

Chapter 11

Factors Influencing Homesite Selection by Gray Wolves in Northwestern Wisconsin and East-Central Minnesota

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Preface One of the most critical aspects of population dynamics in any animal species is the birth and successful rearing of young. Therefore, understanding the characteristics of areas where wolves give birth and rear pups (den and rendezvous sites) is important for proper management. In the Great Lakes region, the gray wolf has made a remarkable recovery, from a small remnant population in northeastern Minnesota to the recolonization of most of northern Wisconsin and the Upper Peninsula of Michigan. In this chapter, we review relevant literature on wolf dens and rendezvous sites and attempt to determine those factors most critical in the selection of homesites in the upper Great Lakes region.

11.1 Introduction

Much research has been conducted on den and rendezvous sites (collectively, “homesites”) of gray wolves (*Canis lupus*). However, with few exceptions (e.g., Norris et al. 2002; Theuerkauf et al. 2003; Capitani et al. 2006), this research has been essentially descriptive in nature, with little or no attempt to quantify those characteristics selected by wolves.

Den sites are often burrows in the ground, but wolves have also been known to den in beaver lodges, hollow logs, beaver dams, caves, or open pits (Joslin 1967; Mech 1970, 1993; Peterson 1977). It has been suggested that the den area is selected for its slope, aspect, sandy soil, and adequate drainage. Norris et al. (2002) found that wolves selected areas of pine and suggested that dens be protected at a relatively large scale. Theuerkauf et al. (2003) found that wolves selected dry conifer forests for both den and rendezvous sites. Rendezvous sites have been described as grassy areas, ~0.5 ha in size, with semiopen canopy. With few exceptions (Van Ballenberghe et al. 1975; Ballard and Dau 1983), rendezvous sites were found in lowland areas bordering bogs, beaver ponds, or wetlands with open water, a large system of trails, and beds or play areas where pups trampled extensive areas of grass (Joslin 1966).

In addition to these habitat characteristics, there is evidence that homesites may also be affected by spatial factors. Ballard and Dau (1983) and Gehring (1995) noted that den sites tended to be located in roughly the center of a wolf's territory. By contrast, Ciucci and Mech (1992) suggested that dens were randomly distributed within the territorial boundaries. Peterson et al. (1984) found that the distance from the natal den to the first rendezvous site was < 2 km, with successive rendezvous sites being located farther and farther from the natal den. Groebner (1991) noted that rendezvous sites fell in the center of a male wolf's territory, but along the edges of a female wolf's territory. Theuerkauf et al. (2003) found that wolves selected areas away from villages, forest edges, and intensively used roads for both den and rendezvous sites.

These findings suggest that multiple spatial and habitat factors affect homesite placement. Characteristics such as location within a wolf's territory and proximity to features such as water, roads, and a particular habitat type may affect the spatial placement of a homesite. Variables such as habitat type, level of fragmentation, human disturbance, and prey density may affect the gross placement of the site within the greater landscape. Microhabitat variables such as vegetation, visibility, availability of water, and other features may determine the specific physical location of the homesite. Others have suggested that it is important to investigate both spatial and habitat factors affecting resource use and homesite placement (Clark et al. 1993; Mladenoff et al. 1995; Arjo and Pletscher 2004).

As homesites may determine the reproductive success of a wolf pack (Harrington and Mech 1982), understanding the factors affecting their placement may prove critical to managers as wolves continue to expand numerically and geographically in the Great Lakes region. Our objectives were to characterize gray wolf den and rendezvous sites in northwestern Wisconsin and east-central Minnesota and suggest what features most strongly affect site selection.

11.2 Study Area

Research was conducted in northwestern Wisconsin and east-central Minnesota (Fig. 11.1). The habitat in the study area (21,591 km²) is primarily a patchwork of second growth northern deciduous (aspen-birch, *Populus tremuloides*-*Betula papyrifera*; sugar maple, *Acer saccharum*) and coniferous (white pine, *Pinus strobus*; balsam fir, *Abies balsamea*) forest, wetland deciduous shrubs (*Alnus rugosa*, *Salix*, *Fraxinus pennsylvanica*), wetland forest (*Thuja occidentalis*, *Picea mariana*, *Fraxinus nigra*, *Ulmus rubra*), emergent wet meadow (*Carex*, *Calamagrostis*), bogs (Ericaceae shrubs, *Sphagnum*), and agricultural lands (Curtis 1959). The topography in the area is a rolling plain with elevations mostly from 250 to 500 m above sea level. Land ownership includes private land, county and state forests, private industrial forest land, tribal lands, and federal land including the St. Croix National Riverway. Road densities within the study area range from 0 to 1.5 km/km² and human density is low, with an average of seven people/km² (Mladenoff et al. 1995).

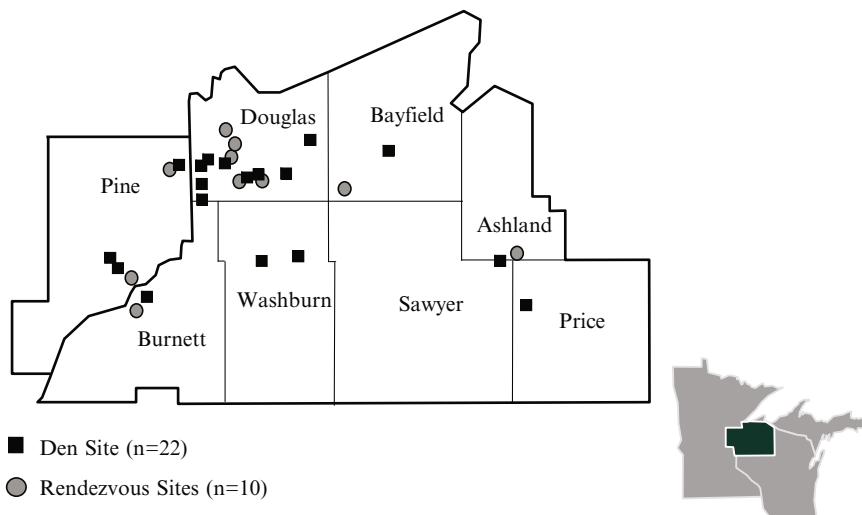


Fig. 11.1 Study area including the locations of timber wolf den and rendezvous sites investigated from July 1994 to August 2001 in counties (*thin lines*) of northwestern Wisconsin and east-central Minnesota (*bold lines*)

Available prey species include white-tailed deer (*Odocoileus virginianus*) and beavers (*Castor canadensis*), both of which have been shown to be primary food sources for wolves in the Great Lakes region (Mandernack 1983; Fuller 1989a; DelGiudice et al., this volume). Estimates of deer densities within the study area have ranged from 9.7 to 13.4/km² ($\bar{X} = 11.7/\text{km}^2$) since 1995 (Wisconsin DNR, unpublished data). Beavers are common in the study area, with helicopter surveys in 1998 estimating 0.61 active beaver colonies per kilometer square in northwest Wisconsin (Wisconsin DNR, unpublished data).

11.3 Methods

Wolf trapping and radio-collaring was conducted as part of the Wisconsin wolf monitoring program (Wydeven et al. 1995, this volume), and a study on impacts of highway development on wolves (Kohn et al. 2000, this volume). Wolves were trapped using modified Newhouse #14 foothold traps (Kuehn et al. 1986) and fitted with VHF radio collars (Telonics, Mesa, Arizona). Wolves were located by radio telemetry from both ground and fixed-wing aircraft two to five times weekly. Those areas that showed a tight cluster of locations (≥ 3 locations in a 1-km² area) within a 3–5 week period were investigated on foot after wolves had abandoned the area.

Homesites were confirmed by the presence of a burrow and excavated soils, scat, tracks, kills, activity areas, and heavily used trails (Joslin 1966; G.B. Kolenosky and Johnston 1967; Mech 1970; Ballard and Dau 1983). Location of the homesite was recorded using a handheld global positioning system (GPS; Garmin™ GPS 45, GPS III, Garmin International, Lenexa, KS) and mapped using Arcview 3.2 and ArcGIS 9.0 (hereafter, GIS; ESRI, Redlands, CA). Homesites were studied at three scales: (1) microhabitat (biotic and abiotic variables measured within 50 m of a site); (2) macrohabitat (location relative to roadways and spatial/structural analysis of habitat cover types located within 1.2 km of site); and (3) location within annual territory relative to an inner 25% core area. Field research was conducted from July 1994 through August 2001.

11.3.1 Location Within Annual Territory

Annual territories were based on locations from May 20 of the pre-den year to May 19 of the denning year. This time period was selected to begin after abandonment of the previous year's den and include only one parturition event. Territory boundaries were determined using the 95% minimum convex polygon method (MCP; Mohr 1947) within the animal movement extension (Hooge and Eichenlaub 1997) in GIS. We used the 95% MCP to maximize the distribution of wolf locations while eliminating outliers. In addition, MCP avoids bias in territory boundary estimation due to concentrations of telemetry locations. Territories were required to have ≥ 30 locations obtained in at least six different months of the year to be included in core analysis (Fuller and Snow 1988).

We used GIS to create a central core that was the same shape as the annual territory but only 25% of its area. The core area was created to determine if wolves were selecting the center of their territory when placing homesites. We recorded the occurrence of homesite and corresponding random sites in relation to this core. To our knowledge, no studies have analyzed specifically whether wolf territorial boundaries are dictated by den site placement or vice versa. Therefore, we also analyzed den site location in territories created from locations obtained between June and December of the previous year (pre-denning), January–May of the same year (denning, including construction and utilization), and June–December of the same year (post-denning).

11.3.2 Macroscale Analyses

Macroscale analyses were conducted within a 1.2-km radius buffer (4.2 km²) around homesites. This buffer was based on the average distance of radio locations for the only radio-collared female from her pup-occupied den (April 1–July 1). While this technique relied on data from only one individual, we believed it was

more tightly tied to the biology of the species than arbitrarily chosen distances used in previous studies (Unger 1999; Norris et al. 2002). Random sites corresponding to each homesite were also selected and buffered to allow comparisons between areas used as homesites and unused sites. The number of random sites in each annual territory varied with the size of the territory, based on one random site per 40 km². This area was chosen because it appeared to give adequate coverage of the home range while minimizing overlap between random sites.

To examine the effect of roads on homesite selection, presence or absence of roads within the buffers around homesites or random sites was recorded. Distance to closest road and density of roads within buffers were also calculated. Road types included in the analysis were highways, other paved roads, and improved (graded) unpaved roads passable by two-wheel drive auto but did not include unimproved forest roads and trails.

Vegetation cover type layers provided by the Wisconsin DNR (<http://dnr.wi.gov/maps/gis/datalandcover.html#overview>) and Minnesota Department of Natural Resources Data Deli (www.deli.dnr.state.mn.us) were used to analyze the habitat surrounding homesites and corresponding random sites. Habitats were grouped into 12 cover types, including 8 forests types (oak, pine, maple, aspen, mixed deciduous/coniferous, mixed other conifers, mixed other deciduous, and forested wetlands), grasslands, upland shrub, lowland shrub, and emergent wetlands. Minor habitat areas (<0.1% of home range) were combined with other habitats, and open water and urban areas were excluded from analysis. The proportion of the area within buffers around each homesite and random site classified as each of the above cover types was calculated and then analyzed to examine the effect of vegetation cover type on the selection of homesites. The GIS-based landscape structure and spatial analysis extension Patch Analyst (Elkie et al. 1999) was used to explore relationships and test for differences in landscape structure and pattern between homesites and randomly selected sites.

11.3.3 Microscale Analyses

Microhabitat variables at homesites were analyzed using a nested sampling technique (Higgins et al. 1994). Variables measured at each site included percent canopy cover, percent visual obstruction, tree species composition, slope, aspect, and whether or not a homesite was within 50 m of a permanent water source. These variables were selected as attributes likely to be biologically important in the selection of a home site (Joslin 1966, 1967; G.B. Kolenosky and Johnston 1967; Mech 1970; Stephenson 1974; Ryon 1977; Ballard and Dau 1983; Fuller 1989b). The type of den structure (burrow, hollow log, beaver lodge, and cave) and den dimensions were also recorded. Den sites were generally analyzed after deciduous trees had shed their leaves in autumn to more closely resemble the vegetative conditions of late winter/early spring when wolves likely selected sites (Thiel et al. 1997). Rendezvous sites were generally investigated within 2 weeks of abandonment.

11.3.4 Statistics

11.3.4.1 Macroscale

The proportions of each cover type within buffers around homesites were compared to the proportions in buffers around random sites within the boundaries of annual territories using a Wilcoxon matched-pairs signed-rank test (SPSS, Inc. 1994). The mean distance to roads from homesites and random sites and the density of roads in buffers were analyzed using this same test.

For homesite location within a territory, we used the binomial probability analysis (SPSS, Inc. 1994) to determine if homesites were more likely to be located within the center 25% core of the territory. For location in relation to roadways, we used Fisher's exact test (Zar 1984) to examine whether buffers around homesites were less likely to contain a road. Data obtained from Patch Analyst were analyzed using the Wilcoxon matched-pairs signed-rank test (SPSS, Inc. 1994) to test for differences in measures of landscape pattern and structure around homesites versus around random sites. Homesites from a particular territory were statistically compared to random sites analyzed in that same territory. A paired analysis protocol was used because at our study scale (1.2-km radius circle) the habitat in one wolf pack territory could differ widely from that of another.

All macroscale variables that demonstrated significant differences ($P < 0.05$) between homesites and randomly selected sites were retained for further multivariable analysis. Spearman rank correlation analysis was used to identify significantly correlated macroscale variables. When two variables were correlated ($|r| > 0.5$), only one was kept, based on its ecological relevance. Noncorrelated macroscale variables were subjected to forward stepwise logistic regression (SPSS, Inc. 1994). Logistic regression was chosen because it is generally robust to violations of normality and can be used with discrete and continuous variables (Gorenzel and Salmon 1995).

11.3.4.2 Microscale

For microscale analysis, two sites located randomly within the annual territory were selected. Data for each variable were then collected in a similar fashion at all sites for statistical analysis. Mann Whitney U tests, Fisher's exact tests, and Spearman's rank correlation analysis were used to test for differences between data collected at homesites and that collected at random sites.

The data presented in this chapter represent combined information from two separate studies conducted by Unger (1999) and Keenlance (2002). Because of methodological differences, much of the data needed to be reanalyzed. Multivariate analysis was not performed on microhabitat scale variables, and in some cases analyses were restricted to only those homesites examined in one of these studies.

11.4 Results

11.4.1 Den Sites

Twenty-two dens in 15 individual packs were identified from July 1, 1994 to August 31, 2001 (Fig. 11.1). Based on territory size, random sites between 1 and 8 were selected within each territory ($n = 63$). We were able to calculate an annual territory ($\bar{X} = 202 \text{ km}^2$, $SD = 115$) for 18 den sites, and 14 fell within the 25% central core ($X^2 = 26.7$, $p < 0.001$). We calculated a pre-denning ($\bar{X} = 133 \text{ km}^2$, $SD = 82$), denning ($\bar{X} = 120 \text{ km}^2$, $SD = 72$), and post-denning ($\bar{X} = 177 \text{ km}^2$, $SD = 69$) territory for 9, 9, and 6 den sites, respectively. Wolves also selected the 25% central core during each of these periods ($p = 0.001$, 0.001 , and 0.005 , respectively). Buffers (1.2-km radius) around dens were less likely to contain a road (7 of 22) than buffers around random sites (40 of 63, $P < 0.001$). Mean distance to roads from a den was more (1,562 m, $SE = 207$) than from a random site (821 m, $SE = 117$, $P = 0.006$). Mean road density within buffers around dens (1.08 km/km^2 , $SE = 1.03$) was not significantly different than in buffers around random sites (1.31 km/km^2 , $SE = 0.86$, $P = 0.37$).

Habitat analysis revealed that buffers around dens contained significantly less jack pine ($P = 0.005$), grassland ($P = 0.009$), emergent wet meadow ($P = 0.043$), and mixed/other coniferous forest ($P = 0.043$), and greater amounts of lowland shrub ($P = 0.047$) than buffers around random sites. There was no statistical difference in the average value of any index of landscape structure in buffers around homesites compared to buffers around random sites.

We entered location within territory, presence/absence of roads, proportion of lowland shrub, open grassland, and jack pine habitats within buffers around dens into a forward stepwise selection procedure within logistic regression to further determine which variables most influence den site selection. Our analysis revealed selection of the central core to be the only significant and most useful predictor of den site placement (Wald Statistic, $P = 0.0045$). The model had $R^2 = 0.29$ and correctly classified 80% of all sites.

We statistically analyzed microscale data from 12 den sites. Wolves selected areas of steeper slope ($p = 0.016$) for den placement. Spearman's rank correlation indicated that the relative percentages of individual tree species between den and randomly selected sites were not correlated, and therefore different ($r = 0.215$, $P = 0.551$). Den sites had higher percentages of upland tree species such as aspen, sugar maple, and balsam fir, while random sites had high percentages of more hydric species such as tag alder, black ash, and tamarack. Of 22 dens investigated, 20 were burrows and two were located under uprooted trees. The entrances of nine of these burrows averaged 50 cm ($SD = 11.2 \text{ cm}$) high by 47 cm ($SD = 10.7 \text{ cm}$) wide. The tunnels generally sloped downward from the entrance into the den. The burrows averaged 230 cm ($SD = 51 \text{ cm}$) in length, 68 ($SD = 19 \text{ cm}$) in width, 47 cm

(SD = 15 cm) in height, with an average volume of 0.79 m³ (SD = 0.52 m³). Dens were found to be clean and dry with no evidence of debris, leaves, or wolf scat. Some dens did have small amounts of porcupine (*Erethizon dorsatum*) scat deposited after wolves had vacated the den. Of nine dens that were entered, seven were found to be simple tubes or round chambers without a separate birthing chamber. Wolves showed no distinct selection for the orientation of the entrance of the burrow or hill aspect. Of 12 burrows, 4 were on a northerly aspect, 5 were on a southerly aspect, and 3 were in flat terrain with no noticeable aspect.

11.4.2 Rendezvous Sites

Ten rendezvous sites in nine pack territories were located (Fig. 11.1). One had a den associated with it, in the form of an uprooted white cedar (*Thuja occidentalis*). Mean distance to roads (1,296 m, SE = 290 vs 1,166 m, SE = 149, $P = 0.68$), and road density in buffers (1.12 km/km², SE = 0.31 vs 1.37 km/km², SE = 0.26, $P = 0.37$) were not significantly different between rendezvous and random sites, respectively.

We calculated an annual territory for nine rendezvous sites. Wolves did not show selection of the 25% central core area of their territory, with four of nine being located within the inner core ($X^2 = 1.81$, $P = 0.337$). Buffers around rendezvous sites were not less likely to contain a road than those around random sites ($P = 1.000$). Wolves selected buffer areas with significantly more aspen ($P = 0.046$). No indices of landscape structure and pattern were found to be significantly different in buffers around rendezvous sites compared to buffers around random sites. Because only one variable (aspen habitat) was shown to be significant, we were unable to perform multivariate analysis on rendezvous sites.

At the microhabitat level, wolves selected rendezvous sites more often associated with water ($P = 0.007$) and higher visual obscurity ($P = 0.050$). Spearman's rank correlation indicated that the tree species between rendezvous sites and randomly selected sites were not correlated and, therefore, different ($r = 0.525$, $P = 0.119$). Rendezvous sites had higher percentages of wetland species such as tag alder, red maple, and black ash while random sites had higher percentages of upland species such as aspen and sugar maple.

11.5 Discussion

11.5.1 Den Sites

Spatial location appears to be crucial in the selection of den sites by wolves in northwestern Wisconsin and east-central Minnesota. Wolves selected the inner core of their annual territory when placing a den. This supports previous assumptions

(Ballard and Dau 1983; Gehring 1995) and findings (Theuerkauf et al. 2003). Dens also were located in the central core of the territory regardless of time of year (pre-den, denning, and post-denning periods) when the territory boundaries were determined. Although wolves will form territories in the absence of a den (Rothman and Mech 1979), our data, particularly our pre-denning results, suggest that territorial boundaries have a strong influence in the placement of a den site.

Possible reasons for placing a den in the central core of an annual territory are optimal foraging and avoidance of interpack strife. Prey abundance may also influence the selection of a den site (Jordan et al. 1967; Lawhead 1983). In the Great Lakes region, wolf pups are generally born in March and April (Fuller 1989b). This coincides roughly with spring deer migration and the abandonment of winter yard areas (Nelson and Mech 1981; Messier and Barrette 1985), resulting in prey that are more widely dispersed (Nelson and Mech 1981). Wolves have been shown to travel long straight-line distances to bring prey to the den (Young and Goldman 1944; Mech 1970; Mech et al. 1999), and must travel repeatedly to food sources to maintain pups (Mech 1970; Groebner 1991). In placing a den near the center of their territory, wolves may be showing a central foraging tendency (Stephens and Krebs 1986) to minimize travel distance to prey, and thus reduce handling time before returning to the den.

Previous research has shown that wolf territories often overlap (Van Ballenberghe et al. 1975; Peterson 1977; Fritts and Mech 1981; Nelson and Mech 1981; Peterson et al. 1984; Jędrzejewski et al. 2007). This tendency also occurred in northwestern Wisconsin and east-central Minnesota (Gehring 1995; Shelley and Anderson 1995; Unger 1999). In these “buffer zones” (Mech 1977), aggression between packs can occur, sometimes resulting in death (Mech 1994). Kohn et al. (2000) reported that aggression between packs accounted for 2 of 18 mortalities of collared wolves in northwestern Wisconsin. Locating the den in the central part of the territory should minimize intrusion on the den area by neighboring packs. In addition, placing the den in the central core would minimize the distance required for reaching all edges of the territory when marking and patrolling these boundaries (Mech 1970; Briscoe et al. 2002).

Theuerkauf et al. (2003) suggested that human disturbance and persecution in and around the Białowieża Forest of Poland resulted in wolves choosing the center of their territory for homesite placement. Lower human population densities and legal protection likely lessened the impact of human disturbance in our study area. Wolves in our study area did choose areas farther from roads. However, we did not detect differences in road density between den and random sites, and road occurrence was not shown to be a significant variable in multivariate analysis. As wolves expand into more human-dominated range, anthropogenic disturbance may become a more important factor in den site selection, necessitating further research.

Twenty of 22 dens studied were burrows in the ground, which have been suggested to be the preferred den structures for wolves (Joslin 1967). Also, 13 of 15 packs used different den sites in subsequent years. These findings suggest that suitable den sites were not limited in our study area.

Ciucci and Mech (1992) determined that wolves in the Superior National Forest in northeastern Minnesota placed dens randomly within their territories. They used a probability distribution of wolf dens within 60% of the mean radius from the approximate center of the territory to the edge using MCP. Our differences could be due to our methodology. Ciucci and Mech (1992) found that den location was related to territory size, with larger territories having dens more centrally located. Our mean annual territory was comparable to previous studies in Minnesota (Van Ballenberghe et al. 1975; Fritts and Mech 1981; Berg and Kuehn 1982; Fuller 1989a), but it appeared wolves in our study selected for the central core of their territory, regardless of size.

More random distribution of dens and traditional den use (used ≥ 2 years) in northern Minnesota may be due to continuous occupation by wolves, and some influence of artificial feeding sources in the form of garbage dumps (Ciucci and Mech 1992). We identified only two packs using traditional dens. The recolonizing nature of the population during our research (1994–2001) may have caused more territorial fluidity than in the established population studied by Ciucci and Mech (1992). We were unaware of any open garbage dumps available in our study area.

Our analysis of habitat showed dens were found in areas with less emergent wet meadow, grassland, jack pine, and mixed conifer/deciduous forest and more lowland shrub. We believe these results were influenced by ease of digging, escape and thermal cover, and the selection of dry upland areas for den sites. Emergent wet meadows precluded digging during den construction, while grasslands and jack pine (mostly plantations <10 years old) lacked adequate cover.

The greater amount of lowland shrub habitat in buffers around dens was due to placement of dens on slightly elevated areas surrounded by dense alder wetlands. Such areas would provide security and escape cover while also placing dens near a water source for the nursing female.

At the microscale level, wolves selected for areas of steeper slope and drier habitats. Den sites were placed in tree communities indicative of upland, well-drained soils (trembling aspen, sugar maple, balsam fir). This finding agrees with previous den site descriptions (Murie 1944; Stenlund 1955; Jordan et al. 1967; Joslin 1967; Mech 1970; Stephenson 1974; Peterson 1977; Ballard and Dau 1983; Fuller 1989b). Steep slope and sandy (dry) soil conditions have been suggested as important for ease of digging and drainage purposes (Jordan et al. 1967; Stephenson 1974). We did not find that visual obscurity was an important attribute for selection in the immediate vicinity of the dens, in contrast to Joslin (1967) and Stephenson (1974). While wolves did select more dense lowland shrub nearby, the area immediately around dens (<20 m) tended to be relatively open. We did not detect selection of a specific aspect for den placement, but as our research was conducted at lower latitudes than most studies, southern exposures may have been less important (Stephenson 1974; Ballard and Dau 1983; Fuller 1989b). Our den dimensions were similar to those reported by Murie (1944), Joslin (1967), Mech (1970), Stephenson (1974), and Ryon (1977), but most dens did not end in an enlarged chamber as described by some (Murie 1944; Joslin 1967; Mech 1970; Stephenson 1974; Ryon 1977; Trapp 2004).

11.5.2 Rendezvous Sites

Rendezvous site selection appeared to be determined mainly by habitat factors as opposed to spatial factors such as territory boundaries and roads. In contrast to our findings on den sites, wolves did not select for the center of their territory or areas devoid of roads for rendezvous site. The increased mobility of maturing pups at rendezvous sites, and therefore their greater ability to avoid danger (predators, humans), may explain this trend. Location of rendezvous sites within aspen habitats may reflect prey availability. Deer, the main food of wolves, feed heavily on forage species found in aspen habitat during spring and summer (McCaffery et al. 1974).

Rendezvous sites were located in wetland community types. Within this wetland, habitat sites were in close proximity to open water, suggesting that available water may play an important role in the site selection process. Wolves usually move from the den to the first rendezvous site when pups are 8–10 weeks of age (Mech 1970; Peterson et al. 1984), which coincides roughly with when they are weaned (Mech 1970; Harrington and Mech 1982). Water is very important to adult wolves for digestion after gorging (Mech 1970). Pups are relatively sedentary at the rendezvous site (Joslin 1967; Theberge and Pimlott 1969). Thus, a permanent water source nearby would be beneficial to pups for digestion, hydration, and evaporative cooling during the warm summer months.

Wolves also selected for higher visual obscurity within this wetland habitat. Higher visual obstruction might be selected to minimize possible conflicts between pups and intruders (Theberge and Pimlott 1969; Harrington and Mech 1982; Veitch et al. 1993; Thiel et al. 1998).

11.6 Summary and Management Recommendations

We studied gray wolf den and rendezvous site selection in northwestern Wisconsin and east-central Minnesota. Spatial location within the wolves' territories appeared the most important factor in the selection of den sites, whereas rendezvous site location was determined primarily by habitat. In the first several weeks after birth, the resource needs of the pups are provided for at the den by the mother. With these needs met, protection of the pups from intruders or competing packs may become the dominant concern in the placement of the den. The increased mobility of pups by 8 weeks of age probably makes variables such as location within the territory and lower road density less important than habitat variables for rendezvous site selection. In addition, as pups mature and are weaned, an increased need for resources may dictate the move to a rendezvous site in wetland habitat where water and higher visual cover are available.

Hierarchy theory is important for studies of habitat selection and foraging behavior (Allen and Starr 1982; Pribil and Picman 1997). Wolves likely select homesites in this manner with the selection of a territory on the landscape followed by selection of an area within this territory, and finally the selection of a specific

microscale location to birth and raise the pups. In our study, wolves selected for the central core of their territory when placing a den site. Within this central core area selected areas of lower road density, upland habitat, and steep slope. Wolves selected areas of aspen habitat for rendezvous sites and within this habitat chose wetland areas in close proximity to water and high visual obscurity.

The data and conclusions presented here provide a further understanding of a factor heavily influencing wolf population dynamics, but must be viewed in the context of larger scale habitat selection by wolves. Without suitable habitat in which to establish a territory, the selection of high quality homesites may become more difficult with a consequent potential reduction in pup production.

Currently, homesite availability does not seem to be a limiting factor in north-west Wisconsin and east-central Minnesota. While areas around dens were less likely to contain a road than areas around random sites, the avoidance of human disturbance does not seem to be driving homesite selection. Based on these findings, the healthy growth of the wolf population in the region during the last 15 years (Erb and DonCarlos, this volume; Beyer et al., this volume; Wydeven et al., this volume), and given current levels of protection and public attitudes toward wolves, broad-scale protection of homesites seems unnecessary. Situations involving vulnerable population segments or areas with a high potential for human–wolf conflict (e.g., the edge of the recolonization front), however, may require protection of homesites. Based on our data, the best indicator of den site location is the identification of the 25% inner core of the annual territory as estimated by the 95% MCP of home range locations of radio-collared wolves.

All discussions of wolf resource selection and population dynamics must be viewed in the context of current levels of legal protection and public acceptance. Changes in either could quickly lead to changes in wolf population levels and resource selection, including homesite selection.

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