LOCATION MATTERS: AN EIGHTEEN YEAR SPATIAL AND TEMPORAL ANALYSIS OF THE RECOLONIZATION OF A DISJUNCT POPULATION OF GRAY WOLVES (CANIS LUPUS)

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AN EIGHTEEN-YEAR SPATIAL AND TEMPORAL ANALYSIS OF
RECOLONIZING GRAY WOLVES (CANIS LUPUS) IN A DISJUNCT POPULATION

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ABSTRACT

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Most gray wolves in the United States live in disjunct populations. Management of isolated populations is important in sustaining the species. The Central Forest Region (CFR) of Wisconsin is home to one such disjunct population. Wolves began recolonizing the CFR in the early to mid-1990s. In this study, wolf recolonization was divided into three distinct Time Periods: Early (1994-1999), Mid (2000-2005), and Late (2006-2012). Habitat Classes of individual pack territories were defined as Optimal, Mixed, and Marginal, based on features known to influence wolf habitat selection or avoidance. These were: (1) percent public land, (2) percent agriculture, and (3) road density. The influence of Time Period and Habitat Class on pack territory size, mid-winter pack size, reproductive performance, wolf-human conflicts, human-caused wolf mortalities, territory persistence and reproductive persistence were analyzed. Pack demographics were similar across Time Periods, except that pup production was slightly lower during the Mid Time Period than during Late. Marginal Habitat packs had smaller mid-winter pack sizes, fewer pups in mid-summer, increased conflicts with humans, five times greater human-caused mortalities, and lower reproductive persistence. Pack territory location matters. Results show how increasingly human-altered landscapes affect wolves’ viability and indicates the extent to which wolf recolonization may or may not be successful.
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CHAPTER I
THE GRAY TIMBER WOLF (*CANIS LUPUS*): AN APEX PREDATOR’S
RETURN TO THE GREAT LAKES REGION

INTRODUCTION

Significance of Top Predators

The importance of top predators in sustaining biodiversity and ecological integrity is well documented (Power *et al.*, 1996; Miller *et al.*, 2001; Wilmers *et al.* 2003, Sergio *et al.*, 2008; Wilmers *et al.*, 2007; Beschta and Ripple 2010; Estes *et al.*, 2011). The interactions that occur between apex predators and their environment influence the full health of the system and form a complex tapestry. In his description of the biotic pyramid, Aldo Leopold first described a trophic cascade by emphasizing the functioning of each layer as dependent on the cooperation and competition of its diverse parts (Leopold 1949). Large carnivores are at the apex of this biotic pyramid. In terrestrial North America these carnivores are black bears (*Ursus americanus*), brown bears (*Ursus arctos*), mountain lions (*Puma concolor*), and gray wolves (*Canis lupus*). In some systems they have the ability to reduce the abundance of their prey. Large carnivores are known to limit populations of their prey, leading to changes in the structure of the whole community (McLaren *et al.*, 1994; Ripple and Beschta 2007; Sergio *et al.*, 2008).

Gray wolves have been characterized as keystone species (McLaren and Peterson 1994, Power *et al.*, 1996; Miller *et al.*, 2001; Eisenberg 2010) with impacts on their ecosystems that are disproportionate to their abundance, and thus their removal often results in a series of changes within the system (Paine 1969; Power *et al.*, 1996; Lee *et al.*, 2012). Paine (1969) states that the activity and abundance of keystone species
determine the structure and integrity of the community. Large predators decrease the
densities of ecologically significant prey species (typically primary consumers) thereby
excluding other species from the community, either through competition or consumption
(Mills et al., 1993). When the density of keystone species falls below some threshold,
community species diversity decreases through competitive exclusion; this triggers an
ecological chain reaction ending in degraded or simplified ecosystems (Estes and
Palmisano 1974; Power et al., 1996).

Wolves are a strongly interactive species whose removal or substantial reduction
leads to significant changes in their ecosystems (Soule et al., 2005; Rooney and
Anderson, 2009). For example, Hebblewhite et al. (2005) observed increased elk
(Cervus canadensis) abundance, lower net twig production by willows (Salix spp.),
decreased density and diversity of songbirds, and decreased abundance of beaver (Castor
canadensis) lodges in Banff National Park, where wolf densities were low.

Keystone species (large carnivores) also affect the population sizes of dominant
ungulate herbivores in many ecosystems (Wilmers et al., 2003a; Hebblewhite et al.,
2005, Soule et al., 2005). Reduced ungulate abundance in turn reduces herbivory
pressure on plants, thereby influencing the structure of plant communities (McLaren et
al., 1994; Beschta, 2004; Ripple and Beschta, 2005; Sergio et al., 2008, Beschta and
Ripple, 2010). Following a severe reduction in the wolf population on Isle Royale,
McLaren and Peterson (1994) observed a depletion of balsam fir (Abies balsamea) forage
as moose (Alces alces) numbers grew. Callan et al. (2013) found increased forb and
shrub species richness, on a local scale, in high wolf areas in Wisconsin. While
Bouchard et al. (2013) found mean leaf size of indicator plants in the Great Lakes region
(GLR) were greater in areas with the longest wolf occupation, they found the effect size too small to suggest that wolves generated a sufficient trophic cascade to halt or reverse plant diversity in the near term. D.G. Flagel et al (2016) noted wolf presence altered deer herbivory in GRL forests. These predator-driven effects may be transmitted to the plant community, affecting species composition and nutrient cycling (Leopold 1933; McLaren et al., 1994, Ripple and Beschta 2007; Sergio et al., 2008).

In addition to direct pressure on prey abundance, top predators can also control prey indirectly by influencing prey behavior and distribution, resulting in a behaviorally mediated trophic cascade (Kauffman et al., 2010). In an effort to be less vulnerable in the presence of predators, prey will alter their group size, length of various activities (e.g. reducing feeding time), foraging patterns, breeding sites, and habitat use (Leopold 1933; Lima and Dill, 1990; Miller et al., 2001; Childress and Lung, 2003; Ripple and Beschta 2004; Fortin et al., 2005; Beshta and Ripple, 2010). Following the reintroduction of the gray wolf in Yellowstone National Park (mid-1990s), Beschta and Ripple (2010) noted increased cottonwood (Populus spp.) recruitment within riparian areas. They hypothesized that such areas were avoided by elk due to their increased vulnerability to wolf predation. In contrast, Kauffman et al. (2010) attributed the failure and pattern of aspen (Populus tremuloides) recruitment to a gradual increase in elk abundance rather than predation risk responses by elk.

Large predators also affect smaller predators in their environment (Miller et al., 2001; Ripple and Beschta, 2005). Large carnivores typically decrease the number of small predators (mesopredators) through predation and distribution (Peterson 1995 and Flagel et al., 2017). Crabtree and Sheldon (1999) noted a 50% reduction in coyote
(Canis latrans) numbers during two winters following the reintroduction of gray wolves in Yellowstone National Park. Conversely, in the absence of top predators, mesopredator abundance and distribution increases, a phenomenon known as mesopredator release. Increased mesopredator abundance, in turn, affects biodiversity and small prey community structure (Miller et al., 2001; Ripple and Beschta 2005; Sergio et al., 2008; and Roemer et al., 2009). The increase in mesopredator abundance leads to increased predation on small native species, which influences their geographical distribution and threatens these conservation-sensitive species with extinction (Sergio et al., 2008; Roemer et al., 2009; Eisenberg, 2010). In Australia, Johnson et al. (2006), found a strong positive relationship between the survival of native marsupials and the density of dingo populations. The dingoes were hypothesized to control populations of introduced mesopredators which decreased the abundance of smaller, native prey items in other areas (Johnson et al., 2006). In the GLR and Wisconsin, wolves seem to effect mesopredator distribution more than abundance (Flagel, et al., 2017; Crimmins and Van Deelen, 2019).

The broader ecological community is additionally influenced by top predators’ ability to moderate the late winter reduction in carrion (Wilmers et al., 2003a; Wilmers and Getz, 2005; Sala, 2006). Wilmers and Getz (2005) found that wolves buffer some effects of climate change, such as the reduction in snow depth and the increase of earlier winter thaws, by inadvertently providing carrion for other scavengers during these light winters when fewer carcasses exist. Wolves also reduce the pool of weak and old animals at the end of severe winters. Furthermore, Wilmers et al. (2003b) observed increased diversity in scavenger species at wolf kills leading to increased biodiversity and
larger populations of scavenger species. By generating carrion throughout the winter, wolves allow scavengers to adapt to the changing environment over a longer, more natural time scale (Wilmers et al., 2003a; Wilmers and Getz, 2005; Wilmers et al., 2007; Sala, 2006).

It has long been argued that large carnivores hold intrinsic value (Olson, 1938; Leopold, 1949; Mech, 1970; Lopez, 1978; Sergio et al., 2008). As far back as 1938, Sigurd Olson wrote of the aesthetic and ecological importance of large predators: “The timber wolf is an integral part of the wilderness community, the destruction of which would destroy the fine balance between related forms. To eliminate as vital a relationship as exists between predatory forms and the animals they prey upon, to destroy mutual dependence, means artificiality has entered the wilderness picture.” Aldo Leopold’s account of the “green fire dying” in an old wolf’s eyes announced a new perspective on our relationship to the land, and the relationship of predator and prey and its ecological significance (Leopold, 1933; Meine, 2009). Before the gray wolf was listed as an endangered species in 1973, Mech (1970) wrote: “Though the gray wolf plays a significant, if not crucial, part in its natural community, some would argue that its mere existence as a species is value enough for its continued presence.” Native Americans, such as the Anishinabeg (Ojibwa), link their existence with their brother, Ma’iiingan, the wolf. Original man was forever linked to Ma’iiingan by their Creator; what happens to one will happen to the other, be it fear, respect, or hatred (USDA-APHIS, 2006; David, 2009). By their inherent charismatic appearance and behavior, large predators also serve as flagship species—poster species—to attract funding and attention to a larger cause (Sergio et al., 2008).
Lastly, large predators provide economic benefits not only as game species, but also aesthetically and financially as a curiosity. Visitors to Yellowstone National Park were estimated to have paid 35 million dollars in 2005 for the opportunity to simply view wolves from a distance and hear them howl (Duffield et al., 2006). For many people, the wolf is important as a symbol of the wilderness; the wolf keeps the wilderness wild (Theberge, 1975; Mech, 1995). Mech and Boitani (2003) summarizes: “This animal that sits on its haunches at the top of the food chain has become a symbol of the wilderness, an icon for environmentalists, and a poster child for endangered species recovery efforts.”

**Wolf Biology**

**General**

The gray wolf has lived and survived in diverse and ever-changing environments throughout most of the Northern Hemisphere, both pre- and post-European settlement (Mech, 1970; Boitani 2003). Mech (1970) describes the gray wolf as a strong, intelligent animal that can travel long distances to seek out, kill, and eat vulnerable game with enough safety and efficiency to maintain its species. It is this intelligence – to quickly learn and retain knowledge for extended periods – that has enabled the gray wolf to endure changes and stresses within its environment by making minor changes in its mode of living (Mech, 1970; Packard, 2003). Primary prey are medium and large mammals that vary by locale; in Wisconsin the primary prey is white-tailed deer (*Odocoileus virginianus*) and beaver (*Castor canadensis*), where the two coexist (Mech, 1970; Peterson and Ciucci, 2003).

Gray wolves are the largest members of the Canidae, or dog family. Gray wolves reach sexual maturity around twenty-two months of age. Mating occurs once a year,
usually February; following an average gestation period of 63 days, litters of five to six pups are born (Mech, 1970; Fuller et al., 2003). While pup (< 5 months) survival rates are difficult to determine (Fuller et al., 2003; Mech, 1977) found that in wolf packs in northeastern Minnesota, pup mortality rates varied from seven to 65 %, with malnutrition and intraspecific strife accounting for 58 % of these deaths. Wydeven et al. (2009) found that pup survival in Wisconsin averaged 28 % from 1979-2007. Few wolves live longer than four or five years, although some females survive and continue to produce pups as late as seven years of age (Fuller et al., 2003; Mech et al., 2016).

Social environment–the pack

Mech (1970) describes a population of wolves as wolf packs occupying adjacent and occasionally overlapping regions within their range. Although packs are strong, close-knit familial groups (parents and off-spring), immigration and emigration into and out of the packs occurs as young wolves disperse (Mech and Boitani, 2003). Packs bud and split, creating new packs and developing a population-scale territorial mosaic. Gaps are created within this mosaic when wolf packs dissolve or when human exploitation occurs (Mech and Boitani, 2003).

Wolf packs are family groups that move within exclusive territories, are hostile to strangers from neighboring packs, and are a function of their social and physical environments (Mech, 1999; Packard, 2003). Pack members are usually offspring of the breeding pair, but can include the wolves that either are siblings to, or unrelated to the breeders (Packard, 2003). Mean pack size in the GLR ranged from 2.6 to 5.5 wolves (Beyer et al., 2009; Erb and Don Carlos, 2009; Wydeven et al., 2009), with a range of two to twelve wolves in Wisconsin (Wydeven et al., 2011). All members of the pack
participate in the care and feeding of the pups. It is this continued contact – caring, playing, teaching – with parents, littermates, and siblings that establishes the strong social bonds between members of a pack (Mech, 1970; Mech and Boitani, 2003; Packard, 2003). For wolves, this social structure provides the support needed to survive and thrive in the challenges of their changing physical environment. Dispersal of offspring generally occurs between 10-54 months but can be as young as five months (Fuller, 1989; Fuller et al., 2003; Mech and Boitani, 2003). Wolves in Wisconsin dispersed between eleven and twenty-six months of age (Treves et al., 2003 and 2009). Food competition and sexual maturity are two driving forces of dispersal from the natal pack (Mech, 1970). As the breeding pair controls the feeding of their offspring, older siblings and subordinate members may choose to strike out on their own when food is scarce and prioritized for the pups (Gese and Mech, 1991).

A breeding pair’s tenancy averages four years, but varies from one to eight (Fuller et al., 2003; Mech et al., 2016). This familial connection, coupled with communal (pack) participation in raising pups, illustrates the intense cohesive nature of pack bonds (Mech, 1970). These strong social bonds make wolf populations more vulnerable, as the death of one or both breeders may cause instability within the pack and may fracture the pack, thereby leaving small packs with very young pups and dispersing pack members more susceptible to mortality (Mech, 1970; Mech and Boitani, 2003; Brainerd et al., 2008).

**Physical environment – territory**

A pack’s territory is the epicenter of its physical environment and provides the necessary resources (food, water, and space) to enhance pack survival. Packs
aggressively defend their territory against neighboring packs in defense of these resources (Fuller et al., 2003; Mech and Boitani, 2003).

Gray wolves are habitat generalists; they exist in a broad range of habitats from grasslands and tundra to forest (Fuller et al., 2003; Mech, 1995; Mech and Boitani, 2003; Mladenoff et al., 1995 and 2009; Treves et al., 2009). Mladenoff et al. (2009) noted that as late as 1980, wolves were believed to require vast wilderness to survive. Thiel et al. (2009) noted that as the wolf population in Wisconsin’s Central Forest Region (CFR) increased, wolves began to inhabit areas within and around human-dominated landscapes (e.g. farms, cranberry and forest industries, and military training areas). In human-dominated landscapes gray wolves incur greater human-caused mortalities through accidental killings (vehicular), deliberate illegal wolf killings (poaching), and legal wolf killing (depredation control – Wydeven et al., 1995 and 2009; Mladenoff et al., 1995 and 2009; Stenglein, 2014; Stenglein et al., 2015 and 2018).

Areas with low road density are preferred by wolves. Gray wolf survival is enhanced in areas with minimal human accessibility (Thiel, 1985; Mech et al., 1988; Mech, 1995; Mladenoff et al., 2009). High road density is a proxy for high human contact levels that may result in human-caused mortality (Kohn et al., 2009). Road density less than 0.60 km/km² is the standard cutoff for areas expected to be preferred and inhabited first by wolves (Thiel, 1985; Mech et al., 1988; Mech, 1995; Mladenoff et al., 2009). Once low road density areas are occupied, wolves settle into areas with higher road densities, especially with road-less areas nearby (Mech et al., 1988; Mladenhoff et al., 1995, 1999 and 2009; Kohn et al., 2009). Though wolves will use low maintenance roads, snowmobile and ATV trails, Mech et al. (1988) determined that the threat from
even these smaller roads resulted in increased human access and increased human-caused wolf mortality. Wydeven et al. (2001) found human-caused mortalities accounted for 60% of wolf mortality at road densities greater than 0.63 km/km², and the predominant form of mortality at road densities greater than 0.78 km/km². Road density is typically associated with developed (urban) and agriculture land use types which pose a risk to wolf security (Mladenoff et al., 2009).

Wolves existing in human-dominated landscapes experience higher wolf-human conflict (Treves et al., 2002; Ruid et al., 2009). The predominant source is wolf depredations on domestic animals including livestock, hunting hounds, and pet dogs. Depredation and harassment of livestock, hunting hounds, and pet dogs, is a source of economic loss to farmers and hunters and emotional stress (Ruid et al., 2009).

Pack territory size varies and may fluctuate in response to prey biomass and availability, pack aggressiveness, and latitude (Fuller et al., 2003; Mech and Boitani, 2003). Fuller et al. (2003) determined that prey biomass accounts for approximately 33 percent of variation in mean pack territory size. Generally, territories of unexploited (non-hunted) packs are relatively stable. Mean pack territory size (1979-1991) was 179 km² in Wisconsin’s re-colonizing wolf population (Wydeven et al., 1995; 2009). Colonizing wolf populations have been found to have larger pack territories than established, saturated populations (Fritts and Mech, 1981; Mech and Boitani, 2003). Since gray wolves are highly territorial (Fritts and Mech, 1981; Fuller, 1989; Mech et al., 1998; Mech and Boitani, 2003), competition for space and resources intensifies as the population increases (Mech and Boitani, 2003).
Pack members are shaped by their experiences within their pack (Packard, 2003). Social experiences shared among pack members differ from pack to pack and these are influenced by the physical environment in which they live. Comparison of pack demographics across the variety of pack habitat quality is vital in determining factors that influence pack viability.

Wolves in the Great Lakes Region and Wisconsin

The gray wolf was essentially extirpated from the northern Great Lakes Region in the 1950’s as a result of habitat loss, hunting and trapping (Thiel, 1993; Mladenoff et al., 1995). By 1960 the species was extirpated from the lower 48 states, except for a small population (<300) in northern Minnesota (Erb and Don Carlos, 2009; Thiel, 1993). The Endangered Species Act (ESA) of 1973 provided protection for the gray wolf in the lower 48 states (Erb and Don Carlos, 2009). Under this protection, gray wolf populations have steadily increased, with populations now inhabiting areas in the GLR (Minnesota, Michigan, and Wisconsin) and the Northern Rocky Mountains (Idaho, Montana, Wyoming, Oregon, and Washington–Mech, 1970; Thiel, 1993; Heilhecker et al., 2008; USFWS, 2012). Gray wolves began to re-colonize Wisconsin by 1975, as individuals dispersed into the area from remaining packs in Minnesota (Wydeven et al., 2009). It took another 20 years before wolves were detected in the CFR (Wydeven et al., 1995). The gray wolf population in Wisconsin grew from a minimum estimate of 25-28 wolves in 1980 to 99-105 wolves in 1996 (Wydeven et al., 2009). Before its removal from the ESA in December 2011, the gray wolf’s status in the GLR shifted between endangered, threatened, and delisted. Under federal and state endangered species protection, only non-lethal control of depredating wolves was permitted. Lethal controls, under federal
and state guidelines, were permitted as the gray wolf’s status changed from endangered to threatened (Refsnider, 2009). By 2012, the minimum population was estimated at 815-880 wolves, over a thirty-fold increase in 32 years (Wydeven et al., 2012).

The gray wolf was listed as a state endangered species in 1975 (Wydeven et al., 2009). Formal WDNR monitoring of the species began in 1979, followed by a state gray wolf recovery plan in 1989 (Wydeven et al., 1995 and 2009). In 1999 the state wolf management plan was approved, setting a state delisting population goal of 250 wolves and a management goal of 350 wolves outside Indian reservations (WDNR, 1999). Wisconsin down-listed the wolf to threatened in 1999, with a further down-listing to a protected (non-game) species in 2004 (Wydeven et al., 2009).

Depredations have increased as the wolf population increased (Ruid 2009). These depredations have strongly impacted human attitudes towards wolves, therefore depredation control is an important component of gray wolf management in the GLR. Under ESA the killing of problem and depredating wolves was prohibited; wolves were subjected to various non-lethal deterrents including guard animals, protective husbandry practices and disruptive stimuli (Ruid et al., 2009; Wydeven et al., 2009). As the GLR gray wolf status changed from an endangered to threatened species, very limited lethal depredation control was permitted. More liberal lethal controls were employed in January 2012 when ESA protection of gray wolves ended and wolf management reverted back to each state (WDNR, 1999, 2006 and 2008; Ruid et al., 2009). Lethal controls – trapping and euthanasia – were administered by United States Fish and Wildlife Services (USFWS) and United States Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS), following the confirmation of probable and
confirmed depredations (WDNR 1999, 2006, and 2008; Treves et al., 2002). The WDNR has also provided financial compensation for verified wolf depredations (killed or injured) of domestic animals since 1985 (Ruid et al., 2009).

Upon removal of the gray wolf from ESA provisions, management reverted back to the individual states (Licht et al., 2010). Since the gray wolf delisting in January 2012 (USFWS, 2011), all three GLR states have instituted wolf hunt seasons, regulating gray wolves as game species (WDNR, 2012). Wisconsin’s present wolf management goal is to reduce the population to the management goal of 350 animals. In 2014, Wisconsin completed its second gray wolf hunt and the 277 wolves harvested were more than twice the number harvested (117 wolves) in the first season (MacFarland and Wiedenhoeft, 2013 and 2014). The effect was a reduction, from an estimated 830 wolves prior to the first season, to 660 following the second season. Understanding and maintaining quality habitat will be essential in managing a viable wolf population above federal recovery levels especially when such a small population is subjected to public harvest and depredation control programs (Mladenoff et al., 2009).

**Importance of Disjunct Wolf Populations**

Haight et al., (1994) observed that wolves live and thrive in a network of disjunct populations and cites the recovering wolf populations in the GLR as an example. These disjunct populations are disconnected from larger wolf populations with little connectivity and restricted animal exchange (Haight et al., 1994; Hanski, 1998). Many of these disjunct wolf populations occupy areas of semi-wilderness – highly altered landscapes close to human occupation (Haight et al., 1994; Mech, 1995); the result is increased exposure to human disturbance and increased human-caused mortality (Thiel,
Understanding the dynamics of wolf occupation within a disjunct population is necessary in predicting population viability and in mitigating human-caused mortalities.

Licht et al. (2010) found that even very small wolf populations, even as small as one pack, can serve as an ecosystem restoration tool for small natural areas. These small populations provide space for dispersers from the larger, regional population, which in turn facilitates population maintenance and geographic expansion (Haight et al., 1998; Hanski 1998). Management of these fragmented wolf populations will become increasingly important in conserving the gray wolf population above recovery levels following delisting from the Endangered Species Act (Bangs et al., 2001).

Assuming habitat consistency and abundant, well-distributed prey throughout the population, Haight et al. (1998) modeled a disjunct wolf population based on the likelihood of human caused mortality. Core (primary) packs were simulated to incur 20% mortalities while peripheral (secondary) packs were simulated to incur 40% mortalities. Haight et al. (1988) found in their simulations that core pack numbers were of particular significance to overall population persistence when immigration was low and pup and dispersal mortality was high. More core packs (with low human-caused mortality) were needed to increase the level of occupancy. Furthermore, population survival can occur even when secondary packs (with high human-caused mortality) outnumber primary packs as long as dispersers replace lost breeders and re-colonize vacant areas. They concluded that wolves can survive and thrive in disjunct populations as long as there is minimal human persecution as well as dispersal movement between populations.
Mladenoff et al. (1995) used geographic information systems (GIS) and spatial data collected from collared wolves to model favorable wolf habitat during wolf recolonization of the northern GLR. With a multiple logistic regression model, they compared known pack areas (territories) and non-pack areas based on such variables as road density, land ownership, land-cover, human population, and landscape indices. They found that road density of less than 0.45 km/km² was the greatest predictor of favorable wolf habitat, followed by habitat fragmentation. Additionally, their results showed pack areas consisted of 46% mixed forest and 2.3% agriculture, while agriculture comprised 28% in non-pack areas. They stress that these primary areas (with less than 0.45 km/km²) are important to successful colonization of marginal habitat, especially if cut off from an abundant source of nearby dispersers in the presence of habitat fragmentation. Similar to Haight et al. (1998), Mladenhoff et al. (1995) stated that continued population maintenance, even within primary habitat areas, is dependent on high levels of immigration.

Since gray wolves colonized most of the predicted core (optimal) habitat areas, Mladenoff et al. (2009) re-assessed the 1990s model utilizing additional re-colonizing wolf data. The new model noted significant changes in predicted areas of gray wolf occupation and expansion from the previous model. Their findings show low road density is still the greatest predictor of gray wolf colonization and population expansion. As primary habitat became occupied, wolves began to settle in areas of higher road density (threshold less than 1.0 km/km²) than the earlier model (threshold of less than 0.45 km/km²). The 2009 model also found that agriculture land cover/use was most negatively correlated with pack areas than any other land cover or use, a reflection of the
high human contact that comes with agriculture. Additionally, deciduous forest (largest forest class) was positively correlated to pack areas, presumably due to its high levels of prey. This change, they summarize, is a reflection of the current gray wolf occupation of most of the core areas (especially in Wisconsin), necessitating the occupation of high-human-contact areas. Thiel et al. (2009) also noted that since 2000, wolves have inhabited areas close to humans with a mean road density of 0.94 km/km². Mladenhoff et al. (2009) further state that due to the fragmented nature of core-quality habitat in Wisconsin, population security will require maintenance of low road density areas, limitation of road development in core (primary) areas, and maintenance of safe corridors to source populations in Minnesota and upper Michigan.

Van Deelen (2009) examined the growth characteristics of the Great Lakes’ recovering wolf population from 1980 to 2007. He noted that while dispersing wolves are successfully navigating across intensive agriculture areas in the Southern Lake Superior (SLS- northern Wisconsin and the Upper Peninsula of Michigan), there is evidence of a density dependent decline in the growth rate of the SLS wolf population in the later years of his study. The saturation of high-quality habitat may explain the decline in growth rate (Haight et al., 1998; Mladenhoff et al., 1999 and 2009). The remaining marginal areas contain higher road densities, subjecting wolves to greater human activity (Mladenhoff et al., 1995), thus higher mortality, less successful pack formation, and less reproduction (Van Deelen, 2009).

The Central Forest Region (CFR, see Figure 1) in west central Wisconsin supports another disjunct population of gray wolves. In winter 1994, the first pack, consisting of a breeding pair with their pups, was detected in the CFR detected in the
CFR, some 109 km south of the nearest pack in Wisconsin’s Northern Forest (Wydeven et al., 2009). Seven wolves, including a breeding pair with pups were detected (Thiel et al., 1997 and 2009). The CFR wolf population increased almost seven-fold in ten years and another three-fold in the subsequent 8 years (Thiel et al., 2009; Wydeven et al., 2012). Their population in 2012 reached an estimated population of 119-135 individuals in 32 known packs. The long delay in initial colonization of the area and the isolation of the CFR packs from other wolf packs within the state suggests that movement of individuals from the northern Wisconsin packs into the CFR was a relatively infrequent event at least during the early phases of wolf recolonization in northern Wisconsin (1970s through early 1990s). Wolves in the CFR live in closer proximity to humans, increasing their vulnerability to human-caused mortalities. Thus, the maintenance of the gray wolf population in the CFR requires that birth and survival rates of pups in CFR packs are sufficient to offset variable rates of dispersal and mortality. This underscores the vulnerability of the CFR wolf packs to population declines and emphasizes the importance of continued conservation of the CFR wolf population. The CFR wolf population is considered important to Wisconsin’s overall wolf population (Fahrig and Merriam, 1994; Mladenoff et al., 1995; Haight et al., 1998; Wydeven et al., 2009; Thiel et al., 2009; Licht et al., 2010). The CFR is a source of dispersing wolves that may reach more distant suitable habitat (Thiel et al., 2009). No study has examined the effects of habitat suitability on the reproductive success, persistent occupation, mortality, and incidence of depredation of known individual wolf packs within a disjunct population of gray wolves, such as the wolves in the CFR.
CHAPTER II
AN EIGHTEEN YEAR SPATIAL AND TEMPORAL ANALYSIS OF THE RECOLONIZATION OF A DISJUNCT POPULATION OF GRAY WOLVES

INTRODUCTION

Wolves are habitat generalists, requiring no specific vegetation or ecosystem type (Mech, 1970; Mladenoff et al., 1995). They display a broad habitat tolerance as long as prey are abundant. Wolves have three requirements of their habitat: (1) food, (2) space, and (3) space from human influence (Mech, 1995; Mladenoff et al., 1995, 1999, and 2009). Studies indicate that wolves preferentially establish in areas with the least anthropogenic pressure. Thiel (1985), Mech (1989), Mladenoff et al. (1995, 1999 and 2009) have shown that recolonizing wolves prefer areas with road density averaging less than 0.60 km/km². Mladenoff et al. (1999, 2009) demonstrated that wolf presence is negatively associated with agricultural land use, while it is positively associated with public land, forest and forest wetland cover. Wolves in Europe exhibit a similar preference for habitat with fewer roads and higher proportions of forest cover and public land use, while avoiding agricultural land use and other areas associated with human disturbance (Blanco & Cortéz, 1997; Corsi et al., 1999; Cayuela et al., 2004; Llaneza et al., 2012; Jedrzejewski et al., 2005; Nowak et al. 2016).

Numerous studies have examined habitat preferences of recolonizing wolves to predict future areas of wolf occupation. Early recolonizing wolves in the Great Lakes Region (GLR) of Minnesota, Wisconsin, and Michigan, USA selected landscapes with forested land cover and low road density (Thiel, 1985; Mech, 1988; Mladenoff et al.,
1995). As recolonization progressed, forested habitat with few roads became limited; wolves then selected less by vegetative land cover and more by land use and anthropogenic features (Mladenoff et al., 1999 and 2009).

Wolves select landscapes that maximize their fitness and enhanced pup production. The presumed positive impact of high-quality habitat, however, may vary with time. As recolonization proceeds, even packs in high-quality habitat may experience pressures from the overall increasing population size. No studies have been conducted to assess the influence of the interacting effects of time and habitat quality on pack demographics.

The Central Forest Region (CFR) in west central Wisconsin is an ideal location in which to examine the impact of time and habitat quality during recolonization on pack demographics. The CFR is home to a disjunct gray wolf population isolated from wolves in northern Wisconsin by a 70 km swath of intense agriculture. The Wisconsin Department of Natural Resources (WDNR) began monitoring CFR wolves upon detection of the first breeding pair in 1994, thus providing over 20 years of wolf pack demographic and spatial data for analysis.

I hypothesized that individual pack demographics in the CFR would change over time, as the population increased. I further hypothesized that wolves with territories in areas with the fewest roads, the greatest percentage of public land and the least percentage of agricultural land would benefit demographically from their high-quality territories. Finally, I hypothesized that the effect of habitat quality would be more important than time in predicting pack demographics, so that the demographics of packs in high-quality habitat would be unaffected by the time of colonization.
METHODS

The Central Forest Region (CFR) of west-central Wisconsin, covering approximately 7,155-km², is comprised of deciduous forest, coniferous swamps, pine barrens, marshes, and sedge and sphagnum bogs (Heilhecker et al., 2007; Thiel et al., 2009). Designated as Wolf Management Zone 2 (WDNR 1999; Fig 1), the CFR encompasses parts of ten Wisconsin counties. County and state forests, state wildlife and natural areas, and federal properties account for 35 percent (2,574 km²) of CFR area (Thiel et al. 2009). Land use in the CFR is predominately outdoor recreation, forestry, wildlife conservation, small dairy operations, and cranberry agriculture (Heilhecker et al., 2007; Thiel et al., 2009). The CFR is separated from the larger northern wolf population by a 22-72 km-wide zone of intensively farmed agricultural land (Wolf Management Zone 3; Fig.1).

Figure 1. Wisconsin DNR Wolf Management zones. The CFR is Zone 2.
Primary prey for wolves in the CFR is white-tailed deer (*Odocoileus virginianus*). White-tailed deer are abundant and vary according to winter conditions (Wydeven *et al*., 1995; Mech and Peterson, 2003; Thiel *et al*., 2009, Kohn *et al*., 2009; Rooney and Anderson, 2009). Wolves supplement their diet with smaller prey, such as snowshoe hares (*Lepus americanus*) and beavers (*Castor canadensis*; Mandernack, 1983; Fuller; 1989; Del Giudice *et al*. 2009). This study did not analyze prey density because it is assumed that prey is sufficient throughout the CFR (Del Giudice *et al*., 2009; Thiel *et al*., 2009; Wydeven *et al*., 2009).

**Wisconsin Department of Natural Resource Wolf Monitoring Data**

The WDNR conducts annual mid-winter wolf censuses, using trained staff and a cadre of volunteer trackers (Wydeven *et al*., 1995, 1999, and 2009). WDNR wolf monitoring data was made available for my use in analyzing wolf occupancy and demographics from winter 1994 through winter 2012.

A wolf pack was defined as a pair of wolves with signs of breeding (raised leg urinations by both the breeding male and female, with or without estrus blood) or presence of offspring (Mech, 1970; WDNR, 1999). Wolf location data were digitized by WDNR using ArcView 3.2 (ESRI software). WDNR created shapefiles for pack territory polygons. Mapped pack territory polygons contained all telemetry, wolf tracks, wolf sign and wolf sightings locations.

**Temporal Analysis: Recolonization Time Periods**

The CFR population went through three transitions—colonization, transition, and saturation—during the study period (1994-2012; Thiel *et al*., 2009). These three
transitions became the Time periods of recolonization: (1) Early Time Period, 1994-1999; (2) Mid Time period, 2000-2005; and Late Time period, 2006-2012 (Fig. 2).

Figure 2. The CFR wolf population each year (A). The number of CFR wolf packs present each year (B). In both figures, Early, Mid and Late indicate the three recolonization Time Periods used for temporal analyses.
Spatial Analysis: Pack Habitat Quality Classes

Landscape data sources

I performed all spatial analyses using ArcMap 10.2, in Esri GIS mapping software. I collected and processed WDNR spatial data sets for the Wisconsin state border, Wisconsin county borders, and the CFR boundary. The WDNR’s CFR boundary is composed of deer management polygons with similar habitat (WDNR 1999). I extended the CFR boundary to include all of Ft. McCoy by hand-digitizing. I removed Sandhill Wildlife Area from the habitat variables data as the entire area is fenced and inaccessible to wolves. These shapefiles became the foundation boundaries for all subsequent spatial analyses of the CFR, for pack territory polygons, and each time period of recolonization (Fig. 3).

I used the National Land Cover Database 2001 (NLCD01) Tile 2 for all land cover and land use analyses. The NLCD01 maps 16 land cover classes at 30-m x 30-m cell size (based primarily on Landsat 5 and Landsat 7 satellite data; Homer et al. 2004, 2007). I used the conterminous United States layer of the NLCD01 for land cover and land use analyses (Fig. 4). I used four sources for public land analyses in the CFR: The Department of Forestry and Natural Resources-Clemson University, Wicland (country forest and public land), and the Conservation Biology Institute (CBI) Version 2 edition of Protect Area Data-United States (PAD-US) (USGS 2004). For road density analyses, I used the U.S. Census Bureau 2000 Tiger Line data (TL2000).

Landscape data preparation

I grouped land cover and land use classes to create two habitat layers – public land and agricultural land – based on two habitat variables known to influence wolf
Figure 3. Distribution of habitat characteristics influential to wolf presence within the CFR (8377.5 km²). Public land makes up 30.2% (2530.2 km²) of the CFR, 27.3% (2297.6 km²) of the area is agricultural land, and the average road density is 1.285 km/km² (10,766.85 km). The fenced Sandhill Wildlife Area ( ) excluded from analyses.
Figure 4. National Land Cover Database (2001) for the state of Wisconsin and the Central Forest Region.
presence or activity levels (Thiel 1985, Wydeven et al. 2001, Mladenoff et al. 1995, 1999, 2009; Table 1). Public land variable included county, state, and federal lands (The Department of Forestry and Natural Resources-Clemson University, Wiscland (country forest and public land), and the Conservation Biology Institute (CBI) Version 2 edition of Protect Area Data-United States (PAD-US) (USGS 2004). I grouped the grassland, hay, pasture, and cultivated crop classes identified in NLCD01 to define the agricultural variable. Cranberry bogs were not included with the agricultural land variable. I created a roads variable (in km/km²) to include county and state recognized, common name, U.S. and interstate roads that were paved, improved, or gravel (U.S. Census Bureau, TIGER/Line ®, 2000). I determined the km² and percent cover within the CFR as a whole for the two habitat variables of agricultural and public land, along with the average road density (km/ km²; Fig.3). I likewise determined km² and percent cover of agricultural and public land and average road density for each pack polygon in each year of the study. I used the same methods to analyze and calculate habitat variables that were part of a pack polygon along the boundary that fell outside the CFR.

**Territory habitat quality classification**

Founder packs in their first year of occupancy within the Early Time Period were assumed to select habitat features most favorable to survival and pup production. I considered these landscape features Optimal Habitat. I then calculated the mean and a 95% confidence interval for these values of 8 packs polygons that became established in the Early Time Period (1994-1999). Mean values ± 95% CI for percent of landscape
features within pack polygons were: 78% ± 15.41% for public land, 8% ± 1.47% for agricultural land, and road density of 0.80 ± 0.131 km/km².

From these I created three Habitat Classes (Table 1):

(1) Optimal Habitat - consisted of (a) ≥ 62.6% public land, (b) ≤ 9.4% agricultural land, and (c) road densities ≤ 0.926 km/km².

(2) Mixed Habitat—which met only one or two of the habitat conditions.

(3) Marginal Habitat—which failed to meet all three of the habitat conditions.

I classified each pack territory polygon for each year as Optimal, Mixed, or Marginal Habitat based on these criteria.

Table 1. Limits of each habitat quality parameter—public land, agricultural land, and road density—required for Optimal, Mixed, and Marginal Habitat.

<table>
<thead>
<tr>
<th>Habitat Parameter</th>
<th>Optimal</th>
<th>Mixed</th>
<th>Marginal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percent Public Lands</td>
<td>≥63%</td>
<td>Meets one or two of the 3 parameters</td>
<td>Meets none of the 3 parameters</td>
</tr>
<tr>
<td>Percent Agriculture</td>
<td>≤9.4%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Road Density</td>
<td>≤0.93 km/km²</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Pack demographic data and analyses

Pack territory size

Pack territory boundaries are dynamic. Shifts occur as packs defend and expand territory boundaries; new packs seize territory between existing packs. Methods for determining pack territory boundaries also create shifts (Fuller 1989, Mech and Boitani,
2003). Even as pack boundaries shift, however, the core usually remains stable for many years (Mech and Boitani 2003).

Pack territory size was determined from packs that had ≥1 radio collared member that remained within that space long enough to allow WDNR to create a pack territory polygon (Mohr 1947, Fuller 1989, Wydeven et al. 1995). I used year-round data and included all years for all pack territories with a radio collared member within the study period (1994-2012).

**Mid-winter pack size**

Based on the location and number of tracks observed in winter track surveys conducted by trained WDNR personnel and volunteers, the WDNR estimated the number of wolves in packs. Aerial observations were also used in estimating the size of packs with a collared member (Wydeven et al. 1999, 2009, 2011). If wolves were detected in an area before the WDNR recognized it as a pack, I included that count if the pack was named and given a pack territory the following year. I censored out the first year if the pack count was two wolves.

**Reproductive performance**

I based reproductive performance (pup production) on number of pups detected during howl surveys. The WDNR determined the number of pups produced per pack each year based on summer howl surveys (performed by two-three highly experienced individuals; Harrington and Mech 1982), aerial pictures of pups, and verified observations of pups. I used all pup counts for all years of the study. Pups detected the
year prior to the WDNR identification as pack were attributed to the identified pack in that territory the subsequent year.

**Wolf-human conflicts**

Management of wolf-human conflicts (WHC) is an essential component of wolf management (Ruid *et al.*, 2009). The WDNR defines WHC as: (1) depredations - killing of domestic animals (livestock, pets or hunting dogs), (2) harassment of domestic animals, (3) property damage, and (4) perceived threats to human safety (WDNR 1999, 2006, and 2008, Ruid *et al*. 2009). For each pack territory, I used only WDNR confirmed wolf conflicts, and grouped all types of confirmed wolf complaints into a single unit (WHC). Each livestock, dog, and hound incident was counted as a single event, even if > 1 animal was involved. I used all WHC, whether located inside or outside of a wolf pack territory and attributed them to the nearest pack.

**Wolf mortalities**

Only collared wolf WDNR mortality data was used to construct mortality rates by Time Period and by Habitat Class. Throughout the study, the WDNR tabulated mortality through field observation and necropsies (Thiel *et al.*, 2009; Wydeven *et al.*, 2009; Stenglein 2014; Stenglein *et al.*, 2015, 2018). The WDNR tabulated 48 collared wolf deaths in the CFR during this study. Since human-caused mortalities (HCM) are a presumed driver in limiting wolf distribution, I limited the analysis to the percent of HMCs by time period and by habitat class. HMC included deaths due to: vehicle collision, train collisions, illegal kill, artillery fire, research capture related, and lethal depredation (Wydeven *et al*. 2012). Collared wolf HCM was standardized by
calculating the number of HCMs per 10,000 radio days. Habitat classification (Optimal, Mixed or Marginal) were assigned to each collared wolf mortality based on their death location. I used ArcMap to create a 10 km radius polygon (average size of CFR wolf pack territories) with the death location (Public Land Survey System or geographic coordinates) as the centroid. I spatially analyzed death locations exactly as I did pack territories. No HMC analyses were conducted by Time Periods (Ruid et al., 2009).

**Territory persistence**

The center of pack territories generally remains constant, though boundaries shift (Mech and Boitani 2003). Territory persistence refers to the occupation of a particular space over time. I used WDNR pack data to assess territory persistence over time by Habitat Class. A year was added if the WDNR pack count was ≥3 wolves in the first year for which data were available, since each pack is assumed to be created by a breeding pair. To calculate a territory’s number of three-year persistence events, during a territory’s “lifespan”, I followed these rules: (1) first year must have ≥2 wolves in the pack (breeding pair and at least one offspring); (2) a persistence event is three years with ≥2 wolves in the pack; (3) area considered continuously occupied with yearly sign of ≥2 wolves or evidence of ≥2 wolves following a year of one wolf sign; (4) restart 3-year event if failure to meet continuous presence; (5) excluded packs whose origin years were either 2011 or 2012 (Table 2). If a territory was classified in more than one Habitat Class, the predominant habitat classification was used. I calculated the percent of territory persistence events of three-year territory persistence events divided by the maximum number of territory persistence events, and averaged by Habitat Class.
Table 2. Rules for a three year territory persistence event.

<table>
<thead>
<tr>
<th>Persistence Event*</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>=3 years</td>
<td>&gt;2 wolves</td>
<td>≥2 wolves</td>
<td>≥2 wolves</td>
</tr>
</tbody>
</table>

* Restart 3-year event if failure to meet event rule

**Reproductive persistence**

Pack reproductive persistence gauges the long-term (year-to-year) trends in output of pups. This minimally requires the presence of pups or a sibling from a previous year. I used the WDNR mid-winter pack count from winter track surveys, since this dataset provides the clearest evidence of reproductive success. I followed the above methods, only with different persistence event rules: (1) first reproductive persistence event must have three years with >2 wolves in the pack; (2) subsequent reproductive persistence event is two years of >2 wolves in the pack; (3) continuous reproductive persistence if a year with a single wolf in a given pack is preceded or followed by >2 wolves in the pack; (4) restart with a three year event if a pack fails to meet rule 3 (Table 3). If a territory was classified in more than one Habitat Class during the study period, the predominant habitat classification was used. I calculated the percent of reproductive persistence of three-year reproductive persistence events divided by the maximum number of reproductive persistence events, and averaged by Habitat Class.
Table 3. Rules for a three year reproductive persistence event.

<table>
<thead>
<tr>
<th>Persistence Event*</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st event =3 years</td>
<td>2 wolves</td>
<td>≥3 wolves</td>
<td>≥3 wolves</td>
</tr>
<tr>
<td>Subsequent event=2 years</td>
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<td></td>
<td></td>
</tr>
</tbody>
</table>

* Restart 3-year event if failure to meet event rule, then 2 year event

Statistical Analysis of Demographic Data

Pack territory size, mid-winter pack size, and reproductive performance

A model-building process was undertaken using a linear mixed effects models with random intercepts of the relationship between the response variables pack territory size, mid-winter pack size (number of individuals) and pack reproductive performance (pup production), and the fixed effect predictors of Time Period and Habitat Class. The random effect due to repeated measures on wolf packs was also accounted for in the model since most packs were evaluated more than once. As no observations were obtained for the Marginal Habitat class at the Early Time Period, two partial models were implemented to study the interacting effects of Time Period and Habitat Class on outcome variables. Model I excluded the Marginal Habitat class for all three Time Periods and Model II excluded the Early Time Period for all three Habitat Classes.

Due to the presence of outliers, the condition of normality of the residuals was not met for the linear mixed regression models for any variables. Therefore, variables were rank-transformed (Baguley, 2012, Conover and Iman, 1981) to reduce the effects of the
outliers and bring the distributions much closer to normality. P-values for fixed effects factors were obtained by F-tests with Satterthwaite’s method, while P-values for post hoc tests were obtained using the t-tests based on Satterthwaite’s approximation for degrees of freedom and Tukey adjustment for pairwise comparisons. When a significant interaction was detected between Time Period and Habitat Class, the eight existing treatment combinations for Time Period and Habitat Class were represented with a single variable and contrasts were constructed to test for pairwise differences among Habitat Classes for each Time Period. A 5% level of significance was used for each modeling scenario and as the family-wise error rate for post hoc multiple comparisons. Models were analyzed using R (R Core Team, 2018) with lme4 (Bates, Maechler, Bolker, and Walker, 2015), lmer Test (Kuznetsova, Brockhoff, and Christensen, 2017), car (Fox and Weisberg, 2011), and emmeans (Lenth, 2019).

Other analyses

I performed separate chi-square analyses to examine the effects of Time Period and Habitat Class on the total number of wolf-human conflicts (WHC; observations per cell were too small to do a Time Period by Habitat Class contingency table). To examine how the increasing population size of wolves in the CFR impacted the frequency of WHC, I also examined the significance of Time Period and Habitat Class on the number of WHC per 100 wolves using chi-square tests. I evaluated the effect of Habitat Class on the number of HCM per 10,000 radio days for collared wolves using a chi-square test.

Persistence calculations generated a single value for each pack, rather than a single total number during the study Time Period, or repeated measures of the same pack. I therefore compared the significance of Habitat Class on territory persistence and
RESULTS

Temporal Patterns in Recolonization

The wolf population in the CFR grew from three or four wolves in a single founding pack in 1994 to 119-135 wolves in 32 packs in 2012. Counting all packs present during each time period (n=287), there were 26 territories in the 6-year Early Time Period, 77 territories in the 6-year Mid Time Period, and 184 territories in the 7-year Late Time Period (Fig.5). Sixty-one percent (n=17) of the Early Time Period territories occupied in Optimal Habitat, thirty-two percent (n=9) occupied Mixed Habitat and zero occupied Marginal Habitat. The majority of the Mid Time Period territories (38, 49%) were in Mixed Habitat, with 27 (35%) in Optimal Habitat. No territories were classified as Marginal Habitat (12, 16%) until the latter part of the Mid Time Period (2002), eight years after initial CFR recolonization. By the end of the Late Time Period (2012), CFR wolf territories were evenly distributed (33%) across all three Habitat Classes (Fig. 6). The majority of territories added to the CFR in Mid Time Period (n=34) were in Mixed (12, 35%) and Marginal Habitat (14, 41 percent). Only eight (23%) new packs established territories during the Late Time Period.

Habitat Analyses

Over the course of the 18-year study, 287 territories were identified and mapped (all pack territories all years they were present—in any one year, the total number of individual territories never exceeded 32 territories). Overall 35% (100) of annual
Figure 5. Number of territories identified during each Time Period. Number and percent of territories in each Habitat Class by Time Period. Early Time Period composed of 17 (61%) Optimal and 9 (32%) Mixed Habitat territories. Mid Time Period composed of 27 (35%) Optimal, 38 (39%) Mixed, and 12 (16%) Marginal Habitat territories. Late Time Period composed of 58 (32%) Optimal, 66 (36%) Mixed, and 60 (33%) Marginal Habitat territories.
Figure 6. CFR public land, agricultural land and roads with Optimal, Mixed and Marginal territories in 2012. One hundred (35%) of CFR’s total territories (n=287) are Optimal Habitat, 117 (41%) are Mixed Habitat, and 70 (24%) are Marginal Habitat.
territories were classified in Optimal Habitat; 41 percent (117) in Mixed Habitat; and 24 percent (n=70) in Marginal Habitat (Fig. 5). The average percentage of public land in territories dropped from 75 percent (n=22) in Early Time Period to 57 percent (n=172) in Late Time Period. The average percent of agricultural land per territory increased from 9.0 percent in Early Time Period to 18.1 percent in Late Time Period. Average road density within territories increased, from 0.84 km/km² in Early Time Period, to 1.0 km/km² in Late Time Period. The habitat content within the CFR varied little over time; habitat content within the territories changed as more territories were established.

Demographic Response to Time Period and Habitat Class

Pack territory size

Ninety pack territories were used in this analysis. Mean pack territory size during the entire length of the study was 101.6 km² (n=90; 10.6-322.7). Mean pack territory size was 105.2 km² (n=7) in Early Time Period; 120.8 km² (n=32) in Mid Time Period; and 89.2 km² (n=51) in Late Time Period (Table 4). Optimal Habitat averaged 97.7 km² (n=33) per territory, Mixed Habitat averaged 97.1 km² (n=38), and Marginal Habitat averaged 112.9 km² (n=19; Table 4). No wolves established territories in Marginal Habitat during Early Time Period; the first pack established in Marginal Habitat occurred in 2003.

Mean pack territory size did not differ over Time Period or Habitat Class (Fig. 7). There were no statistically significant interaction effects between Time Period and Habitat Class on the rank-transformed pack territory size (Model I: $F_{2,59,85} = 0.56, p = 0.5725$, Model II: $F_{2,76,95} = 0.85, p = 0.4297$), nor were main effects observed for Time Period (Model I: $F_{2,62,18} = 1.49, p = 0.2323$, Model II: $F_{1,70,35} = 2.83, p = 0.0971$) or
Habitat Class (Model I: $F_{1,64.56} = 0.44, p = 0.5100$, Model II: $F_{2,57.01} = 1.77, p = 0.1795$).

**Mid-winter pack size**

Two hundred forty-seven packs were used in the pack size analysis. Mean mid-winter pack size for CFR packs was 4.1 wolves ($n=247; 1.0-12.0$). Early Time Period packs averaged 4.8 ($n=16$), Mid Time Period packs averaged 3.5 ($n=68$), and Late Time Period packs averaged 4.2 ($n=163$). Optimal Habitat averaged 4.3 individuals ($n=87$), Mixed Habitat averaged 4.5 ($n=101$), and Marginal Habitat averaged 3.0 ($n=59$; Table 4).

Both Models I and II showed a statistically significant interaction between Time Period and Habitat Class for pack size (Model I: $F_{2,178.4} = 4.19, p = 0.0166$; Model II: $F_{2,206.8} = 4.44, p = 0.0129$; Fig 7). Pairwise tests indicated packs in Marginal Habitat contained significantly fewer individuals than Mixed Habitat during the Mid Time Period, and significantly fewer individuals than both Optimal and Mixed Habitat during the Late Time Period (Fig. 8).

**Reproductive Performance**

Pups were detected in a total of 169 packs during the study time period. The CFR mean number of pups detected per pack was 2.9 ($n=169$). Across all three Time Periods, pups were detected in an average 62.5% of the packs present ($n=169$). During the Early Time Period packs averaged 3.2 pups ($n=14; 1-5.5$). In the Mid Time Period they averaged 2.6 pups ($n=44; 1-6$), and in the Late Time Period they averaged 3.0 pups ($n=111; 1-12$). Packs averaged 3.1 pups ($n=79; 1-7$) in Optimal Habitat, 2.8 pups ($n=76; 1.5-12$) in Mixed Habitat, and 2.3 pups ($n=14; 1-3.5$) in Marginal Habitat (Table 4).
Table 4. Summary of CFR mean pack territory size, pack size, and number of pups detected by Time Period and Habitat Class. The number of packs differs among analyses because all data types are available for all packs throughout the study period (see Methods for more details).

<table>
<thead>
<tr>
<th></th>
<th>Pack Territory</th>
<th></th>
<th>Mid-winter Pack Size</th>
<th></th>
<th>Reproductive Performance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean km²</td>
<td>Range</td>
<td># Packs</td>
<td>SE</td>
<td>Mean size</td>
</tr>
<tr>
<td><strong>Time Period</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early</td>
<td>105.2</td>
<td>34.1-189.1</td>
<td>7</td>
<td>21.83</td>
<td>4.8</td>
</tr>
<tr>
<td>Mid</td>
<td>120.8</td>
<td>25.3-322.7</td>
<td>32</td>
<td>13.18</td>
<td>3.5</td>
</tr>
<tr>
<td>Late</td>
<td>89.2</td>
<td>10.6-243.3</td>
<td>51</td>
<td>6.86</td>
<td>4.3</td>
</tr>
<tr>
<td><strong>Habitat Class</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Optimal</td>
<td>97.7</td>
<td>28.1-216.6</td>
<td>33.0</td>
<td>8.01</td>
<td>4.3</td>
</tr>
<tr>
<td>Mixed</td>
<td>97.1</td>
<td>10.6-322.7</td>
<td>38.0</td>
<td>11.82</td>
<td>4.5</td>
</tr>
<tr>
<td>Marginal</td>
<td>112.6</td>
<td>26.1-243.3</td>
<td>19</td>
<td>13.25</td>
<td>3.0</td>
</tr>
</tbody>
</table>
Figure 7. Overlaid density plots of the mean pack territory and interaction plot showing Models I and II for the effects of pack Habitat Class and Time Period on pack territory. There were no significant differences.
Model I showed no significant interaction effects between Time Period and Habitat Class for territories in Mixed and Optimal Habitat on the rank-transformed data for number of pups per pack ($F_{2,142.96} = 0.92, p = 0.3999$), nor main effects for Time Period ($F_{2,128.82} = 1.72, p = 0.1829$) or Habitat Class ($F_{1,128.35} = 0.35, p = 0.5512$). Similarly, Model II indicated no significant interaction effects ($F_{2,148.93} = 1.25, p = 0.2906$) or main effect due to Habitat Class ($F_{2,132.04} = 2.86, p = 0.0608$; Fig. 9).

In contrast, Model II did show a statistically significant difference in mean ranks for the number of pups between the Mid and Late Time Periods ($F_{1,148.43} = 4.83, p = 0.0294$), with fewer pups produced during the Mid Time Period than during the Late Time Period. This effect is driven by somewhat lower pup production in Mixed Habitat (2.8) and low pup production in Marginal Habitat (2.3) during the Mid Time Period.
Figure 8. Overlaid density plots of the average mid-winter pack size and interaction plot showing Models I and II for the effects of Habitat Class and Time Period on mid-winter pack size. Values sharing a letter (a) are not significantly different from each other in pairwise tests within a given Time Period. Packs in Marginal Habitat had significantly fewer individuals than Mixed Habitat in the Mid Time Period and fewer individuals than Optimal and Mixed habitats in the Late Time Period.
Figure 9. Overlaid density plots of the mean number of pups and interaction plot showing Models I and II for the effects of Habitat Class and Time Period on pup production. Model II indicates that significantly fewer pups were produced per pack during the Mid Time Period than during the Late Time Period.
Wolf-human conflicts

Fifty-two WHC events of various types were confirmed between 1994 and 2012 by the WDNR: five (10%) in Early Time Period; seven (13%) in Mid Time Period; and 40 (77%) in the Late Time Period (Table 5). The total number of WHC events varied over time ($X^2= 45.47$, df = 2, $p<0.01$; Table 5). The total number of WHC events also varied across the three Habitat Classes ($X^2= 6.76$, df =2, $p<0.05$; Table 5): eight (15%) WHC events occurred within Optimal Habitat; 21 (40%) in Mixed Habitat; and 23 (44%) in Marginal Habitat.

Table 5. Summary of the number and types of wolf-human conflicts by territory recolonization Time Period and Habitat Class.

<table>
<thead>
<tr>
<th></th>
<th>Time Period</th>
<th>Habitat Class</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early  Mid  Late</td>
<td>Optimal Mixed Marginal</td>
</tr>
<tr>
<td>Total N of WHC</td>
<td>5 7 40</td>
<td>8 21 23</td>
</tr>
<tr>
<td>Percent of Total WHC (n=52)</td>
<td>10 13 77</td>
<td>15 40 44</td>
</tr>
<tr>
<td># Bear Hounds</td>
<td>5 2 14</td>
<td>4 11 6</td>
</tr>
<tr>
<td># Pets</td>
<td>0 1 11</td>
<td>3 6 3</td>
</tr>
<tr>
<td># Livestock</td>
<td>0 3 12</td>
<td>0 2 13</td>
</tr>
<tr>
<td># Health &amp; Safety</td>
<td>0 1 2</td>
<td>1 1 1</td>
</tr>
</tbody>
</table>
Normalizing for the increased wolf population over time (#WHC/100 wolves) revealed that there were no significant differences among Time Periods in the number of WHC events, which averaged 4.4 WHC per 100 wolves ($X^2 = 1.009, df=2, p > 0.05$; Table 6). There were, however, significantly more WHC per 100 wolves in Marginal Habitat (11.4) than in Optimal (2.0) and Mixed (4.3) Habitats ($X^2 = 6.64, df =2, p< 0.05$; Table 6).

Table 6. Summary of the number of wolf-human conflicts by territory recolonization Time Period and Habitat class. Population and number of territories are the sum of all wolves and all territories across all years for a given Time Period or Habitat Class.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Habitat Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early</td>
<td>Optimal</td>
</tr>
<tr>
<td>Mid</td>
<td>Mixed</td>
</tr>
<tr>
<td>Late</td>
<td>Marginal</td>
</tr>
</tbody>
</table>

| Number of WHC | 5 | 7 | 40 | 8 | 21 | 23 |
| Population    | 96.5 | 257.5 | 737.5 | 400.5 | 489.5 | 201.5 |
| #WHC per 100 wolves | 5.1 | 2.7 | 5.4 | 2.0 | 4.3 | 11.4 |

Wolf mortalities

Human-caused wolf mortalities (HCM) accounted for 30 of the 48 (62.5%) collared wolf mortalities in the CFR during the 18-year study period. Of the 30 HCM, four (13%) occurred within Optimal Habitat, twelve (40%) in Mixed Habitat, and fourteen (47%) in Marginal Habitat. Normalizing for the number of radio days
(Rdays) each collared wolf was transmitting, over six times as many HCM per 10,000 Rdays occurred in Marginal Habitat (25.6) as occurred in Optimal Habitat (3.8), and over 4 times as many occurred in Mixed Habitat (6.0; \( X^2 = 24.53, \text{df} = 2, p < 0.01; \) Table 7).

Table 7. Summary of human-caused mortalities (HCM) per 10,000 radio days (Rdays) by death location Habitat Class. Number of packs and population are the sum of all packs and all wolves across all years and all packs for a given Habitat Class.

<table>
<thead>
<tr>
<th>Habitat Class</th>
<th># HCM</th>
<th>Total Radio Days (Rdays)</th>
<th>HCM per10,000 Rdays</th>
</tr>
</thead>
<tbody>
<tr>
<td>Optimal</td>
<td>4</td>
<td>10671</td>
<td>3.75</td>
</tr>
<tr>
<td>Mix</td>
<td>12</td>
<td>20052</td>
<td>5.98</td>
</tr>
<tr>
<td>Marginal</td>
<td>14</td>
<td>5471</td>
<td>25.59</td>
</tr>
</tbody>
</table>

**Territory Persistence**

Thirty-eight pack territories were included in the analysis. Territory persistence demonstrates that wolf packs (≥2 wolves) continuously occupied that space for a three-year period, understanding that Territory persistence was highest in Mixed Habitat, at 92 (±0.12 SE) percent. Optimal Habitat had 66 (±0.07 SE) percent average pack territory persistence events and Marginal Habitat had a 63 (± 0.14 SE) percent average. There was no significant difference in the average percent of territory persistence events across Habitat Classes (\( F_{2, 35} = 2.23, p > 0.1131; \) Table 8).

**Reproductive persistence**

Thirty-six pack territories were included in the analysis. Reproductive persistence in Marginal (19.4%) Habitat was less than half the average reproductive persistence in Optimal (54.3%) and Mixed (54.9%) Habitat (\( F_{2, 35} = 7.10, p < 0.0027; \) Fig. 10, Table 8).
Figure 10. Mean percent of reproductive persistence across Habitat Classes. Wolves in Optimal or Mixed Habitats had significantly more mean reproductive persistence events than wolves in Marginal Habitat.
Table 8. Summary of territory and reproductive persistence across Habitat Classes. Mean percent territory and reproductive persistence and reproductive persistence calculated individually for each pack then averaged within a given Habitat Class.

<table>
<thead>
<tr>
<th></th>
<th>Territory Persistence</th>
<th>Reproductive Pack Persistence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Optimal</td>
<td>Mixed</td>
</tr>
<tr>
<td>Number of Persistence Events</td>
<td>72</td>
<td>83</td>
</tr>
<tr>
<td>Max Number of Persistence Events</td>
<td>84</td>
<td>87</td>
</tr>
<tr>
<td>Mean Percent Persistence Events</td>
<td>66</td>
<td>92</td>
</tr>
<tr>
<td>Number of packs</td>
<td>12</td>
<td>15</td>
</tr>
</tbody>
</table>
DISCUSSION

Although wolves have been equated with wild lands in North America (Theberge, 1975; Lopez, 1978), wolves do not need wilderness to survive (Mech, 1995; Mladenoff et al., 1995, 2009). Wolves primarily need food, space, and space from human interference. Protection under the Endangered Species Act (1973) lessened wolf persecution, decreasing wolves’ sensitivity to living near humans (Thiel et al., 1998; Fritts et al., 2003; Merrill and Boitani, 2003). Research during more than forty years of wolf recolonization in the GLR has shown that GLR wolf populations can and do live in close proximity to humans, especially if remote areas (inaccessible to humans) are nearby (Mech, 1989; Mladenhoff et al., 1995, 1999, 2009; Heilhecker et al., 2007; Thiel et al., 2009). Road density (< 0.060 km/km²) is the single most important predictor of wolf presence; public land and areas with little agricultural land are also strong indicators of wolf presence (Mladenhoff et al. (1995, 1999, and 2009).

Wolves recolonized the CFR in a selective manner, first establishing pack territories in areas containing low road density with high public land as well as low agricultural land. Early Time Period pack territories had mean road densities 0.80 km/km², compared to the CFR average of 1.29 km/km². These Early territories contained on average 78% public land, while the CFR as a whole was 30% public land. Early Time Period territories also averaged 8% agricultural land, compared to 27% agricultural land within the CFR. By the end of the Late Time Period, mean percent public land (58%) in territories decreased by 30% and mean percent agricultural land (16%) increased by 33%. Mean road density (0.93) increased by only four percent. Results show that CFR wolves first select areas with the least amount of human influence—low road density and low percent agricultural land—as suggested by Mladenhoff et al., (1995-1999, and 2009).
I hypothesized that demographics would change based on Time Period of recolonization. Pack territory size did not vary significantly over time. The number of wolf-human conflicts (WHC) increased significantly from the Early Time Period (four wolves) to the Late (135 wolves). These results support the findings of a positive correlation between wolf population and wolf conflicts (Ruid et al., 2009).

There was no significant difference in the percent mean territory persistence across Habitat Class (based on the number of three-year territory presence events with ≥2 wolves). Across all Habitat Classes, once pack territories were occupied, most remained occupied. Reproductive performance of CFR packs was also fairly uniform in each of the Time Periods and across Habitat Classes, supporting observations of wolves’ high reproductive potential across a wide range of conditions (Mech, 1970; Fuller et al., 2003; Mech and Boitani 2003; Packard, 2003; Mech, 2017).

As I hypothesized, good quality habitat was demographically beneficial to packs in Optimal and Mixed Habitats. Optimal Habitat, signifying the best of the best, met all three habitat limits (high public land, low agricultural land, and fewer roads), while Mixed Habitat met only one or two of the limits. Results showed that having only one habitat parameter within the Optimal criteria was enough to positively influence pack demographics. There was no significant difference in demographics between Optimal and Mixed Habitats.

CFR mean pack size (4.1) was, however, somewhat larger than the mean pack size of 3.6 in northern WI (Wydeven et al. 2009). Overall, packs in Optimal and Mixed Habitat both had significantly larger mean pack sizes than Marginal Habitat. There was no significant difference between mean mid-winter pack size of Optimal and Mixed Habitat packs. In contrast, Kittle et
al. (2015) found wolves in boreal ecosystems did not alter pack size in response to habitat quality.

Good quality habitat had a positive effect on pack reproductive persistence. Packs in Optimal (54%) and Mixed (55%) Habitats had over twice the reproductive persistence of packs in Marginal Habitat (19%). A pack's ability to carry pups past the next breeding season. The loss of auxiliaries (offspring from the previous year) could decrease pup survival (Harrington et al., 1983).

Wolves in the CFR live in relatively close proximity to human activity, compared to most packs in the GLR (Thiel et al., 2009; Mladenhoff et al., 2009). There was significant differences in the number of WHC per 100 wolves across Habitat Classes. Wolves in Optimal Habitat were the least likely to come into conflict with humans; they had one-fifth (2.0) the WHC as wolves in Marginal Habitat (11.4). Wolves in Mixed Habitat had one-third (4.3) the WHC as Marginal Habitat wolves, but were involved in all three (6%) of the public health and safety WHC (52).

The CFR contains two military installations, Fort McCoy (240 km²) and Hardwood Range (31 km²), and borders a military airfield (Volk Field; Heilhecker et al., 2007; Thiel et al., 2009). Understanding these results requires knowledge about individual packs involved. The two livestock WHC events involved the two Fort McCoy packs (Mixed Habitat). These packs depredated calves in dairy farms just off the army installation, likely due to the increased human activity during a summer of intense military training. Conversely, several packs in Optimal Habitat moved in and out of fenced livestock areas with no incidents of depredations (observations from farmers and winter tracking). This provides anecdotal evidence that packs with better quality pack territories may be less likely to prey livestock.
Of the 23 WHC events in Marginal habitat, 13 of them (57%) involved livestock. Packs in Marginal habitat accounted for all but two (87%) of the total WHC events involving livestock during the study period. The other two livestock WHC events occurred in Mixed Habitat. This data supports that of Treves et al., (2002) who observed that WHC occurred at greater rates in areas of higher agriculture-based landscapes.

Hound hunting and training generally occurs in county and state forest lands (Olson et al., 2014; Thiel, 2018). The higher percentage of public forest land in Optimal and Mixed Habitat likely explains why ≥50% of the WHC events in these habitat areas involved hounds. Hunting hounds accounted for four of the eight (50%) WHC events in Optimal Habitat and eleven out of 21 (52%) in Mixed Habitat. In comparison, only six of the 23 (26%) WHC events in Marginal Habitat involved bear hunting hounds. Wolves benefit from public land even though it increases their encounters with hounds. One pack whose territory was classified as Mixed and Marginal Habitats, in different years, was involved in WHC events during all three Time Periods. This pack killed five hunting dogs in the Early Time Period, one in the Mid Time Period and four hunting and three pet dogs in the Late Time Periods.

Human-caused mortality (HCM), is the primary source of wolf mortality in the CFR, accounting for 62.5% (30/48) of collared wolf mortality. Radio collared wolves in Optimal (4.0) and Mixed (6.0) Habitats incurred between four and six times fewer HCM as wolves in Marginal (11.4) Habitat. This inverse relationship between wolf habitat quality and human-caused deaths has not been previously reported. HCM are the most influential demographic variable indicating where wolves live and where they do not: humans.

Road densities exceeding 1.14 km/km² is associated with wolf presence and high wolf HCM (Merrill, 2000; Wydeven et al., 2001; Smith et al., 2010). The mean road density (1.5
km/km²) of both Fort McCoy pack territories (Mixed Habitat) exceed this limit, yet only one collared wolf HCM was documented on the Fort; a dispersing wolf was killed in the artillery impact area (off limits to humans) by military ordinance. The Fort’s limited entrance and use access, combined with its controlled, seasonal land use activities severely restricts human access, and likely mediates the impact of its high road density on wolf HCM (Thiel, 1985; Mech et al., 1988; Mech, 1989).

**SUMMARY**

Wolves have proven to be very adaptable, inhabiting a wide variety of habitats containing an adequate food source and space in which to avoid humans (Mech, 1970; Fuller, 1989; Fritts et al., 2003; Oakleaf et al., 2006). As hypothesized, habitat quality was more important than Time Period. Demographic features examined here varied little over time as the CFR population increased. Time of recolonization was likely important only in securing the most remote areas. Recolonizing wolves first selected low road densities, high percentages of public land and low percentages of agricultural land within the CFR. Examining habitat on a pack territory level, my study shows that territory location—habitat quality—matters. My habitat analyses identified demographic deficiencies within marginal habitats; (1) smaller pack size, (2) increased wolf-human conflicts, (3) increased human-caused mortalities, and (4) decreased reproductive persistence. Wolves can persist and produce pups wherever they are, but pack success and viability in marginal habitats will suffer. Wolves may survive in marginal territories, but they cannot thrive.

Wolf populations are vulnerable if wolves fail to reproduce and sustain a breeding population (Thiel 1978, 1985, Wydeven et al., 2001). High HCM in marginal habitat territories
may have a ripple effect, suppressing mean pack size through high turn-over of breeders and offspring (Thiel et al., 2009) as well as reducing reproductive persistence in Marginal Habitat.

This study provides the limitations in habitat quality beyond which wolves cannot thrive. Management agencies should focus wolf protection efforts in areas with optimal habitat restricting increased economic activity, as well as limiting the addition of new roads and human disturbance. Territories in optimal areas likely serve as population source areas to offset the increased mortality in marginal areas (Mladenhoff et al., 1995, 1999, 2009). States with wolf harvests should focus wolf harvests in marginal habitat and wolf conflict areas first, with no harvest in optimal habitat areas.
REFERENCES


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APPENDIX A

TERRITORY DEMOGRAPHIC PERFORMANCE BY TIME PERIOD

AND HABITAT CLASS
Summary of territory demographic performance across Time Periods and Habitat Classes. Marginal Habitat territories had significantly different mean mid-winter pack size, mean number of pups, number of wolf-human conflicts per 100 wolves, number of human-caused mortalities per 10,000 radio days, and mean reproductive persistence.

<table>
<thead>
<tr>
<th>Demographic Parameter</th>
<th>Time Period</th>
<th>Habitat Type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Early</td>
<td>Mid</td>
</tr>
<tr>
<td>Mean Territory Size (km²)</td>
<td>105.2</td>
<td>120.8</td>
</tr>
<tr>
<td>Mean Mid-winter Pack Size</td>
<td>4.8</td>
<td>3.5</td>
</tr>
<tr>
<td>Mean # Pups per Pack</td>
<td>3.2</td>
<td>2.6*</td>
</tr>
<tr>
<td># WHC per 100 Wolves</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td># HCM per (#/10,000 Rdays)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Territorial Persistence (Mean %)</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Reproductive Persistence (Mean %)</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* Significance