



## Management and Conservation Article

# Surveying Predicted Rendezvous Sites to Monitor Gray Wolf Populations

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**ABSTRACT** We used rendezvous site locations of wolf (*Canis lupus*) packs recorded during 1996–2006 to build a predictive model of gray wolf rendezvous site habitat in Idaho, USA. Variables in our best model included green leaf biomass (Normalized Difference Vegetation Index), surface roughness, and profile curvature, indicating that wolves consistently used wet meadow complexes for rendezvous sites. We then used this predictive model to stratify habitat and guide survey efforts designed to document wolf pack distribution and fecundity in 4 study areas in Idaho. We detected all 15 wolf packs (32 wolf pack-yr) and 20 out of 27 (74%) litters of pups by surveying <11% of the total study area. In addition, we were able to obtain detailed observations on wolf packs (e.g., hair and scat samples) once we located their rendezvous sites. Given an expected decrease in the ability of managers to maintain radiocollar contact with all of the wolf packs in the northern Rocky Mountains, rendezvous sites predicted by our model can be the starting point and foundation for targeted sampling and future wolf population monitoring surveys.

**KEY WORDS** *Canis lupus*, gray wolf, monitoring, northern Rocky Mountains, rendezvous site, resource selection function, stratification.

Monitoring large carnivores is notoriously difficult because they tend to be elusive, occur in low densities, and can live in remote and inaccessible terrain where surveying is difficult (Long and Zielinski 2008). Further, because many large carnivores are territorial (i.e., maintaining exclusive use of home ranges, excluding conspecifics; Powell 2000), the challenge of locating an individual, or even sign of an animal, or group of social animals within a large territory can be daunting.

Radiotelemetry is an effective tool for monitoring large carnivores where funding and manpower are sufficient to collar and track a large proportion of a population. Radiotelemetry has been used almost exclusively for monitoring the reintroduced population of gray wolves (*Canis lupus*) in Idaho, USA (Bangs and Fritts 1996). The United States Fish and Wildlife Service (USFWS) sought to maintain  $\geq 1$  radiocollared member within each wolf pack, allowing documentation of wolf abundance and reproductive success through regular relocations. This monitoring effort has been expensive, with annual budgets for wolf recovery in the northern Rocky Mountains (NRM) of  $\geq$  \$2 million (E. Bangs, USFWS, personal communication). Maintaining such intense monitoring has become more difficult as the wolf population has grown and expanded since reintroduction ( $\geq 1,645$  wolves; USFWS et al. 2009). Idaho will be required to report annual wolf population size and distribution for 5 years following removal of wolves from the Endangered Species list (USFWS 2009). An expected decrease in federal funding following delisting, however, will compound the difficulties

of monitoring wolves in Idaho with traditional capture and radiotelemetry techniques.

Surveying for animal populations at a time of year when movements are constricted and animals are congregated (e.g., elk [*Cervus elaphus*] on winter range; Samuel et al. 1987) can increase efficiency of population monitoring techniques. The habits of reproductively active wolf packs provide such an opportunity because, during pup-rearing, reproductive packs are constrained in their movements and individuals in the pack congregate at the pup-rearing site (Packard 2003). Thus, the ability to find pup-rearing sites would allow collection of information needed for monitoring. Trapp (2004) identified broad areas of denning habitat for wolves in Idaho, but the breadth and generality of such areas preclude using them as predictors of den sites. Furthermore, surveying for wolves during denning season is difficult because wolves are typically not responsive to howling at that time of year and both pup and alpha female movements are constrained to the den site (Harrington and Mech 1982, Packard 2003). Once pups are weaned but still too small to travel with adults, the pack will relocate the pups to a rendezvous site where they remain while adults leave to hunt and return with food (Joslin 1967, Mech and Boitani 2003). Wolf packs with pups will typically occupy a rendezvous site for several weeks, occasionally moving to new rendezvous site locations until the end of summer when pups are large enough to travel with the pack (Mills et al. 2008).

Habitat characteristics associated with rendezvous sites have not been well documented. Wolf rendezvous sites in Poland typically contained glades, although this term was

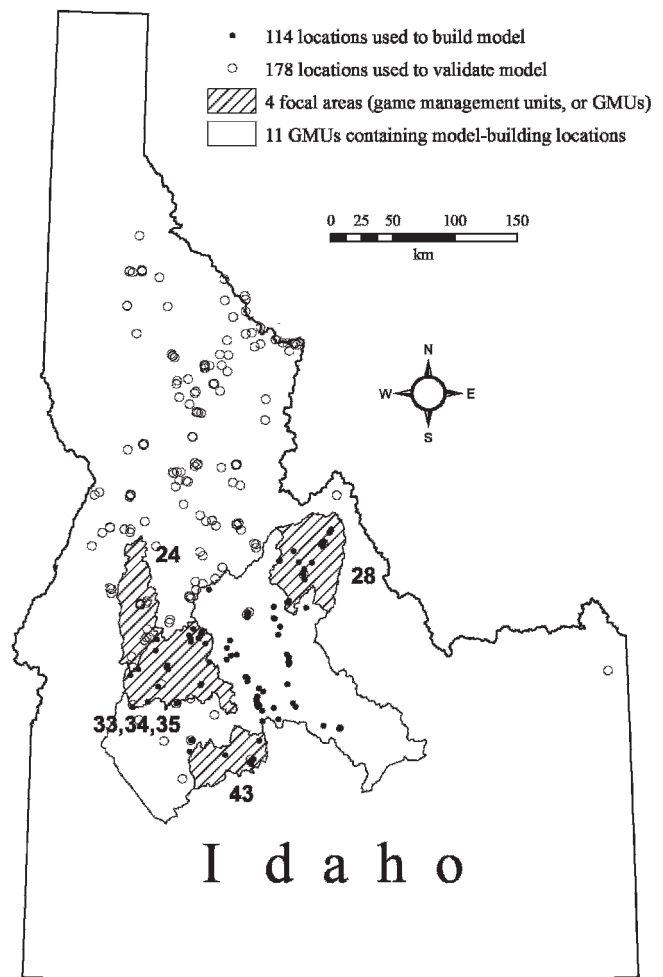
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undefined by the authors, and in eastern and midwestern North America wolves commonly use meadows for rendezvous sites (Joslin 1967, Kolenosky and Johnston 1967, Unger 1999, Theuerkauf et al. 2003). Biologists have observed similar patterns and general use of meadows for wolf packs in the NRM (J. Holyan, Nez Perce Tribe [NPT], unpublished data). Unger (1999) found wolves in Wisconsin and Minnesota, USA, selected wetland habitat (hereafter, wet meadows) for rendezvous sites and hypothesized this was because young pups are unable to travel far and require ample water to process a diet high in protein. Unger (1999) also hypothesized dense grasses at wet meadows decreased detection of pups by intruders. Conceivably, wolves could also select wet meadows because they provide abundant small mammal and insect prey for pups and because the lack of overstory vegetation and loud, swift-moving water could permit acoustic communication between pups and adults and facilitate detection of intruders.

Though several investigators have described wolf rendezvous sites generally, none have attempted to predict locations of rendezvous sites based on habitat and landscape characteristics (Joslin 1967, Kolenosky and Johnston 1967, Unger 1999). Such a predictive model could be used to locate rendezvous sites and serve as a base for wolf population survey efforts. In addition, surveying at predicted rendezvous sites could allow collection of genetic material (scats and hairs) from most pack members, yielding valuable population metrics ranging from pack size and abundance to measures of genetic diversity. We hypothesized that wolves in Idaho, like those in Ontario, Canada, and Minnesota and Wisconsin, would select wet meadows for rendezvous sites, despite size, abundance, and distribution of wet meadows being strongly restricted by mountainous terrain. Specifically, we predicted wolves would select areas for rendezvous sites that were dominated by grasses with little overstory canopy, were topographically flat, and held abundant water during summer months. Our goals were to 1) develop and test a model for predicting rendezvous sites of wolves in Idaho, and 2) use model predictions of rendezvous site habitat to effectively and efficiently document wolf pack distribution and fecundity.

## STUDY AREA

We modeled rendezvous sites for 115,219 km<sup>2</sup> of occupied wolf range in Idaho using historic rendezvous site location data from 11 Game Management Units (GMUs 27, 28, 33, 34, 35, 36, 36A, 36B, 39, 43, 50; Idaho Department of Fish and Game [IDFG] 2007) that represented the core area of wolf reintroduction and early colonization (Fig. 1). To field-test predictions of our model, we chose 4 study areas in central Idaho (GMUs 24, 28, 33, 34, 35, 43; Fig. 1) that had established wolf populations and reasonably good access to facilitate our field testing. The 4 study areas were mountainous and dominated by a mix of ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), and spruce (*Picea engelmannii*) forests and sagebrush (*Artemisia tridentata*) steppe. Annual precipitation ranged from 89 cm to



**Figure 1.** Map of Idaho, USA, and gray wolf rendezvous site locations we used to build a predictive wolf rendezvous site habitat model. Hatched areas are the 4 study areas where we field-tested the predictive model, 2007–2009. Current wolf distribution roughly extends from the southernmost study area through the entire state to the Canadian border on the north.

178 cm, and temperatures ranged from  $-34^{\circ}\text{C}$  in winter to  $38^{\circ}\text{C}$  in summer (Western Regional Climate Center 2009).

## METHODS

Wolves in Idaho were either radiocollared when reintroduced (1995 and 1996 only) or more typically captured in foot-hold traps and fitted with radiocollars (USFWS et al. 2000–2009). Monitoring of radiocollared wolves from 1996 to 2006 allowed observers to record the location of 300 rendezvous sites (some sites were used by packs  $\geq 1$  yr) from the air during radiotelemetry flights and from the ground when conducting pup counts for radiocollared packs.

We estimated wolf pack abundance and number of litters produced by monitoring radiocollared wolves in our 4 study areas. Wolves were captured and radiocollared as part of annual monitoring by IDFG and NPT; each pack had  $\geq 1$  animal fitted with very high frequency or Global Positioning System radiocollars (USFWS et al. 2001–2006). During pup-rearing season (generally 1 Jun–15 Aug), observers located wolves at rendezvous sites during biweekly radiotelemetry flights. Ground searches conducted during denning

and pup-rearing seasons, based on aerial radiotelemetry locations, allowed observers to confirm locations of dens and rendezvous sites and to document numbers of pups and pack sizes for wolves inhabiting our 4 study areas.

We used habitat and landscape characteristics at 122 known rendezvous sites distributed across 11 GMUs that represented the core area of wolf reintroduction and early colonization (Fig. 1) to develop a predictive model of rendezvous site habitat (Manly et al. 2002, Johnson et al. 2006). If 2 known rendezvous site locations were within 100 m of one another, we randomly excluded one location to ensure independence among used sites, resulting in 114 points used to build our model. To determine habitat availability and to ensure sites were truly representative of the habitat available to wolves for establishing rendezvous sites, we randomly chose more than twice the number of used points ( $n = 244$ ), within the 11 GMUs, excluding areas  $>2,765$  m in elevation because no rendezvous site has been found above this elevation in Idaho (C. Mack, NPT, unpublished data). We also excluded from analyses random points that fell on large bodies of water.

At each used and available point, we measured habitat and landscape characteristics with a digital elevation model and Landsat 7 TM imagery (15-m<sup>2</sup> grain) and identified variables that we expected would be consistent with wet meadows. Specifically, we used green leaf biomass (Normalized Difference Vegetation Index [NDVI]) as a measure of greenness, where high values indicated areas of grass with little overstory canopy. We calculated NDVI using the algorithm provided in ERDAS Imagine (Norcross, GA) version 9.3.2, and we calculated surface roughness and profile curvature using ArcGIS functions surface roughness and curvature, respectively. We also used profile curvature and surface roughness as indicators of the capacity of terrain to gather and hold water. A negative value for profile curvature indicated a concave, water-gathering topography, whereas a positive value indicated a convex, water-shedding topography. A high profile curvature value indicated a topographically variable landscape, whereas a low value indicated the low topographic variability characteristic of flat meadows. We merged all imagery to create one high-resolution color image (pan-sharpened) at 15-m<sup>2</sup> pixels.

We used logistic regression across used and available sites to create competing resource selection functions (RSFs) for predicting suitable locations for rendezvous sites based on all combinations of our 3 variables (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). For each model, the probability an area contained suitable rendezvous site habitat was predicted by:

$$\text{logit}(\pi) = \beta_0 + \beta_1 x_1 + \dots + \beta_k x_k, \quad (1)$$

where  $\pi$  represents the probability of being a rendezvous site and  $\beta_1, \dots, \beta_k$  are estimated regression coefficient(s). We used Akaike's Information Criterion (AIC) to evaluate relative support for each model and assessed model likelihood given the data using model weight ( $w_i$ ; Burnham and Anderson 2002).

We translated the model with the lowest AIC into a spatially explicit model that could be linked to a Geographic Information System (GIS) as an RSF:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k), \quad (2)$$

where  $w(x)$  represents relative suitability of a location as a rendezvous site,  $x_1, x_2, \dots, x_k$  represent values for vegetation and topography variables generated from a moving-window analysis for each pixel, and  $\beta_1, \dots, \beta_k$  are model parameters estimated from logistic regression (Boyce et al. 2002, Manly et al. 2002, Johnson et al. 2006). We applied  $\beta$ -coefficients from equation 1 to GIS layers identified in model selection in ArcView 9.2 Spatial Analyst. The resulting GIS map represented the relative suitability as rendezvous site habitat.

To test model predictions, we evaluated ability of the model to predict 178 rendezvous site locations not used to build the model. We categorized  $w(x)$  values for each 15-m<sup>2</sup> pixel in our study area into 10 classes of equal area that represented increasing predicted suitability as a rendezvous site (Boyce et al. 2002). We regressed the proportion of 178 independent historical rendezvous sites not used to build the model that geographically fell into each  $w(x)$  class against the proportion of sites used to build the model in each  $w(x)$  class and used squared correlation ( $R^2$ ) to evaluate model fit (Johnson et al. 2006). A model with good predictive abilities should show similar patterns between data used to build the model and independent data used to test the model, have a high validation  $R^2$  value, a slope not different from 1, and an intercept not different from zero (Johnson et al. 2006). A model with poor predictive ability would be no better than random and, in our case, have 10% of rendezvous site locations in each class (Johnson et al. 2006).

After constructing and testing our model against independent data, we used our predictive model to locate wolf pack rendezvous sites in our study areas. From approximately 15 June to 20 August 2007–2009, we surveyed predicted rendezvous site locations in the top 3 equal-area classes once per summer throughout our 4 study areas, with the exception of sites on private lands. We surveyed only the top 3 equal-area classes because of time and logistical constraints. We surveyed only sites with contiguous patches  $\geq 1.0$  ha and did not survey GMUs 24 and 43 in 2009.

At each site a technician gave a series of howls (Harrington and Mech 1982); if wolves responded by howling, technicians attempted to obtain a visual observation. If they did not detect wolves after howling, technicians surveyed for wolf sign along the perimeter of the site where daybeds and high-use areas are commonly found and on trails leading away from or through the site. If a potential site was too large to survey its entire perimeter and all trails, 2 technicians conducted sign surveys in the site for 30 minutes. Predicted rendezvous sites were sometimes large meadow complexes encompassing several square kilometers. We divided such sites into 1.6-km<sup>2</sup> blocks and technicians surveyed alternating blocks because we assumed unsurveyed portions were within the broadcast range of technicians' howls (Harrington and Mech 1982). When

**Table 1.** Total number of sites surveyed, type of sign, and number of litters detected during field testing of predicted gray wolf rendezvous site model in Idaho, USA, 2007–2009.

Yr	Game management units	No. sites surveyed	No. sites wolves detected	No. sites scats detected	No. sites tracks detected	No. sites howling detected	No. sites hairs detected	No. litters detected	No. verified litters
2007	24	112	28	16	22	3	1	1	1
	28	110	24	21	6	2	1	3	4
	33, 34, 35	210	67	35	44	9	2	3	4
	43	44	8	6	4	0	0	0	0
	Annual total	476	126	83	76	14	4	7	9
2008	24	120	48	29	27	1	2	0	2 <sup>a</sup>
	28	148	29	17	12	3	7	2	3
	33, 34, 35	173	71	55	38	2	10	3	5
	43	47	11	6	5	0	1	0	0
	Annual total	488	159	107	82	6	20	5	10
2009	28	149	40	32	12	3	2	4	4
	33, 34, 35	166	43	37	21	5	4	4	6
	Annual total	315	83	69	33	8	6	8	10

<sup>a</sup> These 2 litters of pups inhabited private land and their rendezvous sites were not surveyed by the study area crew.

sites contained drivable roads, we conducted sign surveys in vehicles at 20 km/hr along all roads within the site (Crete and Messier 1987). The minimum observed distance between historical rendezvous sites of adjacent packs in Idaho was 6.4 km (C. Mack, NPT, unpublished data); we therefore placed a 6.4-km-radius circle around predicted rendezvous sites occupied by wolves and did not survey additional sites within that buffer.

We considered canid scats  $\geq 2.5$ -cm-diameter to be wolf scats (Weaver and Fritts 1979). Because coyote (*C. latrans*) scats and wolf pup scats overlap in size, we did not consider scats  $< 2.5$  cm to be wolf pup scats unless there was abundant wolf sign (e.g., pup play areas; Joslin 1967) or live wolves at the site.

## RESULTS

Independent observers monitored 15 wolf packs (32 wolf pack-yr) inhabiting our 4 study areas and documented 29 litters of pups (2/29 litters were on private land not surveyed when field-testing our model) during 2007–2009 (Table 1). Our global model including green leaf biomass, profile curvature, and surface roughness had the strongest statistical support ( $w_i = 0.85$ ) out of our candidate set for predicting rendezvous sites (Table 2). Rendezvous sites in Idaho were best characterized by high green leaf biomass associated with

grasses and the concave and gentle topography needed to retain water (Table 3).

Predictions from our model were strongly correlated ( $R^2 = 0.86$ ; Fig. 2) and there was strong fit ( $\chi^2 = 0.24$ ,  $P = 0.99$ ) with the locations of 178 independent rendezvous sites not used to build the model. Slope of the regression did not differ from 1 (1.14, 95% CI = 0.77–1.50) and the intercept did not differ from zero ( $-0.01$ , 95% CI =  $-0.06$  to 0.03), indicating a strong relationship between our candidate variables and rendezvous site selection by wolves. Our model showed a similar pattern of increasing use in the 10 equal-area categories for both build and independent test data sets. The top 4 equal-area classes of predicted probabilities (40% of the landscape) included 67.5% of the 114 locations of rendezvous sites used to build the model and 79.8% of the 178 independent rendezvous site locations used to test the model (Fig. 2). Wolves in Idaho did not always select wet meadows for rendezvous sites, with approximately 10% of historic sites falling in the 4 lowest predicted equal-area classes (Fig. 2).

We surveyed 476, 478, and 315 locations in our study areas predicted by our model to be highly suitable for rendezvous sites (79% of sites predicted to have selection probabilities  $\geq 70\%$ ; Table 1) during summers of 2007, 2008, and 2009, respectively. We detected wolves at

**Table 2.** Log-likelihood (LL), number of parameters ( $K$ ), Akaike's Information Criterion value (AIC), change in AIC value ( $\Delta$ AIC), and Akaike weight ( $w_i$ ) of habitat model predicting gray wolf rendezvous site locations, Idaho, USA, 1996–2006.

Model	LL	$K$	AIC	$\Delta$ AIC	$w_i$
Vegetation and topography models					
Green leaf biomass + profile curvature + roughness	-188.37	4	384.74	0	0.846
Green leaf biomass + roughness	-191.09	3	388.18	3.44	0.151
Green leaf biomass + profile curvature	-209.63	3	425.26	40.52	0.000
Topography models					
Profile curvature + roughness	-195.15	3	396.3	11.56	0.003
Roughness	-197.97	2	399.94	15.2	0.000
Profile curvature	-220.6	2	445.2	60.46	0.000
Vegetation model					
Green leaf biomass	-212.8	2	429.6	44.86	0.000

**Table 3.** Logistic regression parameters (SE) and odds ratios from the highest ranked model describing gray wolf rendezvous sites in Idaho, USA, 1996–2006.

Parameter	Estimate	SE	Odds ratio	Lower 95% CI	Upper 95% CI
Constant	−13.589	4.28			
Green leaf biomass	0.083	0.025	1.086	1.035	1.14
Profile curvature	0.492	0.211	1.636	1.081	2.475
Roughness	−0.537	0.09	0.585	0.49	0.698

approximately 30% of these potential rendezvous sites (Table 1). Scats were the most common form of wolf sign we detected, with tracks the second most common; we rarely detected howling or hairs (Table 1). Comparing locations where we detected wolves during field testing to radiotelemetry data and ground observations we collected during summer showed we detected all 15 packs known to inhabit our study areas, while surveying <11% of the total study area. In addition, we detected 20 of the 27 (74%) litters of pups in those years (Table 1). We did not observe litters from 2 packs in 2008 because their rendezvous sites were on private lands. Nevertheless, radiotelemetry verified that our model accurately predicted the rendezvous sites of these 2 packs.

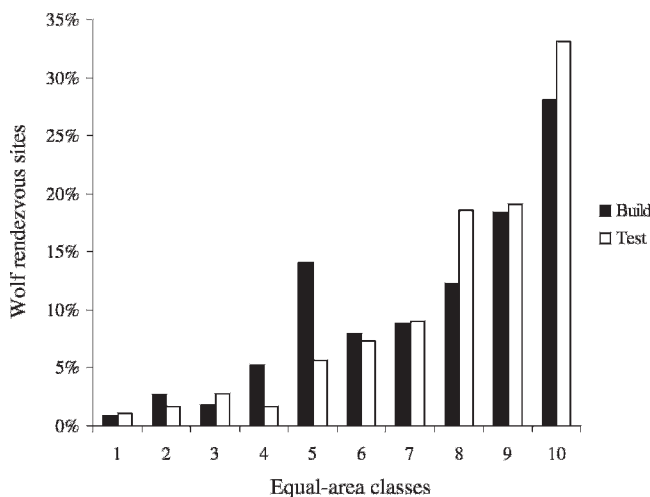
## DISCUSSION

We developed and field-tested an a priori, predictive habitat model that not only effectively narrowed the search for wolves, a low-density carnivore, but also helped locate individuals at a time of year when information about a critical vital rate (reproduction) could be obtained. Becker et al. (1998) and Patterson et al. (2004) found that wolf populations could be monitored through the use of aerial track transects when wolf pack movements and snow conditions permitted observation of tracks in open habitats (e.g., tundra, frequently frozen waterways and lakes). The aerial track transects method has limited utility in Idaho because of a lack of widespread open habitat and inconsistent snow conditions. Furthermore, unless surveys

are conducted annually and pack sizes are continuously tracked using this method, little inference about reproduction within the population can be obtained. By contrast, our predictive model allowed us to detect nearly 75% of the litters of pups in our study areas over 3 years, demonstrating that our approach can provide substantive information about reproduction within the population. We consistently located wolf packs and their litters and were able to obtain a wealth of genetic information from each pack through collection of scat and hair deposited at occupied sites without the use of radiotelemetry (Stenglein et al. 2010).

As we predicted, wolves in Idaho chose wet meadows for rendezvous sites. Both historical (1996–2006) and extant rendezvous site locations for wolves in our study areas were found in areas of high habitat suitability for rendezvous sites, giving us confidence in the predictive power of our model. Profile curvature was the dominant predictive variable in our model (odds ratio = 1.6; 95% CI = 1.1–2.5), presumably because of its association with ability of a site to retain the water essential for pup rearing. Green leaf biomass was also an important variable (Table 3) because higher values likely represented a lack of forest cover and presence of grass common at wetter sites. Although present in our model with the lowest AIC score, roughness of terrain contributed little based on the odds ratio alone (Table 3), suggesting that relative flatness alone does not predict a rendezvous site location but can complement profile curvature and green leaf biomass when making predictions. Wolves in Idaho did not always select wet meadows for rendezvous sites, with approximately 10% of historic sites falling in the 4 lowest predicted equal-area classes. Therefore, due to model uncertainty, we would expect to miss approximately 10% of locations of wolf pack rendezvous sites over a 10-year period using this model if we were not surveying the lowest predicted equal-area classes. This variability could be because wolves also select rendezvous sites based on proximity to prey that may not always be convenient to wet meadows, whereby wolves will use forested areas with slow-moving streams as we have occasionally observed in central Idaho. Including prey availability as a covariate in our models could have addressed this possibility and perhaps improved model fit, but these data were unavailable for much of our area.

Our model allowed us to reduce the area searched by 89%, but surveying the remaining 11% required 260 person-days to survey 11,337 km<sup>2</sup> (2007, 2008) with technicians working in pairs. Averaging across 3 years of field testing, this method required 34.6 person-days (with technicians working in pairs) to detect a litter of pups.



**Figure 2.** Percentage of gray wolf rendezvous site locations in each of 10 equal-area categories we used to build ( $n = 114$ ) and test ( $n = 178$ ) a predictive wolf rendezvous site habitat model ( $R^2 = 0.86$ ), Idaho, USA, 1996–2006.

Our field effort, however, was based on naive survey of potential rendezvous sites (i.e., we surveyed every predicted site in our top 3 equal-area classes); we could have improved efficiency by narrowing our search further based on readily available information such as historical knowledge, public reports, and observations by agency personnel. Furthermore, Stenglein et al. (2010) showed that abundance estimates derived from genetic samples collected during our field effort remained accurate (with reduced precision) even when only 50% of the predicted sites in our study areas had been sampled.

Although a few studies (Joslin 1967, Kolenosky and Johnston 1967, Unger 1999) have described wolf rendezvous sites, none have attempted to identify influential variables, predict rendezvous site habitat over a large area, and then use subsequent spatial predictions to locate wolves. Wolves in Idaho, like those in eastern and midwestern North America, chose wet meadows for rendezvous sites, supporting earlier descriptive work and the generality of this behavior for wolves occupying similar latitudes (approx. 40°–50°N; Joslin 1967, Kolenosky and Johnston 1967, Unger 1999). Capitani et al. (2006) found that wolves in the Apennines in Italy, however, had rendezvous sites on steep slopes in forested cover farther from roads and borders of protected areas and showed that proximity to human activity rather than habitat better predicted rendezvous site locations in the Apennines. Theuerkauf et al. (2003) also found habitat characteristics were secondary to human activity for determining wolf pack rendezvous site locations in Poland. Wolves are highly adaptable, and we hypothesize that high levels of human-caused mortality cause wolves to use suboptimal habitat for rendezvous sites to avoid human activity. If our hypothesis is correct, the relative protection of endangered wolves from human-caused mortality in Idaho could explain why habitat features alone were powerful predictors of rendezvous site locations. We assumed that characteristics of rendezvous sites documented from 1996 to 2006 would predict habitat found at future rendezvous sites and this assumption was met during field testing in 2007–2009. Recently, however, wolves have transitioned from protected status under the Endangered Species Act to a big game species, which can be legally hunted in Idaho. If hunting and human-caused mortality cause wolves to select different habitat for rendezvous sites, as Theuerkauf et al. (2003) and Capitani et al. (2006) found for wolves in Europe, then our model will lose efficacy until it is updated to incorporate this new behavior.

Predicting suitable habitat through modeling is not a novel concept (Manly et al. 2002, Schlossberg and King 2009), and although many habitat models are rigorously tested (Boyce et al. 2002, Johnson et al. 2006, Sawyer et al. 2009, Thatcher et al. 2009), few studies have used model predictions for subsequent surveys of animal populations. In contrast, Rachlow and Svancara (2006) demonstrated a predictive habitat model could be used to effectively narrow the survey area for pygmy rabbits (*Brachylagus idahoensis*) and suggested biologists could use this approach to focus

survey efforts across broad geographic areas for a species of interest. Our results support this notion for low-density carnivores and we further demonstrate that predictive habitat models can be rooted in the animal's behavioral and life-history patterns so that subsequent ground searches are not only spatially narrowed, but also provide data that illuminate vital rates of interest for both management and research.

## MANAGEMENT IMPLICATIONS

Because wolf packs congregate at predictable rendezvous sites in summer, our model can be used to narrow the search for wolves considerably when information is needed in areas of high management interest or uncertainty. The ability to find rendezvous sites facilitates sampling dependent on the level of information needed by managers, from howling or sign surveys, to determine presence to obtaining genetic material to assess pack size, composition, and diversity. This information can be used as part of a population monitoring program (e.g., estimating distribution and fecundity of wolves), or to address questions about pack dynamics in areas of strong human interest (e.g., on the frontier of colonization by wolves or on landscapes with high potential for conflicts).

Where resources limit sampling every rendezvous site predicted by our model, we suggest the following criteria be considered when subsampling potential sites: 1) survey in the vicinity of known historic rendezvous sites where packs have been well established because wolves often return to areas used in previous years; 2) overlay public sightings or agency personnel reports during summer onto the predictive map and survey predicted sites within a 6.0-km radius (the approx. upper 95% CI of the average distance moved between late-summer rendezvous sites and final rendezvous sites used by packs in Ontario; Mills et al. 2008); and 3) without the benefit of other information, where surveys must be conducted naively, randomly survey 50% (yielding reliable but imprecise results) to 75% (increasing precision of results by 20–30%) of predicted sites (Stenglein et al. 2010).

## ACKNOWLEDGMENTS

We thank The NPT, The Regina Bauer Frankenberg Foundation for Animal Welfare, IDFG, Montana Fish, Wildlife and Parks, Montana Department of Natural Resources and Conservation, The Mountaineers Foundation, Wolf Recovery Foundation, Defenders of Wildlife, Oregon Zoo Future for Wildlife Grants, and the MILES Program at The University of Montana for funding and assistance. We also thank S. Nadeau, M. Hart, W. Gustafson, and L. Waits for their advice, and J. Stenglein, M. Anderson, N. Carter, M. Connors, A. Fahnestock, B. Fannin, A. Greenleaf, Q. Harrison, S. Howard, C. Jacobs, J. Joyce, R. Kalinowski, S. Longoria, T. Loya, D. Miles, B. Nelson, A. Roadman, L. Robinson, C. Rosenthal, J. Ruprecht, A. Sovie, R. Wilbur, and B. Wojcik for their dedication and perseverance in the field. We also extend thanks to L. Bradley and M. Lucid for earlier manuscript

reviews that greatly strengthened this paper. Lastly, we are grateful for the critical yet respectful reviews provided by anonymous reviewers. Our paper is much better because of their thorough review.

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Associate Editor: Millsaugh.