 2022). We used Gaussian curvature to characterize the general curvature and water-gathering capacity of the topography. Gaussian curvature is a product of the minimum and maximum curvatures at a given point of a surface (Minár et al. 2020), where positive values indicate a convex surface (i.e., water-shedding), negative values indicate a concave surface (i.e., water-gathering), and a value of 0 indicates a flat surface. We calculated Gaussian curvature in ArcGIS Pro version 3.1.0 with the Surface Parameters toolbox (Esri, Redlands, CA, USA). We calculated slope from the SRTM digital elevation data in program R version 4.2.1 (R Core Team 2022) using the terra package version 1.6.17 (Hijmans 2022).

Documented water sources may offer more reliable access to water than terrain features capable of holding water, so we identified waterbodies (e.g., lakes, ponds, water tanks) using the National Hydrography Database (U.S. Geological Survey and National Geospatial Program 2023*a*, *b*) and used the distance function in Google Earth Engine (Gorelick et al. 2017) to generate a raster (30-m resolution) representing distance to nearest perennial waterbody (hereafter, distance to water). This variable represented accessibility of reliable water sources across the study area.

We used the Global Human Modification dataset (Kennedy et al. 2019) and the TIGER roads layer (U.S. Census Bureau 2016) to characterize anthropogenic factors hypothesized to influence den and rendezvous site selection. The Global Human Modification dataset ranges 0–1 and represents intensity of human modification of terrestrial lands (1-km^2 resolution) based on 13 factors (e.g., human settlement, agriculture, and infrastructure; Kennedy et al. 2019). We filtered the TIGER roads layer to neighborhood and rural roads (S1400) and 4-wheel drive roads (S1500; U.S. Census Bureau 2016) and used the distance function in Google Earth Engine (Gorelick et al. 2017) to generate a raster (30-m resolution) representing distance to nearest local, rural, or 4-wheel drive road (hereafter, distance to road). Although the TIGER roads layer included residential roads in urban and suburban areas, we excluded areas of high human density from what was considered available to Mexican wolves, so the distance to road variable was primarily composed of rural and 4-wheel drive roads. We focused on rural and dirt roads instead of highways or primary arterial roads because wolves often travel low-use roads (Dickie et al. 2017) and because human activities that may disturb wolf dens and rendezvous sites (e.g., antler gathering, turkey hunting, or other recreational activities) generally occurred in remote regions with primitive roads.

We used the normalized difference vegetation index (NDVI) to represent green leaf biomass (Didan and Munoz 2021). The NDVI measures terrestrial photosynthetic vegetation activity, where higher values are typically associated with areas of higher green leaf biomass like grasslands with little canopy cover (Didan and Munoz 2021). Areas of higher green leaf biomass, in combination with less rugged and more concave terrain, were associated with wet meadows in Idaho (Ausband et al. 2010), and we expected a similar suite of variables could be predictive of areas used by Mexican wolves for rendezvous sites. After masking out clouds, we calculated mean NDVI for the rendezvous site season (mean NDVI from June–August) per year from 2000–2023 using the Moderate Resolution Imaging Spectroradiometer (MODIS) Terra vegetation indices 16-day global 250-m grid (MOD13Q1.061; Didan and Munoz 2021) in Google Earth Engine (Gorelick et al. 2017). We did not mask out conifers when calculating mean NDVI and we acknowledge that tree cover may have influenced our mean NDVI estimates. We resampled the mean NDVI datasets to 30-m resolution to match other terrain and habitat variables and then used a moving-window analysis to calculate the average mean NDVI (hereafter, NDVI) value within a 250-m radius of each pixel (based on the average radius of a rendezvous site). This variable represented the presence of green leaf biomass that Ausband et al. (2010) found was associated with wet meadows. The NDVI varied annually and thus resource availability changed over our study. To control for availability dependence in annual responses to vegetation, we also generated a study area-wide average NDVI value per rendezvous site season by averaging NDVI (hereafter, average NDVI) across the entire buffered MCP per year.

We used the Hansen Global Forest Change dataset (v1.10, 2000–2022) to approximate annual percent tree canopy cover (Hansen et al. 2013). This dataset comprised tree canopy cover in 2000 (30-m resolution), defined as percent canopy closure for vegetation taller than 5 m, and the year that full canopy loss occurred owing to stand-replacement disturbance (Hansen et al. 2013). Using a moving-window analysis in Google Earth Engine (Gorelick et al. 2017), we calculated the average percent canopy cover in 2000 and the total area of canopy loss per year within a 250-m radius of each pixel. We then generated a dataset in Program R (R Core Team 2022) representing annual mean canopy cover (hereafter, canopy cover) by adjusting the average percent canopy cover in 2000 by the proportion of canopy lost per year, as canopy loss accumulated over time from 2000 to 2022. This variable represented forested areas that could provide protection from predators and heat exposure (Trapp et al. 2008) and habitat associated with the distribution of the primary ungulate prey (i.e., elk) in Arizona and New Mexico (Martínez-Meyer et al. 2021, Smith et al. 2023). High-severity wildfires have reduced ponderosa pine forests and increased non-forest vegetation types in Arizona and New Mexico (Woolman et al. 2022), changing mean canopy cover availability over time. We therefore generated a study area-wide average mean canopy cover per year by averaging mean canopy cover (hereafter, average canopy cover) across the entire buffered MCP per year to control for availability dependence in annual responses to vegetation.

We matched the annual NDVI and canopy cover datasets to the year each site was used (and their associated available locations), allowing us to characterize the annual variability of available habitat at the time each den and rendezvous site was used. However, the remotely sensed NDVI and canopy cover data were not available before 2000 and the canopy cover data were also unavailable after 2021. We therefore matched NDVI and canopy cover data from 2000 to pup-rearing sites used from 1998–2000 and canopy cover data from 2022 to pup-rearing sites used from 2022–2023.

Resource selection functions

We assigned a binary value to each used (1) and available (0) location and extracted covariate data at each location, ensuring time-varying covariates were matched to the appropriate year each pup-rearing site was used. We then assigned a weight of 5,000 to available locations and a weight of 1 to used locations following recommendations by Fieberg et al. (2021). We standardized all covariates by centering around their individual means and scaling by 1 standard deviation, and checked for collinearity among covariates. We tested for collinearity among all covariates used in the den and rendezvous site analyses, respectively, and found none were correlated ($|r| < 0.6$). We then fit resource selection functions (RSF; Fieberg et al. 2021) to the data using logistic regression models fitted with the lme4 package (Bates et al. 2015) in Program R (R Core Team 2022).

We analyzed the den and rendezvous site datasets separately because resource selection may differ during the 2 stages of the pup-rearing season. In the denning season, we hypothesized that resource selection for Mexican wolves would be influenced by physical protection, a combination of physical protection and access to reliable water sources, or human disturbance (Trapp et al. 2008, Sazatornil et al. 2016). We therefore developed a set of *a priori* competing models that included different combinations of elevation, slope, surface roughness, canopy cover, distance to water, human modification, and distance to road as covariates in the den RSF model set (Table 1). Because canopy cover changed over the course of our study, we modeled canopy cover as a function of the annual average canopy cover, effectively allowing the strength of selection to vary nonlinearly based on average availability each year (i.e., functional response; Matthiopoulos et al. 2011). In the rendezvous site season, we hypothesized that resource selection for Mexican wolves would be influenced by the presence of wet meadows (following Ausband et al. 2010), physical protection and access to water (including wet meadows), or human disturbance (Sazatornil et al. 2016). We developed *a priori* competing models for the rendezvous site RSF that included elevation, surface roughness, surface curvature, NDVI, distance to water, human modification, and distance to road as

TABLE 1 List of competing logistic regression models used to estimate resource selection functions (RSF) for Mexican wolf pup-rearing (den or rendezvous site) site selection in Arizona and New Mexico, USA, 1998–2023. Linear predictors included elevation, slope, terrain roughness (roughness), annual percent canopy cover (cover), distance to nearest waterbody (dist. to water), an index of human modified landscape (human), distance to nearest road (dist. to road), surface curvature (curvature), and annual mean normalized difference vegetation index (NDVI; averaged over the rendezvous site season). Functional responses were included on canopy cover and NDVI predictors where coefficients were modeled as a function of the annual average percent canopy cover (avg cover) and annual average NDVI (avg NDVI), respectively.

Pup-rearing site	Model	Linear predictors
Den	Null	Intercept only
	Protection	Elevation + elevation^2 + slope + roughness + cover + cover:avg cover[a]
	Protection and water	Elevation + elevation^2 + slope + roughness + cover + cover:avg cover[a] + dist. to water[b]
	Human disturbance	Human + dist. to road[b]
	Global	Elevation + elevation^2 + slope + roughness + cover + cover:avg cover[a] + dist. to water[b] + human + dist. to road[b]
Rendezvous site	Null	Intercept only
	Wet meadows[c]	Roughness + curvature + NDVI + NDVI:avgNDVI[a]
	Protection and water	Elevation + elevation^2 + roughness + curvature + NDVI + NDVI:avgNDVI[a] + dist. to water[b]
	Human disturbance	Human + dist. to road[b]
	Global	Elevation + elevation^2 + roughness + curvature + NDVI + NDVI:avgNDVI[a] + dist. to water[b] + human + dist. to road[b]

[a]Model included a functional response to changes in the available average canopy cover or average NDVI over time.

[b]Models were built with and without natural log transformations on distance to nearest waterbody and roads. We used corrected Akaike's Information Criterion (AIC_c) to assess which model was more supported. Models without a natural log transformation were included in the final model set owing to lower AIC_c values.

[c]Model represents a modified version of the Ausband et al. (2010) model, which included a measure of terrain roughness, surface curvature, and NDVI when predicting habitat for gray wolf rendezvous sites in Idaho, USA.

covariates (Table 1). Like the den RSF analyses, we included a functional response for annual variation in average NDVI in the rendezvous site RSF analyses (Matthiopoulos et al. 2011). For both den and rendezvous site RSF analyses, we included a quadratic term on elevation to account for potential nonlinear responses (i.e., use of higher but not the highest elevations in the region). We also considered a natural log transformation on distance to water and distance to road to account for potential attenuation in the effect to water and roads as distance increased. Finally, we used corrected Akaike's Information Criterion (AIC_c) to select the best supported model for the den and rendezvous site RSF analyses. We interpreted slope coefficients of the underlying RSFs as statistically significant if the P-value ≤ 0.05.

We mapped the best supported den and rendezvous site models across the study area (buffered MCP). Specifically, we exponentiated the linear component of each logistic regression, excluding the intercept, and predicted the relative probability of selection across the extent of the study area at a 30-m resolution. We reclassified the predictions into 10 equal-area bins where bin 10 represented the most suitable conditions for Mexican wolf dens and rendezvous sites (Ausband et al. 2010). Finally, we used the Boyce et al. (2002) method for K-fold cross-validation to assess the predictive capacity of the top models (refer to Supporting Information for full details).

RESULTS

From 1998–2023, we documented 255 den sites used by 77 different Mexican wolf packs (277 pack-years) in Arizona and New Mexico, USA. From 2005–2023, we documented 129 rendezvous sites used by 44 different packs (84 pack-years). Of those, 211 den sites and 122 rendezvous sites were included in the final RSF analyses. After excluding low-elevation regions determined to be unsuitable for Mexican wolves (Martínez-Meyer et al. 2021), the elevation of available locations in the study area ranged 1,023–3,296 m.

The global model was best supported in the den RSF analysis, carrying 99% of the model weight in the model set (Table 2). Elevation, elevation^2, slope, roughness, distance to water, and distance to road affected selection of den sites by Mexican wolves. Specifically, the relative probability of selection increased with elevation until approximately 3,100 m, then declined (Table 3). This means that for every 323.75-m (1 SD) increase in elevation, the odds of selection increased by a factor of 5.58, until approximately 3,100 m, at which point the odds of selection decreased by a factor of 0.75 for every 323.75-m increase in elevation. Mexican wolves also selected for steeper slopes and rougher terrain, where the odds of selection increased by 89% for every 9.63 degree increase in slope and by 21% for every 0.22 increase in vector ruggedness measure (Table 3). Relative probability of den site selection decreased with increasing distance to the nearest waterbody, where the odds of selection decreased by 48% for every 1.47-km increase in distance from water (Table 3). Conversely, distance to nearest road had a positive effect on Mexican wolf selection, where the odds of selection increased by 21% for every 1.86-km increase in distance from roads (Table 3), indicating wolves were more likely to select habitat for denning farther from secondary roads. The magnitude of the effect of elevation was largest on selection, followed by slope and distance to water (Table 3).

The protection and water model was best supported in the rendezvous site RSF analysis, carrying 78% of the model weight in the model set (Table 2). Mexican wolf rendezvous site resource selection was influenced by elevation, elevation^2, distance to water, and a functional response to NDVI (Table 3). Like the top den RSF, relative probability of selection increased with increasing elevation until approximately 2,800 m, then declined, and wolves were less likely to select areas farther from water during the rendezvous site season (Table 3). More specifically, the odds of selection increased by a factor of 15.57 for every 319.97-m increase in elevation until approximately 2,800 m, then decreased by a factor of 0.51 for every 319.97-m increase in elevation. The odds of selection decreased 33.69% for every 1.46-km increase in distance from water. In addition, the relative probability of

TABLE 2 Logistic regression models representing resource selection functions for Mexican wolf den and rendezvous sites in Arizona and New Mexico, USA, 1998–2023, ranked by corrected Akaike's Information Criterion (AIC_c) from lowest to highest.

Pup-rearing site	Model	AIC_c	ΔAIC_c	Model weight
Den	Global	5,553.81	0.00	0.99
	Protection and water	5,563.58	9.77	0.01
	Protection	5,617.28	63.47	0.00
	Human disturbance	5,947.56	393.74	0.00
	Null	5,961.64	407.83	0.00
Rendezvous site	Protection and water	3,242.74	0.00	0.77
	Global	3,245.14	2.41	0.23
	Wet meadows	3,396.10	153.36	0.00
	Human disturbance	3,447.67	204.94	0.00
	Null	3,447.86	205.12	0.00

TABLE 3 Estimated coefficients, standard errors (SE), and *P*-values of best supported resource selection functions for Mexican wolf den and rendezvous site selection in Arizona and New Mexico, USA, 1998–2023. All coefficients were estimated using standardized covariates.

Pup-rearing site	Parameter	Estimate	SE	*P*
Den	Elevation*	1.72	0.19	<0.001
	Elevation^2*	−0.29	0.08	<0.001
	Slope*	0.64	0.07	<0.001
	Roughness*	0.19	0.09	0.036
	Distance to water*	−0.65	0.09	<0.001
	Canopy cover	0.06	0.07	0.351
	Human modification	−0.21	0.19	0.269
	Distance to road*	0.19	0.07	0.004
	Canopy cover:Average canopy cover	0.05	0.04	0.247
Rendezvous site	Elevation*	2.75	0.42	<0.001
	Elevation^2*	−0.66	0.17	<0.001
	Roughness	0.08	0.10	0.413
	Surface curvature	0.12	0.09	0.197
	NDVI	0.02	0.12	0.846
	Distance to water*	−0.41	0.11	<0.001
	NDVI:Average NDVI*	−0.18	0.08	0.026

*$P \leq 0.05$.

selection declined with increasing NDVI when the average NDVI was higher, meaning selection for areas with higher NDVI was weaker in years when availability was higher (i.e., odds of selection decreased 16% for every 0.03 increase in average NDVI; Table 3). The magnitude of the effect of elevation and elevation^2 was largest on rendezvous site selection, followed by distance to water. The global model was the second-best supported model, with 22% of the weight, and contained the same significant variables as those in the top model.

Our models were highly predictive considering we included only 221 used den locations and 122 used rendezvous site locations in the respective models (Figure S5). Based on the 5-fold cross-validation analysis, the den RSF was on average more predictive of used den locations (mean r_s = 0.90, SE = 0.025) than the rendezvous site RSF was of used rendezvous site locations (mean r_s = 0.81, SE = 0.045; Table S1). After predicting the top den and rendezvous site RSFs and binning the predictions into 10 equal-area bins, the most suitable den and rendezvous site habitat (bin 10) comprised 5,682.85 km^2 (9.99%) of the land area considered suitable for Mexican wolves within the 56,866.51 km^2 we predicted across (Figure 2). This corresponded to 12.27% of the land area within the defined study area (Figure 2).

DISCUSSION

Success of the Mexican wolf recovery strategy is measured by population growth, survival of released captive wolves, and genetic health of the population (USFWS 2022). With the population growing by 23% in 2022 (USFWS 2022), there is a clear need for more efficient methods to locate and monitor Mexican wolves as the

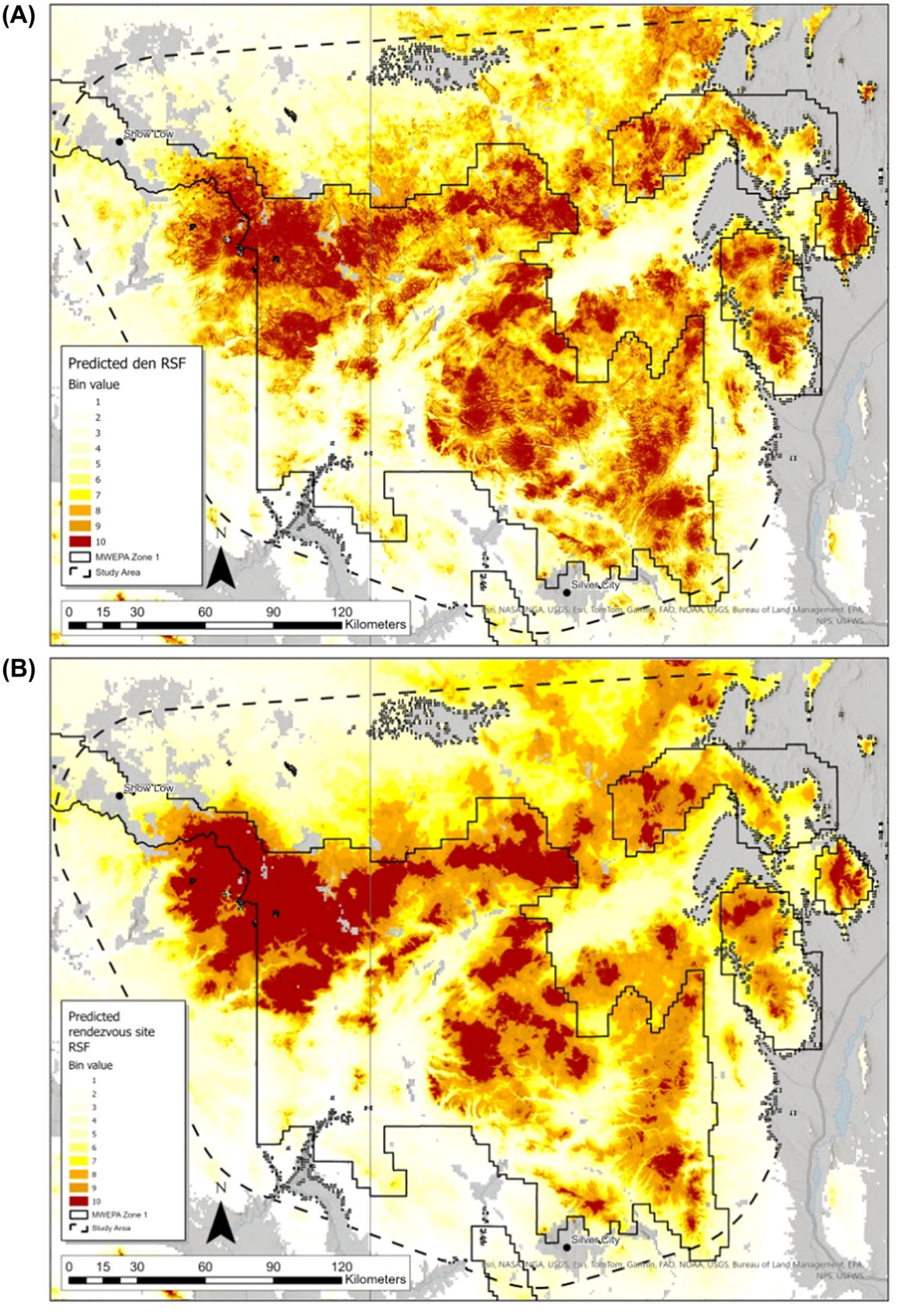

FIGURE 2 Predicted (A) den and (B) rendezvous site habitat for Mexican wolves in the occupied portion of the Mexican Wolf Experimental Population Area (MWEPA) in Arizona and New Mexico, USA, 1998–2023. The top den and rendezvous site resource selection functions (RSF) were predicted across the study area and discretized into 10 equal-area bins where bin 10 represented the most suitable habitat and bin 1 represented the least suitable habitat.

population expands (Russo et al. 2023). We developed resource selection functions to predict highly suitable den and rendezvous site habitat to help guide future monitoring of the Mexican wolf population. Consistent with our expectations, we found site characteristics associated with physical protection and reliable access to water were most important in characterizing pup-rearing habitat for Mexican wolves. In addition, we found denning sites to be more predictable than rendezvous sites for Mexican wolves.

Terrain characteristics tended to have the greatest influence on selection of den and rendezvous sites. Mexican wolves selected denning sites at higher elevations that had steeper slopes and rougher terrain, relative to what was available. They also selected locations at higher elevations for rendezvous sites, which likely reduced exposure to extreme summer temperatures. Mid- to high elevations were also associated with elk calving (May - June; Wallace and Krausman 1992) in the recovery area, which would allow wolves easier access to their primary prey source when wolves were relatively anchored to pup-rearing sites (Benson et al. 2015, Smith et al. 2023). Pups are also particularly vulnerable to predation risk and disturbance from humans during the denning season (Sazatornil et al. 2016). Steeper, rougher terrain may have limited predator access to den sites and provided more protective structures (e.g., rock crevices, boulder piles) and easier tunneling for dens compared to flatter, gentler terrain (Benson et al. 2015, Llaneza et al. 2018). Finally, the locations of rendezvous sites were likely influenced by the location of den sites owing to the limited mobility of pups, which may further explain the importance of elevation in the rendezvous site model. For instance, of the dens and rendezvous sites located within the same year and used by the same pack (n = 115 den–rendezvous site pairings) between 2015 and 2023, >50% (n = 59 pairings) were located within 2.5 km of each other and 80% (n = 92 pairings) were within 5 km of each other.

The relative probability of selecting den and rendezvous sites declined with increasing distance to nearest waterbody, indicating that reliable access to water was an important predictor of pup-rearing habitat for Mexican wolves. Conversely, we did not find evidence that terrain features associated with water retention (roughness and curvature) were predictive of rendezvous sites. Access to reliable water is likely important during the denning season because lactation demands are highest for the breeding female at this time but pups cannot be left unattended for long (Packard 2003, Benson et al. 2015). In the rendezvous site season, access to reliable water becomes important for the pups as they begin to consume high-protein diets but still have limited mobility (Unger et al. 2009, Ausband et al. 2010). Permanent waterbodies, like ponds, water tanks, and springs, may hold water more consistently throughout the pup-rearing season than areas simply capable of holding water. Even when ephemeral water sources were periodically available during the rendezvous site season following monsoonal rains (Nolin and Hall-McKim 2006), reliable access to water via permanent water sources appears to be an important feature of rendezvous site habitat. These results highlight that access to water is a common factor influencing selection of pup-rearing sites across wolf populations, even if the exact source of water differs depending on the species and region (e.g., water tanks for Mexican wolves vs. wetlands and wet meadows for gray wolves; Theuerkauf et al. 2003, Unger et al. 2009, Ausband et al. 2010).

The influence of green leaf biomass (NDVI) on rendezvous site selection varied by its average availability each summer. Namely, the relative probability Mexican wolves selected greener areas declined as the overall average green leaf biomass increased across years, indicating that wolves select more strongly for green leaf biomass when its availability is limited. In Idaho, the influence of green leaf biomass was associated with wet meadows and wolf rendezvous sites when in combination with the additive effects of terrain roughness and curvature (Ausband et al. 2010). But in our study area, terrain variables did not influence selection of rendezvous sites, suggesting the importance of green leaf biomass was not tied to wet meadows specifically. We hypothesize the influence of NDVI was instead related to its association with the general distribution of elk (Smallidge et al. 2010) and precipitation from monsoonal rains (Birtwistle et al. 2016) in Arizona and New Mexico. Prey and water may have been more widely distributed in greener years, potentially explaining the weaker selection for green leaf biomass by Mexican wolves compared to their Rocky Mountain counterparts.

Contrary to expectation, factors associated with human disturbance had the smallest impact on den and rendezvous site selection for Mexican wolves. Human-related risk can strongly influence wolf distributions and selection of pup-rearing sites in some populations (Sazatornil et al. 2016), but we found limited evidence that Mexican wolves avoided areas modified by humans when selecting pup-rearing locations. This finding is consistent with research on gray wolves in the Northern Rocky Mountains, which found road density and harvest did not influence use of highly suitable habitat for pup-rearing (Jacobs and Ausband 2018). The strength of resource selection can vary across spatial scales (Johnson 1980); by avoiding human-dominated areas at higher orders of selection (Martínez-Meyer et al. 2021), the strength of avoidance may have been dampened at lower orders of selection (e.g., selection of pup-rearing sites) for Mexican wolves (Sazatornil et al. 2016, Ciucci et al. 2018). We also masked out areas of high human density when defining availability in our study, which likely contributed to this apparent scaling effect. Alternatively, the relative importance of higher, steeper, rougher terrain in the den model may reflect selection of refuge habitat (Capitani et al. 2006, Llaneza et al. 2018) that was not sufficiently captured by the human modification variable. Mexican wolves selected areas farther from roads during the denning season, suggesting that they avoided rural and 4-wheel drive roads when pups are most vulnerable and human activities associated with antler gathering and turkey hunting are high and perhaps dangerous to wolves. We found no evidence of an effect of distance to nearest road during the rendezvous site season when human activity patterns were perhaps more benign (e.g., hiking and fishing). Wolves frequently use linear features (Zimmermann et al. 2014, Dickie et al. 2017) and access to low-use roads likely facilitated travel to and from pup-rearing sites when hunting. By denning farther from roads but not avoiding them during the rendezvous site season, this pattern may suggest wolves balance the risks and rewards of roads differently depending on the vulnerability of pups and adults over the course of the summer.

As expected, denning locations were more predictable than rendezvous sites for Mexican wolves. Highly suitable denning habitat appears to be more specific and thus predictable compared to rendezvous site habitat owing to the importance of multiple terrain and anthropogenic features associated with dens. Water was also more widely available during the rendezvous site season owing to frequent monsoonal rains, likely contributing to the lower predictability of the rendezvous site model compared to the den model. Wolf pups are also relatively immobile during the denning season; thus, selecting an optimal pup-rearing site may be more critical during this time compared to the remainder of the summer when pups can travel with the pack for short distances. Finally, the smaller sample size in the rendezvous site model may have also contributed to lower predictive success.

Future development

Although our top den and rendezvous site RSFs were predictive of pup-rearing sites used by Mexican wolves, our definition of availability may have influenced results. We drew available points from the entire study area because we were interested in the availability and selection of pup-rearing sites across the occupied range of the Mexican wolf population and because we lacked information on all annual, pack-specific territory boundaries. Our analysis therefore assumed the entire study area was available to all wolf packs (following a Design 2 resource selection study design; Manly et al. 2002; Thomas and Taylor 1990, 2006). However, wolves are territorial and once a territory is established, wolves generally only use locations within their pack's defined home range (Packard 2003); site conditions available to an individual pack may differ compared to those across the entire study area. The definition of availability can strongly influence estimates in an RSF (Manly et al. 2002) and it is possible our results would differ if we had drawn available locations from pack-specific territories. Future work focusing on availability within individual pack territories when predicting suitable pup-rearing habitat would provide helpful information. Accounting for territory-specific availability would allow researchers to estimate pack-specific variation in selection of pup-rearing sites that may be driven by differences in availability (Thomas and Taylor 1990, 2006).

Our choice of predictors and imperfect detection of den and rendezvous sites may have further influenced our results. The distance to nearest water variable was based on permanent waterbodies documented in the National Hydrography Database (U.S. Geological Survey and National Geospatial Program 2023*a*, *b*). However, some water sources (e.g., dammed streams and drinkers for livestock) may have gone undocumented or became unavailable over time (e.g., dried up). Missing or non-existent waterbodies would have affected our distance measurements and potentially influenced our results. In addition, the strength of selection for waterbodies may vary spatially depending on the density of waterbodies within a wolf pack's territory. We did not account for this in our analyses because we did not know the spatial scale at which waterbody density could influence den and rendezvous site selection. Several predictors were time-varying, even within a season (e.g., NDVI). Although we included functional responses to these variables at an annual timescale, wolves use multiple rendezvous sites within a single season (Ausband et al. 2016). Accounting for dynamic environmental predictors at finer timescales may further improve the predictive capacity of our RSFs (Milanesi et al. 2020). The distribution of abundant prey may also influence den and rendezvous site selection (Benson et al. 2015). Elk are considered the primary prey source for Mexican wolves (Smith et al. 2023), but we were unable to incorporate associated variables into our models given the large spatial extent of the Mexican wolf experimental population area and available elk data. Variation in prey availability and diversity, including domestic prey, may further influence selection (Milanesi et al. 2019, 2022; Zabihi-Seissan et al. 2022). Inclusion of such variables may improve RSF predictions even further. In addition, variables more directly associated with human-related risk (e.g., human settlements, recreational use patterns) may influence selection of pup-rearing sites more than the variables we used in our analyses.

CONSERVATION IMPLICATIONS

We developed resource selection functions to identify highly suitable den and rendezvous site habitat for Mexican wolves. Our models can streamline future monitoring of the Mexican wolf population in multiple ways. First, our models identify areas across the landscape that have the highest relative probability of being selected by wolves at specific times of year. If managers focus surveys in the highest suitable habitat class (bin 10), our models can reduce the search area for Mexican wolf dens and rendezvous sites by approximately 90% of the area otherwise identified as suitable for Mexican wolves. This would be particularly helpful when searching for uncollared wolves as the Mexican wolf population expands into new areas. Second, our models will help managers locate active dens and rendezvous sites, increasing the probability of detecting all pack members at these sites because every adult in the pack returns periodically to guard and provision the pups (Packard 2003). When coupled with non-invasive genetic surveys (e.g., sampling scats; Stenglein et al. 2010), locating dens and rendezvous sites can aid in documenting population growth and survival of released captive wolves. Den and rendezvous site surveys can also be used in an occupancy modeling framework to monitor the distribution and abundance of wolf packs using a variety of sampling methods and data streams (Bassing et al. 2019; Ausband et al. 2014, 2023). These methods may be particularly important in Mexico where recovery and counts of Mexican wolves is dependent upon access to private land and varying levels of landowner cooperation. Sampling in areas where access is allowed by private landowners may provide for robust population estimates across a patchwork of accessible and inaccessible areas. Finally, our model predictions show a limited portion of the Mexican wolf recovery area is considered highly suitable den and rendezvous site habitat, which may influence the distribution and density of Mexican wolf packs in the United States. If Mexican wolves do not show plasticity in their pup-rearing habitat requirements (e.g., not selecting sites in lower bins as density increases; O'Neil et al. 2019) and are constrained by the relatively extreme environmental changes across elevations (e.g., desert habitat in lower elevations), there may be a limit to how many reproductive wolf packs can successfully occupy the recovery area.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Animals were handled under USFWS permits and protocols (permit number TE091551) in accordance with the Endangered Species Act.

DATA AVAILABILITY STATEMENT

Den and rendezvous site location data are sensitive. The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions. Complete data are available to qualified researchers by contacting the Mexican Wolf Field Projects Coordinator at U.S. Fish and Wildlife Service.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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