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Reproduction and Den Site Selection by Wolves in a Disturbed Landscape

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Abstract

We studied litter sizes, den characteristics, and den site selection by wolves (*Canis lupus ligoni*) on Prince of Wales and adjacent islands in Southeast Alaska, USA. The study area was extensively logged and roaded enabling us to examine effects of those factors on den site selection. We counted pups in dens during May using an infrared video camera with a flexible-shaft. We recorded habitat features at dens and used logistic regression to compare den site characteristics within 100-m and 1000-m circular buffers around dens with randomly matched unused locations. Litter size averaged 4.1 (SD = 1.7) pups, however, average litter sizes of six first-time breeding females were smaller ($\bar{x}$ = 3.0, SD = 2.5). Dens were located in root wads of large living or dead trees within old-growth forest stands <150m from freshwater. Within 100-m and 1000-m buffers, wolves selected coarse-canopy old-growth forest stands and muskegs adjacent to lakes, ponds or streams, on gentle slopes, that were farther from logged stands and roads than unused locations. Landscape features such as elevation and slope, and proximity of fresh water had the greatest effects on den site selection. Covariates tabulated within 100-m buffers had much greater influence on den site selection than variables tabulated within 1000-m buffers indicating that wolves mostly responded to features within the immediate vicinity of dens. Wolves generally avoided clearcuts and roads but they tolerated intense disturbances of short duration during our den visits. We suggest wolves prefer locations away from roads and clearcuts but will select them if suitable alternative locations do not exist. Once established at den sites, wolves will tolerate some human disturbance at least of short duration.

Introduction

The coastal temperate rainforests of Southeast Alaska support a population of about 1000 gray wolves (*Canis lupus ligoni*) (Person et al. 1996) that are genetically distinct from interior continental populations in Alaska and Canada (Weckworth et al. 2005). The cool, wet climate, island topography, and forest habitat of the region present unique conditions to which wolves have adapted. Most of southeast Alaska is within the Tongass National Forest, the largest national forest in the United States. About 400,000 ha of old-growth forest were clearcut logged between 1955 and 2005, mostly on the islands in the southern portion of the national forest (U.S. Forest Service 1997). Industrial-scale timber harvest may affect deer populations, the primary prey of wolves, and increase mortality of wolves because roads built for logging facilitate hunting and trapping (Person et al. 1996, Person 2001, Person and Russell 2008). Consequently, the wolf is considered a management indicator species in the Tongass Land Management Plan (U.S. Forest Service 1997) and information concerning effects of habitat change and harvest on demographic rates is critical to conserving populations.

Reproduction is a primary demographic component affecting population change in wolves. Most data concerning litter sizes of free-ranging wolves in North America are from populations within the boreal forest biome (Fuller et al. 2003) or within the montane forests of the Greater Yellowstone Ecosystem (Smith et al. 2008). There is no published information concerning litter sizes of wolves inhabiting the vast coastal temperate rainforests of southeast Alaska. Some segments of the wolf population in that region, such as those on Prince of Wales Island, are heavily harvested by hunters and trappers (Weckford et al. 2005, Person and Russell 2008) and subject to extensive habitat changes owing to logging and road building (Person et al. 1996, Person 2001). Consequently, litter size is important information needed to evaluate the resilience of those wolves to habitat changes and harvest. In addition, characteristics of dens and denning sites in coastal temperate rainforests have not been described previously, nor has anyone examined the effects of timber harvest and roads on den site selection by wolves within the biome. Studies of wolves in other temperate forest landscapes have yielded contrasting results with respect to effects of habitat composition,

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topography, and human disturbance on den site selection. For example, several studies indicated that wolves selected coniferous forest patches away from roads and development (Norris et al. 2002, Theuerkauf et al. 2003) but near sources of fresh water (Norris et al. 2002). Other studies emphasized elevation and slope but reported little effect of vegetative or forest characteristics on den site selection (Matteson 1992, Unger 1999). In contrast, one study in Montana concluded that thick vegetative cover sufficient to hide dens was a significant predictor of den site selection by wolves but elevation and slope had little influence (Trapp 2004). Several studies suggested wolves avoided roads and human disturbances (Unger 1999, Norris et al. 2002, Theuerkauf et al. 2003) whereas others found little effect of roads or human activity on den site selection (Matteson 1992, Trapp 2004). Clearly, multiple factors influence the selection of den sites and those determinants likely vary depending on environmental conditions that are specific to different regions. Identifying landscape and habitat characteristics common to den sites within the temperate rainforests of Southeast Alaska will assist local biologists with locating areas in which those sites are likely and enable development activities such as timber harvest to be planned in ways that minimize impacts on wolf populations.

We examined litter sizes of wolves in an area where extensive road construction and logging have occurred on Prince of Wales and adjacent islands in southeast Alaska. We described habitat characteristics of dens and investigated the influence of variables related to habitat composition, habitat arrangement and distribution, topography, and distances from fresh water, roads, and logged habitat on selection of den sites. Specifically, we wanted to determine if wolves avoided roads or logged stands when selecting locations for den. Wolves likely integrate information about their environment at very large scales, and it is logical that they would react to environmental conditions both in the immediate vicinity of dens and at much larger landscape-level scales (Norris et al. 2002). Therefore, we compared the relative influences on den site selection of habitat, landscape, and topographic characteristics within 100 m of dens with those tabulated within a radius of 1000 m of dens. Our study provided important demographic information for wolves in coastal temperate rainforests and described some patterns of den site selection that are general to all wolves and others that are specific to the environment of Southeast Alaska. Our results are applicable to many wolf populations situated in areas where landscapes are undergoing extensive change from human activities.

Study Area

Southeastern Alaska comprises a narrow strip of mainland and a chain of islands, known as the Alexander Archipelago, which is oriented roughly parallel to the mainland (Figure 1). The archipelago consists of thousands of islands ranging in size from <0.01 to >6000 km^2 with distances between islands and the mainland ranging from several meters to 13–15 km. The study area encompassed Prince of Wales, Kosciusko, Heceta, and other smaller adjacent islands (between 54° 40' and 56° 20' north and 132° 00' and 134° 00' west). The topography included rugged mountains up to 1160 m and long deep fiords. Prince of Wales is the third largest island in the United States (about 6000 km^2) and contains the towns of Craig, Klawock, Hydaburg, and Thorne Bay, as well as several smaller villages and settlements. During our study, temperatures in January were usually >0° C, temperatures in July were usually >18° C, and annual precipitation ranged from 279–505 cm.

The study area supported highly productive forest growth, dominated by Sitka spruce and western hemlock, with lesser amounts of western redcedar (*Thuja plicata*), shore pine (*Pinus contorta*), and Alaska yellow cedar (*Chamaecyparis nootkatensis*). Alaback (1982) and Alaback and Juday (1989) described the understory characteristics and ecology of those forests. More than 4800 km of road were built within the study area and approximately 150,000 ha have been clearcut logged since 1955. About 25% of the land area encompassed by the home ranges of wolf packs that we monitored was clearcut logged. Generally, clearcuts ≤29 years post logging were brushy with sparse forest canopies of conifers, and clearcuts >29 years old had closed forest canopies and sparse understory vegetation. Density of roads averaged 1.03 km/km^2 but ranged 0.15–1.86 km/km^2 within the home ranges of monitored wolf packs. All roads that likely affected wolves at dens were gravel and constructed to facilitate logging. Logging and silvicultural thinning occurred near

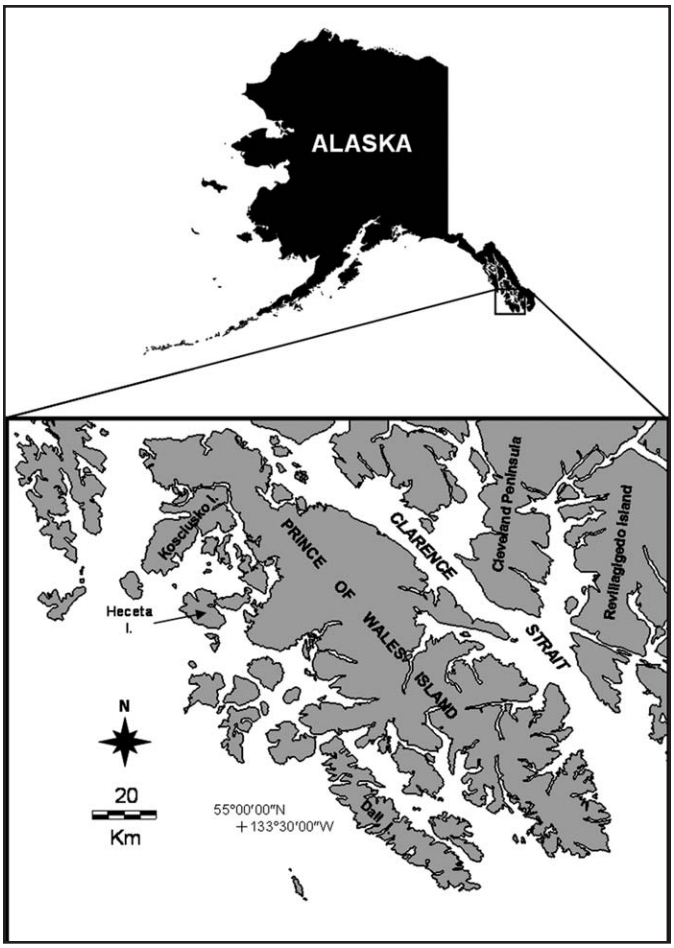

Figure 1. Map of Prince of Wales and adjacent islands in southeast Alaska.

our sample of den sites throughout the study. Both activities resulted in noise from chainsaws and machinery as well as vehicle traffic at regular intervals throughout the day. In addition, during spring and summer, U.S. Forest Service personnel, anglers, black bear hunters, and other recreationalists frequently used roads near den sites. Most roads were open for highway vehicle use but some were closed by gating, or removing bridges and culverts after logging had ceased. Other mammals that commonly occurred within the study area were Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), black bears (*Ursus americanus*), beaver (*Castor canadensis*), river otters (*Lutra canadensis*), other mustelids, and several species of small rodents (MacDonald and Cook 1999). The study area contained many streams and rivers that supported abundant salmon (*Oncorhynchus* spp.) populations.

Methods

We captured and radiocollared fifty-five wolves on Prince of Wales, Heceta, and Kosciusko Islands between March 1993 and August 2003. Capture and handling methods were described in Person (2001) and Person and Russell (2008). All procedures followed guidelines specified by the University of Alaska Fairbanks Institutional Animal Care and Use Committee and the American Society of Mammalogists (Animal Care and Use Committee 1998). We monitored radiocollared wolves 2-6 times each month aerially and from the ground. The greatest intensity of monitoring occurred during denning between April and July. All dens sites were located aerially in April or May. Den locations were overlain on geographically referenced orthophotographs and assigned coordinates (UTM Zone 8N, North American Datum 1927). All locations were entered into a geographic information system (GIS) database (IDRISI, Clark University, Worcester, MA) for analysis.

Active wolf dens were visited when pups were between 3–5 weeks old. Survey crews numbered 2–4 individuals and we spent <45 minutes at each den. Prior to 2000, we counted pups by inspecting dens with headlamps or observing them outside dens. That technique enabled us to obtain complete counts of pups only at relatively shallow and simple dens; therefore, we could not count pups at all dens that were located. After 2000, we used an infrared-illuminated video probe attached to a 8-m long flexible shaft (Fuhrman Diversified Inc., Seabrook, TX) to survey den interiors and obtain counts of pups. That technique enabled us to survey all but the deepest and most complex dens. In some cases we had to crawl into dens up to 2–3 m to direct the probe into all chambers. We mapped each den, recorded diameter and species of trees forming den structure, canopy closure, direction of main entrance, depth of main chamber, distance to fresh

water, and evidence of beaver activity. We also categorized dens as obscured by thick cover if the den entrances could not be seen from a distance of 20 m from any direction. We transformed the bearing direction of the main entrances to dens into 2 variables representing degrees along a north-south axis and degrees along a west-east axis using the following formulas adapted from McCune (2007):

degrees N–S = 180 – abs(azimuth – 180)
degrees W–E = abs[180 – abs(azimuth – 90)] .

That enabled us to determine if den entrances were oriented southerly or easterly, which potentially could maximize solar radiation.

Classification of Habitat Features

One hundred meter and 1000-m radii buffers were placed around den locations, which were matched with random points selected from areas 1.5 times the size of 95% adaptive kernel home ranges (Worton 1989) for wolf packs that were monitored (Person 2001). We inspected each random location to make sure none had been used for denning. Circular buffers also were placed around all matched unused locations. Habitat variables evaluated within buffers around dens were grouped into 3 covariate groups: 1) habitat composition, 2) landscape characteristics, and 3) distance measures (Tables 1 and 2). We considered all roads to be open to motor vehicle use. We could not reliably identify roads as open or closed because the classification of roads changed frequently during the duration of our study and their status was poorly documented by the U.S. Forest Service. Indeed, the status of many roads changed multiple times within periods as short as one year without our being aware of it. Moreover, many "closed" roads were used by people driving all-terrain vehicles (ATVs) and motorbikes. They also provided trails for hunters, trappers, subsistence harvesters, and hikers.

Digital habitat and topographic maps used in our analyses were derived from U.S. Forest Service GIS coverages for the Tongass National Forest and 7.5 minute series digital elevation models for Alaska from the U.S. Geological Survey. Geographic analyses were conducted using IDRISI Andes edition raster GIS software. The raster cell resolution was 20 m.

Statistical Analyses

We used a chi-square test to compare the frequency that vegetation obscured dens with a frequency

TABLE 1. Grouped variables used to assess den site selection by wolves on Prince of Wales and adjacent islands, Alaska, 1995–2004.

Variable Group[a] Variable	Description
Habitat Composition	Vegetation class[b] proportion of buffer composed of a particular vegetation class
Landscape Characteristics	
Fragmentation	(n-1) ÷ (c-1), where n = number of vegetation classes in 7x7 pixel kernel and c = 49; result is averaged over buffer
Edge density	(total perimeter of all vegetation classes - perimeter of buffer) ÷ area of buffer
Patch size (by vegetation class)	Area of largest patch of particular vegetation class intersecting buffer
Southing aspect	average degree (0-180) that buffer faces south, 0 = 100% north facing, 180 = 100% south facing
Easting aspect	average degree (0-180) that buffer faces east, 0 = 100% west facing, 180 = 100% east facing
Slope	average degrees of slope within buffer
Elevation	average elevation (m) within buffer
Distance Measures	
Riparian distance	average distance (m) from any point within buffer to lakes or streams
Road distance	average distance (m) from any point within buffer to roads
Logged land	average distance (m) from any point within buffer to lands on which timber harvest has occurred

[a] Variables were summed or averaged within circular buffers around each radio relocation.

[b] Table 2.

TABLE 2. Descriptions of vegetation classes on Prince of Wales and adjacent islands, Alaska.

Vegetation Class	Description
Beach	nonforested tide lands, open habitat consisting mostly of rocky, sandy, or muddy beaches. Any area within buffers that overlapped shoreline and ocean was considered to be beach or tideland.
Alpine	nonforested, open habitat >600m elevation.
Muskeg	predominantly heath or bog-like muskegs with sparse distribution of conifers.
Lake or Stream	fresh water lake, pond or stream.
Open-canopy old-growth forest	primarily uneven aged hemlock-cedar forest <58.3 m^3/ha gross timber volume.
Coarse-canopy old-growth forest	primarily uneven aged hemlock-spruce forest ≥58 m^3/ha gross timber volume.
Clearcut	thick brushy even-aged shrub or shrub-sapling stage second-growth stands ≤29 years post logging.
Second-growth Forest	clearcuts >29 years post logging had sparse understory vegetation and closed canopies of coniferous trees.
Private Land	unspecified private lands; most were clearcuts 1–29 years old.
Grass	fresh or salt water marsh and grassy meadows.
Road Corridor	paved and unpaved roadways and adjacent habitats within 20 m road right-of-way; included all mapped roads regardless of level of human use. Twenty meter width was determined by the minimum cell resolution of raster GIS layers.

of 50%, which would be expected from a simple binomial random event. We used nonparametric Mann-Whitney statistics to compare bearing directions that main entrances faced on west–east and north–south axes to equal-sized samples of random bearings along those axes. We also used Mann-Whitney tests when comparisons between mean values of grouped variables were required.

We evaluated the effects of habitat, landscape, and distance variables on den site selection by wolves using logistic regression of used versus matched unused locations (Hosmer and Lemeshow 2000) using SPSS (SPSS 2004). We analyzed data for each covariate group separately so that we could evaluate the relative influences of habitat composition, landscape features, and distance measures on den site selection. The analyses were repeated for buffers of 100-m and 1000-m. Variables were screened for strong correlations ($-0.7 \geq r \geq 0.7$) with other variables within covariate groups prior to model selection. If strong correlations were observed, covariates with the weakest relations to the outcome variables were dropped from the models. We fit models containing all possible combinations of covariates that had not been eliminated during the screening for correlations with other covariates. The fit of models to logistic functions was evaluated using Hosmer-Lemeshow goodness of fit tests and adequate fit was assumed if $P>0.1$ (Hosmer and Lemeshow 2000). We tested models for over-dispersion because some packs were monitored over several denning seasons and data for those packs represented repeated measures. In all models the ratios of deviance to degrees of freedom were slightly <1 indicating that we overestimated standard errors for some parameters; however, that simply implied our models tended to be conservative with respect to inclusion of covariates (Menard 2002). We used AIC_c criteria (Burnham and Anderson 1998) to select the best multivariate models and calculated AIC weights (w) to compare models within each covariate group and buffer scale. We only considered models to be valid if $\Delta AIC_c \leq 4$ (Burnham and Anderson 1998). We used model averaging techniques for all valid models in each variable group and scale to derive composite model coefficients and their unconditional standard errors (Burnham and Anderson 1998). We calculated the relative effect size for each covariate included in composite models by evaluating the odds ratio (relative effect) for an increase in the covariate equal to 10% of its range of values (Riggs and Pollock 1992). For example, a relative effect (RE) >2.0 for a covariate indicated that a 10% increase in that variable within a buffer more than doubled

the probability of selection of a location for a den site. In contrast, a RE <0.5 indicated that a 10% increase in a covariate reduced the probability of selection by more than 50%. That enabled us to directly compare the relative magnitudes of influence that individual covariates had on the probability of den site selection and determine which covariates had the greatest effect.

Results

Den Visits

We visited 26 active dens used by 12 wolf packs on Prince of Wales, Kosciusko, and Heceta Islands between 1995 and 2004. On two occasions, wolves removed pups from dens after our visits and took them to other den sites <1 km away. In both cases, all of the pups were observed again in late summer indicating that moving had not compromised their survival. Of 6 wolf packs whose dens we surveyed >1 year, 4 used the same dens for at least one consecutive year. Two wolf packs used the same dens for 3 consecutive years despite our annual visits. Intervals between use of specific dens ranged 1–5 years.

Reproduction

Natal dens were occupied as early as April 21 and as late as July 15. We successfully counted pups at 23 of 26 active dens surveyed. Pups were 3–5 weeks old when dens were visited indicating that parturition occurred between the last week of April and the second week of May. Sizes of litters ranged from 1–8 pups. The average litter size was 4.1 pups (SD = 1.7) and the median and mode were 4 pups. We observed that new mothers produced fewer pups ($\bar{x}$ = 3.0, SD = 2.5) than experienced mothers ($\bar{x}$ = 4.8, SD = 0.9, Mann-Whitney Z = -2.3, P = 0.024). Six litters were produced by first-time mothers and 12 were from females that previously had given birth. We did not know if mothers were new or experienced breeders for the other 5 litters. Five of the new mothers produced ≤3 pups. Three new mothers were wolves that had settled along with their mates in vacant territories after dispersal. Three others were resident pack members that produced litters after the previous breeding female had died. One of those wolves produced 8 pups, the largest litter we observed. In two instances, wolf packs failed to exhibit denning behavior or produce litters. In one case, a change in the breeding pair likely occurred the year they failed to breed. In the other instance, a dispersing pair had recently settled but did not produce a litter during their first year within the new home range. We saw no evidence of multiple litters within packs but we certainly could not rule them out. After July 8, most dens were abandoned and pups were located near temporary rendezvous sites usually <1 km from the natal dens. All rendezvous sites were located in estuarine meadows or muskeg heaths and were used from July to as late as October.

Den Characteristics

We examined 25 dens that were used in a total of 33 denning events. Den sites were mostly at low elevations, on relatively flat terrain, and all were within 150 m of freshwater streams, ponds, or lakes (Table 3). Thirteen (52%) dens were located on lake shores, 5 (20%) along streams, and 7 (28%) near muskeg ponds or pools. Most dens on lake shores were on islands or peninsulas. Flow of streams adjacent to 5 (20%) wolf dens was altered by beaver activity. Indeed, evidence of recent beaver activity was observed at 17 (67%) den sites (Table 3). Most den sites were >776 m from roads and >580 m from logged stands (Table 3). Nonetheless, one den was only 170 m from a road and 12 m from a clearcut that had transitioned into second-growth forest (>29 years post logging). All dens were located immediately adjacent to open spaces created by lake shores, stream banks, beaver meadows, or muskegs. Dens were elevated above the surrounding ground either on top of small mounds or on gently sloping hillsides. Fifteen (60%) dens were in stands of coarse-canopy old-growth forest and 10 (40%) were in open-canopy old-growth forest. Fourteen (56%) dens had entrances that could be seen 20 m away from at least one direction and 11 (44%) did not but those frequencies did not differ from what would be expected due to random chance (χ^2 = 0.081, df = 1, P = 0.777). One den was in the hollow of a downed rotting log but all others were excavated from the soft dirt under the root wads of living or dead trees. Most dens were under live trees with diameters at breast height >60 cm, and canopy closures >70% (Table 3). Most dens had multiple entrances and several chambers. The main entrances tended to face south and east (Table 3), however, that relation was not statistically different from what would be expected from a random distribution of bearings on a west–east

TABLE 3. Characteristics of 25 dens surveyed on Prince of Wales and adjacent islands, Alaska, 1995–2004.

	Mean or %	SD	Median	Range
Distance from roads (m)	1351.0	1248.0	776.0	170.0–2681.0
Distance from fresh water (m)	20.6	31.2	10.0	2.0–150.0
Distance from logged stands (m)	988.0	1047.0	580.0	12.0–3914.0
Slope (degrees)	4.9	4.0	4.0	0.4–13.7
Elevation (m)	86.0	71.0	55.0	11.0–296.0
Dens on islands (%)	17.0	7.4	--	--
Dens on peninsula (%)	25.0	8.5	--	--
Beaver present (%)	67.0	9.2	--	--
Dens under live trees (%)	77.0	8.3	--	--
Canopy closure (%)	70.2	14.1	75.0	25.0–90.0
Obscured (%)	44.0	9.9	--	--
Dbh largest tree (cm)	68.8	21.3	71.1	22.9–101.6
Direction main entrance (easting °)	99.3	49.6	92.5	0.0–180.0
Direction main entrance (southing °)	101.4	56.6	110.5	5.0–180.0
Length of tunnel to natal chamber (m)	3.9	2.4	3.0	1.0–8.0

axis (Mann Whitney, $Z = 0.611$, $P = 0.54$) and a north–south axis (Mann-Whitney, $Z = 0.846$, $P = 0.393$). Indeed, 7 (28%) dens faced northward. Tunnels leading to primary natal chambers varied in length from 1–8 m (Table 3) and the number of chambers ranged from 1–5. In several dens, tunnels connected root wads (elevated buttresses composed of roots) of different trees. Elevated bedding sites used by adult wolves were evident at all den sites. Well used trails radiated from most dens and scat was often abundant along those trails.

Den Site Selection

Analyses of habitat characteristics within 100-m buffers around den sites indicated that wolves strongly selected relatively flat areas near lakes and streams at low elevations (Tables 4 and 5). They tended to locate dens within or near larger stands of coarse-canopy old growth adjacent to riparian habitats that were further from logged stands than unused sites. We originally categorized logged habitat into two age classes because of structural changes that occur over time owing to forest succession. However, few buffers around den locations overlapped any of those individual age classes and maximum likelihood estimates of logistic regression coefficients did not exist owing to quasi-separation between those covariates and the binary outcomes (Allison 2004). Consequently, we combined both age classes of clearcuts into one vegetative class representing the proportion of a buffer logged to permit model estimation. We also did the same for variables representing patch sizes of clearcuts and second-growth forest. After combining classes, the regression coefficient for proportion logged still could not be estimated but the coefficient for patch size could. The presence of clearcuts or second-growth forest within 100-m buffers essentially was a perfect predictor that a location would not be selected by wolves for a den site. They also avoided roads, although distance to roads and logged stands was highly variable. Large patches of muskeg frequently intersected den buffers but that characteristic was also highly variable. Wolves selected sites with greater density of edge than unused sites at the 100-m scale but the influence was small. Clearly, slope, elevation, nearness of lakes and streams, presence of coarse canopy old-growth forest, proximity of muskegs, and absence of clearcuts were the major influences on den site selection at the 100-m scale. The best fitting model representing landscape characteristics was overwhelmingly supported ($AIC_c = 38.405$, $w = 0.963$) when compared with best fitting models for habitat composition ($AIC_c = 44.944$, $w = 0.037$) and distance measures ($AIC_c = 57.560$, $w < 0.001$) (Table 4). That reflected the strong influences of slope, elevation, and patch sizes of clearcuts, coarse-canopy old growth, and muskegs on den site selection.

Patterns of habitat selection within 1000-m buffers around den sites were similar to those at

TABLE 4. Comparison of habitat characteristics within 100-m buffers around wolf den sites and matched unused sites on Prince of Wales and adjacent islands, Alaska, 1995–2004. Results are for logistic regression of used versus matched unused sites. Separate models for individual variable groups are shown. Shown are covariates for all models for which AIC_c $\Delta < 4.0$, their AIC_c scores, differences in AIC_c scores from the best model (Δ), and AIC_c weights (w).

Model[a]	AIC_c	Δ	w
Habitat Composition Model[a]			
%L&S, %CCOG, %Musk	44.944	0	0.834
%L&S, %CCOG	48.166	3.222	0.166
Landscape Characteristics Model[b]			
Slope, Elev, Patch CCOG, Patch CC, Edge density	38.405	0	0.367
Slope, Elev, Patch CCOG, Patch CC	38.722	0.317	0.313
Slope, Elev, Patch CC, Patch Musk	39.721	1.316	0.190
Slope, Elev, Patch CC	40.485	2.080	0.130
Distance Measures Model[c]			
Distance L&S, Distance Logged	57.560	0	0.529
Distance L&S, Distance Roads	57.793	0.233	0.471

[a] %L&S = proportion of buffer composed of lakes and streams, %CCOG = proportion coarse canopy old growth, %Musk = proportion muskeg.

[b] Slope = average slope in buffer, Elev = average elevation of buffer, Patch CCOG = patch size of coarse canopy old growth, Patch CC = patch size of clearcuts, Patch Musk = patch size of muskeg.

[c] Distance L&S = average distance within buffer from lakes or streams, Distance Logged = average distance within buffer from logged stand, Distance Roads = average distance within buffer from roads.

TABLE 5. Comparison of habitat characteristics within 100-m buffers around wolf den sites and matched unused sites on Prince of Wales and adjacent islands, Alaska, 1995–2004. Results are for logistic regression of used versus matched unused sites. Separate models for individual variable groups are shown. Model averaged covariates and unconditional standard errors based only on those models for which AIC_c $\Delta < 4.0$.

Covariate	β [a]	SE [b]	RE [d]	90% C. I. [e]	Δ10% [f]
Habitat Composition Model					
% Lakes & streams	0.372	0.125	31.804	4.511–224.214	9.3%
% Coarse-canopy old growth	0.046	0.021	1.584	1.113–2.254	10.0%
% Muskeg	0.038	0.020	1.462	1.045–2.046	10.0%
Constant	-3.622	2.405			
Landscape Characteristics Model					
Slope	-0.523	0.229	0.234	0.080–0.681	2.7°
Elevation	-0.015	0.006	0.331	0.157–0.696	73.8 m
Patch size coarse-canopy old growth	0.0005	0.0003	1.495	0.997–2.212	790.7 ha
Patch size clearcut	-0.003	0.0015	0.582	0.369–0.917	180.5 ha
Patch size muskeg	0.003	0.004	2.169	0.383–12.289	258.1 ha
Edge density	0.003	0.002	1.156	0.983–1.361	48.4 ha
Constant	6.625	2.642			
Distance Measures Model					
Distance to lakes & streams	-0.010	0.003	0.373	0.227–0.613	98.7 m
Distance to logged land	0.0011	0.0007	1.538	0.971–2.437	391.4 m
Distance to roads	0.0009	0.0007	1.443	0.894–2.329	407.2 m
Constant	0.728	0.482			

[a] Coefficient of covariate in logistic regression model.

[b] Standard error of coefficient.

[c] *P*-value of coefficient.

[d] Relative effect size; odds ratio evaluated for 10% increase in covariate.

[e] 90% confidence interval for relative effect size.

[f] Value and units of 10% increase used to calculate relative effect size for covariates.

TABLE 6. Comparison of habitat characteristics within 1000-m buffers around wolf den sites and matched unused sites on Prince of Wales and adjacent islands, Alaska, 1995–2004. Results are for logistic regression of used versus matched unused sites. Separate models for individual variable groups are shown. Shown are covariates for all models for which AIC_c $\Delta < 4.0$, their AIC_c scores, differences in AIC_c scores from the best model (Δ), and AIC_c weights (w).

Model	AIC_c	Δ	w
Habitat Composition Model[a]			
%L&S, %CCOG, %Musk, %OCOG	67.482	0	0.410
%L&S, %Musk, %CC	67.571	0.089	0.392
%L&S, %CC	68.930	1.448	0.198
Landscape Characteristics Model[b]			
Slope, Elev, Patch CCOG, Patch CC	61.187	0	0.289
Slope, Flat Terrain, Elev, Patch CCOG, Patch CC, Patch L&S	61.228	0.041	0.283
Slope, Elev, Patch CCOG, Patch CC, Patch L&S	61.550	0.363	0.241
Slope, Elev, Patch CCOG, Patch Musk, Patch CC, Patch L&S	62.049	0.862	0.187
Distance Measures Model[c]			
Distance L&S, Distance Roads	65.000	0	0.590
Distance L&S, Distance Logged	65.726	0.696	0.410

[a] %L&S = proportion of buffer composed of lakes and streams, %CCOG = proportion coarse canopy old growth, %Musk = proportion muskeg, %OCOG = proportion open canopy old growth, %CC = proportion clearcut.

[b] Slope = average slope in buffer, Flat Terrain = proportion of buffer with no slope, Elev = average elevation of buffer, Patch CCOG = patch size of coarse canopy old growth, Patch CC = patch size of clearcuts, Patch Musk = patch size of muskeg, Patch L&S = patch size of lakes and streams.

[c] Distance L&S = average distance within buffer from lakes or streams, Distance Logged = average distance within buffer from logged stand, Distance Roads = average distance within buffer from roads.

the 100-m scale although the overall magnitude of the effects was much smaller (Tables 6 and 7). Wolves selected gently sloping areas adjacent to lakes and streams at low elevations. As mentioned above for models at the 100-m buffer scale, we combined clearcuts and second-growth forest into one vegetative class to permit model fitting. Wolves avoided logged stands and roads but the effects were relatively small compared to elevation and the presence of lakes and streams. The other predictors included in the models also had relatively small effects on den site selection. The best fitting model included covariates representing landscape features ($AIC_c = 61.187$, $w = 0.839$) followed by measures of distance ($AIC_c = 65.000$, $w = 0.125$) and habitat composition ($AIC_c = 67.482$, $w = 0.036$, Table 6).

Discussion

We provide the first published information concerning litter sizes, den characteristics, and den site selection for wolves occupying temperate rainforests in the Pacific Northwest. In addition, we evaluated effects of anthropogenic habitat change on den site selection, information which should be valuable when assessing the implications of development activities for the conservation of wolves.

Reproduction

Average litter size in our study was smaller than reported elsewhere for free-ranging wolves shortly before or after parturition. For example, 6.6 pups was the average litter size reported by Fuller (1989) for wolves in north-central Minnesota. Boertje and Stephenson (1992) examined reproductive tracts from wolves killed by trappers and hunters in Alaska. They reported average numbers of fetuses ranging from 6.9 in areas where ungulate densities were high to 4.6 where those densities were low. McNay et al. (2006) used ultrasonography and post-mortem examinations of 46 pregnant females to determine litter sizes in wolves from interior Alaska. They reported litter sizes averaging 5.1 pups using ultrasound and 5.6 pups using post-mortem examinations. Litter sizes ranged from 1–9. Average litter sizes from 17 studies in North America ranged from 4.2–6.9 with an overall average of 5.5 pups (Fuller et al. 2003).

Litter size may be affected by abundance of prey (Boertje and Stephenson 1992, Fuller et al.

TABLE 7. Comparison of habitat characteristics within 1000-m buffers around wolf den sites and matched unused sites on Prince of Wales and adjacent islands, Alaska, 1995–2004. Results are for logistic regression of used versus matched unused sites. Separate models for individual variable groups are shown. Model averaged covariates and unconditional standard errors are based on only those models for which AIC_c $\Delta < 4.0$.

Covariate	β [a]	SE [b]	RE [d]	90% C. I. [e]	Δ10% [f]
Habitat Composition Covariate					
% Lakes & streams	0.356	0.119	2.435	1.477–4.014	2.5%
% Coarse-canopy old growth	0.013	0.009	1.126	0.981–1.292	9.1%
% Muskeg	0.052	0.027	1.395	1.043–1.865	6.4%
% Open-canopy old growth	0.038	0.031	1.151	0.949–1.396	3.7
% Clearcut	-0.020	0.012	0.820	0.672–1.002	9.9
Constant	-2.454	2.008			
Landscape Characteristics Covariate					
Slope	-0.245	0.132	0.525	0.293–0.941	2.6°
Elevation	-0.011	0.005	0.485	0.280–0.843	65.7 m
Patch size lakes & streams	-0.005	0.003	0.821	0.673–1.002	39.5 ha
Patch size coarse-canopy old growth	0.0003	0.0004	1.268	0.745–2.157	790.7 ha
Patch size clearcut	-0.002	0.001	0.888	0.502–0.942	187.2 ha
Patch size muskeg	0.0006	0.0007	1.168	0.862–1.582	258.1 ha
Constant	3.356	1.441			
Distance Measures Covariate					
Distance to lakes & streams	-0.011	0.003	0.440	0.302–0.641	74.6 m
Distance to logged land	0.0004	0.0004	1.161	0.904–1.491	372.4 m
Distance to roads	0.0006	0.0004	1.276	0.971–1.677	406.2 m
Constant	2.001	0.674			

[a] Coefficient of covariate in logistic regression model.

[b] Standard error of coefficient.

[c] *P*-value of coefficient.

[d] Relative effect size; odds ratio evaluated for 10% increase in covariate.

[e] 90% confidence interval for relative effect size.

[f] Value and units of 10% increase used to calculate relative effect size for covariates.

2003); however, deer were moderately abundant within our study area with densities ranging from 7–11 deer/km^2 (Person et al. 1996, Farmer 2002). Indeed, ungulate biomass index per wolf (*sensu* Fuller 1989) was about 270. Based on an analysis relating ungulate biomass with litter size described by Fuller et al. (2003), that value should correspond to litter sizes >5 pups. In addition, salmon producing streams were located within all of our wolf pack home ranges and beavers were widely available. Therefore, it is unlikely that small average litter size was because of low densities of prey. Mortality of pups may have occurred before we surveyed dens each year, which if frequent would bias our counts low when compared to litter sizes observed *in utero*. We saw no evidence of prior pup mortality, although dead pups likely would have been removed from dens without a trace. One factor that clearly affected litter size was the number of first-time breeders in our sample. Small litters were produced by new mothers that recently settled in vacant territories or replaced previously breeding females. We can only speculate why that was the case. Female wolves that recently settled after dispersal may not have been in prime condition during gestation and parturition. All females that survived dispersal and settled produced small litters or did not reproduce at all during their first year in a new territory. For other first-time breeding females, our observations may simply be a consequence of small sample size. Indeed, despite mostly small litters, one of those wolves produced the largest litter observed during the study. Regardless of cause, the net effect was that most first-time breeders produced smaller litters and the frequency of new mothers was related to

turnover in packs owing to harvest. Therefore, harvest of wolves that induces turnover of breeding females may reduce average litter sizes. Intense harvests during predator control programs that eliminate packs over large areas may increase the number of breeding wolves in an area temporarily as colonizing wolves scramble to fill vacant habitat (Hayes and Harestad 2000). Surviving or colonizing wolves simultaneously may benefit from high ratios of ungulate prey to wolves stimulating large litter sizes (Boertje and Stephenson 1992) and multiple litters within packs (Ballard et al. 1987). Those factors can dramatically increase reproduction in wolf populations that have been reduced to very low numbers (Ballard et al. 1987, Hayes and Harestad 2000). Within our study area, however, individual wolf packs were occasionally eliminated and others reduced, but large-scale removal of wolves did not take place. There also was no substantial increase in deer population. We did not observe an increase in the number of successfully breeding females after intense harvests nor did we find evidence of multiple litters within packs. Consequently, wolf harvest in our study area induced turnover of breeding individuals and likely reduced reproduction overall.

Den Characteristics

In other portions of the continent, wolves have been observed denning in elevated, dry areas with loose soils near fresh water (Mech 1970, Ballard and Dau 1983, Lawhead 1983, Matteson 1992, Cluff et al. 2002). Wolves clearly adopted a similar strategy for locating dens in the coniferous forests and rainy climate of southeast Alaska. Trees were shallow rooted and the elevated buttresses or wads of roots of large live or dead trees offered convenient cavities that usually were filled with loose organic soil. They were above the water table and were dry. Other researchers have indicated that dens tend to be on southern aspects that may maximize solar radiation (Ballard and Dau 1983, Matteson 1992). We found no strong evidence for that relation in our study. We believe that protection from rain was the major factor influencing the location of den entrances. Canopy cover was dense and in most instances, dens were in thick, forested stands that often restricted sunlight from reaching the entrances but intercepted rain. Trapp (2004) suggested that wolves in Idaho and Montana selected locations with thick brushy cover in which to dig dens because those locations offered security and hiding cover. Others have observed wolves constructing dens in open forests or exposed ridges devoid of ground cover that would obscure dens (Ballard and Dau 1983, Lawhead 1983, Norris et al. 2002). We found no relation between dens and understory cover. Thick forest canopies often precluded development of understory vegetation. Moreover, most dens could be located easily from distances >20m because well used trails leading to them were highly visible. Thus, hiding cover did not offer any real security, whereas placement of dens on peninsulas and islands probably did. We believe the most important characteristics of dens were nearness of fresh water, thick forest canopy over the den, and availability of loose, dry soils in which to dig. All other features were of secondary importance or site-specific correlates of those attributes.

Den Site Selection

Wolves never located dens within clearcuts and second-growth forests and generally preferred sites further from logged stands than our sample of unused sites. They also selected den sites that were at low elevations and on gradual slopes, a pattern also observed by Matteson (1992) in Montana, and Norris et al. (2002) in southeastern Ontario. Similar to Unger's (1999) results from Wisconsin, wolves also selected locations closer to freshwater lakes and streams than our unused sites. Those attributes were primary influences on den site selection measured at both the 100-m and 1000-m buffer scales. Wolves selected expansive areas with gentle slopes at low elevations rather than small flat pockets or elevated benches nestled in rugged terrain. Habitat composition around dens was less important as a predictor of den site use, however our models indicated that wolves selected areas that encompassed coarse-canopy old-growth forest stands and muskegs within 100-m and 1000-m of dens. Wolves also selected areas with greater density of edge between vegetation classes near dens. Edge was due largely to the interspersion of muskegs, lakes, streams, and forest around dens and may have enhanced visibility and thus security. The location of numerous dens on islands and peninsulas suggested the security they provided was somewhat important.

Wolves selected den sites based on characteristics at multiple scales. Similarly, Norris et al. (2002) reported that habitat characteristics within 500-m and 1000-m buffers influenced den site

selection by wolves in Algonquin Provincial Park, Canada. In our study, variables such as proportion of buffers composed of lakes and streams, slope, and elevation were important predictors of den site selection within 1000-m buffers indicating wolves were influenced by those habitat features within a radius of 1 km around dens. Nonetheless, AIC_c scores of models for the 100-m buffer scale were much lower than those of models for 1000-m buffers indicating that den site characteristics tabulated within the smaller buffers discriminated between used and random sites much better than variables tabulated within the larger buffers. Clearly, conditions immediately surrounding dens were the most important factors predicting location of den sites. We believe that for many wolf packs, large proportions of the landscape were unsuitable for den sites owing to logging and topography. Consequently, the size of suitable areas was small and options for selecting den sites based on characteristics at larger scales was more limited.

Effects of Human Disturbance and Habitat Change

We investigated how landscape and habitat changes affected den site selection by wolves. It was not our intent to address the effects of human activity at active dens on the behavior of wolves. We can make a few observations, however, about the effect that our intrusive sampling activities had on wolves at dens. Thiel et al. (1998) reported that wolves tolerated relatively intense human activity near dens throughout the denning season. Frame et al. (2007) experimentally tested the response of wolves to human intrusion nears dens and observed that tolerance by wolves related to the ages of pups. Wolves tended to remain at disturbed dens if pups were very young (<6 weeks old) and to move pups when they were older and more mobile. During our study, wolves were intensely disturbed during our visits to active dens. Indeed, we usually climbed part way into dens to move the video probe into deep, winding chambers. Nonetheless, our presence lasted only a few minutes and we did not return again that season. Wolves moved pups to new dens after our visits on only two occasions and in both cases pups were 5 weeks old. Some wolves returned to the same dens year after year despite our repeated annual visits. Clearly, our brief but intense disturbance did not force many wolves to abandon dens and our experience was similar to that reported by Frame et al. (2007).

Despite the tolerance of wolves to our visits, they generally avoided roads and logged stands when selecting den sites. Theuerkauf et al. (2003) and Norris et al. (2002) reported similar patterns of avoidance of roads and logged stands for wolves in the Bialowieza Forest in Poland and in Algonquin Provincial Park in Canada; respectively. Those factors, however, were of secondary importance for wolves in our study compared with presence of freshwater, gentle slopes, and low elevation. Wolves likely avoided habitats near roads and logged stands only if those other preferences were satisfied first. Indeed, one den that we located was 170 m from a road and only 12 m from a clearcut. Despite that exception, most dens were much farther from roads and logged stands. We suggest that the long-term use by humans of logged areas and roads was a factor influencing where wolves selected den sites, but once wolves had committed to den sites during parturition and pup weaning, they were resistant to short periods of intense human disturbance. They also successfully denned within landscapes heavily modified by human development. Nonetheless, wolves probably selected those modified landscapes out of necessity given limited availability of alternatives, and preferred to den in areas with less human disturbance. Therefore, biologists should be careful not to dismiss the effects of resource developments such as timber harvest and roads on wolves simply because they find dens in disturbed areas. Retaining roadless forested buffers >100m wide around low elevation major lakes and streams likely would preserve some den site options for wolves in extensively logged watersheds. Closing roads, wherever feasible, within that buffer likely would reduce the effects of existing roads on den site selection. Finally, with respect to both den site selection and reproduction by wolves, watershed-scale habitat reserves that encompass productive habitats for ungulate prey and suitable denning locations, and that at least partially protect wolves from harvest would likely be an effective strategy to reduce turnover in wolf packs and ensure wolf populations are resilient to habitat change owing to human activity (Person et al. 1996, Person 2001, Person and Russell 2008).

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Literature Cited

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. Ecology 63:1932–1948.

Alaback, P. B., and G. P. Juday. 1989. Structure and composition of low-elevation old-growth forests in research natural areas of southeast Alaska. Natural Areas Journal 9:27–32.

Allison, P. D. 2004. Convergence problems in logistic regression. *In* M. Altman, J. Gill, and M. P. McDonald (editors), Numerical issues in statistical computing for the social sciences. John Wiley and Sons, Hoboken.

Animal Care and Use Committee. 1998. Guidelines for capture, handling, and care of mammals. Journal of Mammalogy 74:1416–1431.

Ballard, W. B., and J. R. Dau. 1983. Characteristics of gray wolf, *Canis lupus*, den and rendezvous sites in Southcentral Alaska. Canadian Field-Naturalist 97:299–302.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south to central Alaska. Wildlife Monograph 98.

Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology. 70:2441-2443.

Burnham, K. P. and D. R. Anderson. 1998. Model Selection and Inference: a Practical Information-Theoretic Approach. Springer-Verlag New York Inc., New York.

Cluff, H. D., L. R. Walton, and P. C. Paquet. 2002. Movements and habitat use of wolves denning in the central Arctic, Northwest Territories, and Nunavut, Canada. Final report to West Kitimeot/Slave Lake Study Society, Yellowknife, Northwest Territories.

Farmer, C. J. 2002. Survival and habitat selection of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in a fragmented coastal temperate rainforest. Ph.D. Dissertation, State University of New York, Syracuse.

Frame, P. F., H. D. Cluff, and D. S. Hik. 2007. Response of wolves to experimental disturbance at homesites. Journal of Wildlife Management 71:316–320.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monographs. 105.

Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. *In* L. D. Mech and L. Boitani (editors), Wolves: Behavior, Ecology, and Conservation. University of Chicago Press, Chicago.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Hosmer, D. W., and S. Lemeshow. 2000. Applied Logistic Regression, 2nd edition. John Wiley and Sons, New York.

Lawhead, B. E. 1983. Wolf den site characteristics in the Nelchina Basin, Alaska. M.S. Thesis, University of Alaska Fairbanks, Fairbanks.

Matteson, M. Y. 1992. Denning ecology of wolves in Northwest Montana and southern Canadian Rockies. M.S. Thesis, University of Montana, Missoula.

McCune, B. 2007. Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. Journal of Vegetation Science 18:751–754.

McNay, M. E., T. R. Stephenson, and B. W. Dale. 2006. Diagnosing pregnancy, in utero litter size, and fetal growth with ultrasound in wild, free-ranging wolves. Journal of Mammalogy 87:85–92.

MacDonald, S. O., and J. A. Cook. 1999. The land mammal fauna of Southeast Alaska. Canadian Field-Naturalist 110:571–598.

Mech, L. D. 1970. The Wolf: The Ecology and Behavior of an Endangered Species. University of Minnesota Press, Minneapolis.

Menard, S. W. 2002. Applied Logistic Regression Analysis, 2nd edition. Sage Publications Inc., Thousand Oaks, CA.

Norris, D. R., M. T. Theberge, and J. B. Theberge. 2002. Forest composition around wolf (*Canis lupus*) dens in eastern Algonquin Provincial Park, Ontario. Canadian Journal of Zoology 80:866–872.

Person, D. K. 2001. Alexander Archipelago wolves: ecology and population viability in a disturbed, insular landscape. Ph.D. Dissertation, University of Alaska Fairbanks, Fairbanks.

Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. Journal of Wildlife Management 72:1540–1549.

Person, D. K., M. D. Kirchhoff, V. Van Ballenberghe, G. C. Iverson, and E. Grossman. 1996. The Alexander Archipelago wolf: a conservation assessment. USDA Forest Service General Technical Report, PNW-GTR-384.

Riggs, M. R., and K. H. Pollock. 1992. A risk ratio approach to multivariable analysis of survival in longitudinal studies of wildlife populations. *In* D. R. McCullough, and R. H. Barrett (editors), Wildlife 2001: Populations. Elsevier Applied Science, New York.

Smith, D. W., D. R. Stahler, D. S. Guernsey, M. Metz, E. Albers, L. Williamson, N. Legere, E. Almberg, and R. McIntyre. 2008. Yellowstone wolf report 2007. National Park Service, Yellowstone Center for

Resources, Yellowstone National Park, Wyoming, YCR-2008-01.
SPSS. 2004. SPSS 13.0 Brief guide. SPSS Inc., Chicago.
Theuerkauf, J., S. Rouys, and W. Jedrzejewski. 2003. Selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest, Poland. Canadian Journal of Zoology 81:163–167.
Thiel, R. P., S. Merrill, and L. D. Mech. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. Canadian Field-Naturalist 122:340–342.
Trapp, J. R. 2004. Wolf den site selection and characteristics in the northern Rocky Mountains: a multi-scale analysis. M.A. Thesis, Prescott College, Prescott, AZ.
Unger, D. 1999. A multi-scale analysis of timber wolf den and rendezvous site selection in northwestern Wisconsin and east-central Minnesota. M.S. Thesis University of Wisconsin, Steven's Point.
U.S. Forest Service. 1997. Tongass Land Management Plan Revision. USDA Forest Service R10-MB-338b.
Weckworth, B. V., S. Talbot, G. K. Sage, D. K. Person, J. Cook. 2005. A signal for independent coastal and continental histories among North American wolves. Molecular Ecology 14:917–931.
Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164-168.

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