Chapter 12
Dispersal of Gray Wolves in the Great Lakes Region

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12.1 Introduction

In less than 40 years, gray wolves (*Canis lupus*) rebounded from a population of <700 wolves restricted to northeastern Minnesota to >4,000 wolves across northern Minnesota, Wisconsin, and Michigan (Chaps. 4–6, this volume). This recovery is due in part to changing human attitudes toward wolves, protection by the U.S. Fish and Wildlife Service (USFWS) under the Endangered Species Act (ESA), and favorable ecological conditions (Mladenoff et al. 1997; USFWS 2007; Schanning, this volume). Furthermore, two features intrinsic to wolf life history facilitated rapid recovery: long-range movements and broad habitat tolerance. The wolf is a habitat generalist, using all habitat types of the northern hemisphere except tropical rain forests and deserts (Mech 1970). Equally important is their tremendous capacity for rapid, long-distance movement, allowing them to colonize distant, suitable areas rapidly. Mech and Boitani (2003) describe wolf packs as "dispersal pumps" that convert prey into wolves and scatter these dispersers across the landscape, "pumping out" half of their pack each year.

Long-range movements of wolves deserve scrutiny by managers and scientists because such movements are driving recolonization of their historical range. Wolf populations in the western Great Lakes and the northern Rocky Mountains have been assigned to distinct population segments proposed for removal of federal protections under the ESA (USFWS 2007, 2008), but would continue to produce dispersers that reach states were wolves still would receive ESA protection. Predicting where such long-range movements take wolves requires an understanding of dispersal and habitat selection during long-range movements.

Dispersing gray wolves can travel vast distances, and have moved as far as 1,092 km in a straight-line distance from their original pack territories (Wabakkan et al. 2007). One wolf radio-collared in Wisconsin dispersed >689 km into eastern Indiana, a trip that likely entailed skirting the greater Chicago metropolitan area (Thiel et al., this volume). Certainly, short-range movements are more common among wolves, but long-range movements are disproportionately important from a management perspective because they create the possibility of recolonizing historic

range and new regions. Indeed, it took Minnesota wolves <30 years to recolonize the northern third of Wisconsin and Upper Peninsula (UP) of Michigan (Wydeven et al., this volume; Beyer et al., this volume).

With few exceptions, unless a wolf attains alpha status, it will eventually leave its pack (Mech 1970, 1999). However, the appealing story of wolves setting out on lengthy voyages of discovery is misleading. Most extraterritorial movements (ETMs), short or long, do not result in new packs or immigration into an existing pack. Indeed, when a wolf leaves its natal pack, it may return with or without encountering other wolves. Wolves that do not return to the natal pack may spend years as loners before joining packs or being joined by other wolves. Some long-range movements do result in residence in a new pack (dispersal). Because intentions are inscrutable and initial ETMs do not seem to predict the eventual outcomes, wolf movements defy easy classification. Furthermore, efforts to predict future dispersal and colonization are hindered by methods available for monitoring wolves. Radio telemetry remains the current best option, but transmitters fail, batteries weaken, and people cannot search everywhere when a wolf goes missing (Mech 1974, 1983; Coffey et al. 2006). All these factors make it challenging to predict future sites of colonization or dispersal.

In this chapter, we review findings on wolf dispersal, and examine a subset of long-range movements from Wisconsin that illuminates habitat selection by wolves when they disperse long distances. Understanding habitat use by dispersing wolves in this human-dominated ecosystem is important for planning wolf conservation and habitat protection, particularly for regions outside of vast wilderness areas.

12.2   Review of Wolf Dispersal in the Great Lakes Region

Long-range wolf movements have been critical to recolonization of the Great Lakes region. Before breeding packs were detected in Wisconsin and Michigan, individual wolves were detected, probably dispersing from Minnesota or Ontario (Hendrickson et al. 1975; Thiel 1978; Thiel and Hammill 1988). Extensive data on wolf dispersal in Minnesota, Michigan, and Wisconsin have been collected (Table 12.1), although definitions of dispersal, starting and ending points, and methods for estimating movement have varied across studies. Nevertheless, comparisons between studies illuminate consistent patterns that help us to infer specific regional characteristics relating to sex and age of dispersers and travel patterns.

Studies conducted in the Great Lakes region (Table 12.1) reveal no clear pattern in the sex ratio of dispersers. Fuller (1989) and Gese and Mech (1991) detected no difference in the numbers of males and females dispersing in Minnesota. This corroborates research in Montana and Alaska where male and female wolves were equally likely to disperse (Boyd and Pletscher 1999; Peterson et al. 1984). In central Alaska, males dispersed at higher rates than did females (Ballard et al. 1987). Peterson et al. (1984) found males from the Kenai Peninsula dispersed farther than females, whereas Ballard et al. (1987) found that females from central Alaska

Table 12.1 Summary of gray wolf dispersal patterns in the Great Lakes region

Location	n	Mean distance (km)	Mean age (years)	Sex ratio (♂:♀)	Percentage of yearling	Percentage of success	Reference
Northwestern Minnesota	9	NA[a]	NA	0.5:1.0	78	44	Fritts and Mech 1981
North-central Minnesota	15	148	1.7	2.5:1.0	60	NA	Berg and Kuehn 1982
North-central Minnesota	28	29	NA	NA	39	42	Fuller 1989
Northeastern Minnesota	75	88 (♂) 65 (♀)	1.5	1.1:1.0	53	63	Gese and Mech 1991
Northern Wisconsin	16	114	1.7	0.8:1.0	50	31	Wydeven et al. 1995
Central Wisconsin	15	83 (♂) 67 (♀)	2.2 (♂)[b] 1.7 (♀)	0.9:1.0	NA	58	Thiel et al., this volume

[a]*NA* not available
[b]Excluding a 7.8-year-old male

dispersed farther. Costs and benefits of dispersal are likely to differ between males and females given differences in costs of reproduction and competition for mates, as well as local variation in breeding vacancies (Shields 1987).

In most studies, only small percentages of pups dispersed, and mostly at the end of winter when they neared 1 year of age. Percentages of yearlings among dispersers ranged from 38% to 78% across studies (Table 12.1). In Wisconsin, average age at dispersal was between 1.5 and 2.2 years, and appeared slightly higher for males in central Wisconsin (Thiel et al., this volume). The percentage of yearlings dispersing changed with population status in northeastern Minnesota. Seventy percent of yearlings dispersed during population declines, 47% when the population was stable, and 83% while the population was increasing (Gese and Mech 1991). Average age of dispersal was higher and percent of yearlings dispersing was lower in Quebec, Alaska, and Montana (Messier 1985; Ballard et al. 1987, 1997; Boyd and Pletscher 1999). Dispersal rates may be higher for pups of eastern wolves (*Canis lycaon,* see Nowak, this volume, for discussion of taxonomic status) in Ontario, where dispersal was suspected to have occurred in 20% of monitored pups and occurred as early as 4.5 months of age (Mills et al. 2008).

The oldest disperser detected by Gese and Mech (1991) in northeastern Minnesota was 4.5 years old. In contrast, one male in central Wisconsin joined a new pack at 7.8 years of age. In Minnesota and Wisconsin, older wolves generally were more successful at establishing new territories or joining other packs, and usually traveled shorter distances (Gese and Mech 1991; Wydeven et al. 1995). Individual success in establishing new home ranges and attaining breeding status varied from 31% to 63% across studies (Table 12.1).

Dispersal distances in Alaska and Montana were similar to those in north-central Minnesota in the 1970s (Berg and Kuehn 1982), and in Wisconsin during early colonization (Wydeven et al. 1995). Radio-collared wolves in the Great Lakes states have shown tremendous ability to disperse long distances (Table 12.2). The longest known dispersal in North America occurred when an adult male moved 886 km northwest from north-central Minnesota through Manitoba and eventually to eastern Saskatchewan (Fritts 1983). A dispersing Scandinavian wolf topped this, moving 1,092 km from southern Norway to the Finnish–Russian border (Wabakkan et al. 2007). Scandinavian wolves averaged 313 km per dispersal

Table 12.2 Long-distance movements of gray wolves in the Great Lakes region (1976–2004)

Wolf/sex/age[a]	Origin	Final destination	Minimum distance (km)	Movement duration (years)	Reference
5167/M/P	Northwestern Minnesota	Western Ontario	390	2.8 (1976–1979)	Fritts and Mech 1981
555/M/Y	North-central Minnesota	Southern Manitoba	432	0.7 (1979)	Berg and Kuehn 1982
/M/Y	North-central Minnesota	Eastern Saskatchewan	886	0.82 (1981)	Fritts 1983
035/F/A	Northwestern Wisconsin	Central UP Michigan	227	1.0 (1985–1986)	Thiel 1988
177/F/A	Eastern Minnesota	Northwestern Wisconsin	304	0.13 (1993)	Wydeven 1994
113/F/Y	North-central Wisconsin	Western Ontario	480	1.0 (1988–1989)	Wydeven et al. 1995
/M/A[b]	Northern Minnesota?	Southern South Dakota	530+	1991[c]	Licht and Fritts 1994
/M/A[b]	Northern Minnesota?	Western North Dakota	343+	1992[c]	Licht and Fritts 1994
395/M/P	Northeastern Minnesota	Central UP Michigan	275	2.8 (1991–1994)	Mech et al. 1995
487/F/Y	Northeastern Minnesota	Southern Wisconsin	555	0.33 (1994)	Mech et al. 1995
7809/F/A	Central Minnesota	Central Minnesota	494[d]	0.49 (1999)	Merrill and Mech 2000
0071/F/P	Eastern UP Michigan	Southern Wisconsin	483	0.16 (2001)	WDNR/MI DNR files
0018/M/P	Western UP Michigan	North-central Missouri	720	1.6 (2000–2001)	Mech and Boitani 2003
409/M/P	Central Wisconsin	Eastern Indiana	689	0.43 (2003)	Thiel et al., this volume
4914/M/A	Eastern UP Michigan	Northwestern Wisconsin	435	0.12 (2004)	WDNR/MI DNR files
2061/M/A	Central UP Michigan	Eastern Minnesota	427	0.25 (2004)	WDNR/MI DNR files

[a]Age at start except as listed below; P <1 year, Y >1 & <2 years, A >2 years
[b]Age at time of death
[c]Year found dead
[d]Straight line from origin and furthest point; actual movements were > 4251 km before return to original territory

movement, longer than averages for North American wolves (Linnell et al. 2005). Wolves from newly established subpopulations, such as Wisconsin (1979–1992, Wydeven et al. 1995) and north-central Minnesota (1970–1980, Berg and Kuehn 1982), moved farther than dispersers from established subpopulations.

Total distances moved by wolves during dispersal significantly exceeded minimum straight-line distances between start and end points (Table 12.2). For example, a Minnesota wolf tracked by satellite telemetry for 179 days traveled at least 4,251 km from northwestern Wisconsin eastward to Green Bay, then west again to LaCrosse, then northwest to Grantsburg, before leaving the state and returning to her home territory in Camp Ripley, Minnesota. The straight-line distance from her original territory to her farthest destination was 494 km (Merrill and Mech 2000). She traveled through at least 27 of Wisconsin's 74 counties in <3 months. The above-mentioned Scandinavian yearling may have traveled >10,000 km with at least 3,471 km traversed over 271 days (Wabakkan et al. 2007). Clearly, end points of movements capture only portions of the extensive movements made by dispersing wolves.

In addition to traveling long distances, wolves readily cross human-altered landscapes and areas without resident wolves. Wolves from the Great Lakes states of the United States have moved into three Canadian provinces (Ontario, Manitoba, and Saskatchewan), and into at least five surrounding states (Illinois, Indiana, Missouri, North Dakota, and South Dakota). Before 1992, 43% of dispersing wolves from Wisconsin ($n = 14$) moved into Minnesota (Wydeven et al. 1995). In winter 2006–2007, 11 of 63 (17%) radio-collared wolves monitored in Wisconsin came from the UP of Michigan. Between 1994 and 2006, dead wolves were detected in 47 of 72 counties in Wisconsin, despite packs occurring in only 13 (1994)–30 (2006) counties. The likelihood that these long travels result in colonization of new areas depends on finding safety, a mate, food, and suitable habitat.

12.3 Habitat Used in Long-Range Movements by Wisconsin Wolves

Landscape features that characterize areas of wolf colonization are popular topics of research (e.g., Mech et al. 1988; Massolo and Meriggi 1998; Corsi et al. 1999; Jędrzejewski et al. 2004; Potvin et al. 2005), particularly in Wisconsin (e.g., Thiel 1985; Mladenoff et al. 1995; Wydeven et al. 2001). Despite keen interest from researchers, habitat selection by wolves during long-range movements remains poorly understood (Mladenoff et al. 1999). Early work suggested that dispersing wolves use areas previously thought unsuitable for establishment of wolf packs (Licht and Fritts 1994; Wydeven 1994; Mech et al. 1995). At least three studies have attempted to characterize suitable landscapes for dispersing wolves (Harrison and Chapin 1998; Wydeven et al. 1998; Oakleaf et al. 2006), and assumed that dispersing wolves tolerated poorer quality habitat than wolves in pack territories.

Underlying predictions about habitat selection by wolves are basic models of animal movement behavior. Fretwell and Lucas (1970) predicted that animals select the most suitable habitats first. As population density in those habitats increases,

relative suitability decreases proportionally until habitats of originally lower suitability become equivalent in quality to those selected initially. Following saturation of more suitable habitats, animals occupy less suitable habitats. This idea of relaxing criteria for habitat selection has been tested and is useful in understanding habitat use by animals (Whitham 1980; Petit and Petit 1996). Because animals on the move must avoid danger, locate resources (food, water, shelter, etc.), and search for mates, intermediate steps likely reflect choices between available habitat patches. This conceptual model informed our analysis of long-distance movements by wolves in Wisconsin.

12.3.1   Methods

Managers and researchers have trapped and radio-collared wolves in Wisconsin since 1979 (Wydeven et al., this volume). These wolves have been tracked mainly by aerial radio telemetry. Radio-collared wolves were generally located once per week from the air by Wisconsin Department of Natural Resources (WDNR) pilots with fixed-wing airplanes, but wolves detected outside their packs and translocated wolves were sometimes located two to three times per week (Treves et al. 2002; Wydeven et al. 2004). Between 1981 and 2004, the WDNR recorded 20,006 locations from 202 wolves.

If a wolf left a known pack or territory to establish or join another pack or territory, we classified that wolf as an unambiguous disperser. Unfortunately, only 32 wolves provided such clear examples of individual wolf dispersal, including 18 with intermediate locations and 14 providing only start and end points within packs. To estimate dispersal distance in each of the 32 unambiguous cases, we measured the distance between the last location in the known territory and the first location in the destination territory (Gese and Mech 1991).

Most movements were ambiguous because we could not determine outcomes. To increase our sample of habitat used during long-term movements, we inspected all ETMs of Wisconsin wolves. We classified ETMs as movements that occurred >5 km beyond estimated territory boundaries (Messier 1985; Fuller 1989), and 63% of radio-collared wolves had ≥1 ETM (Martin 2007). The Wisconsin dataset contained 295 ETM segments from 127 wolves. Given that time required for confirmed dispersals is longer than for temporary ETMs (Gese and Mech 1991), we used 29 days as a threshold for defining "long-term movements" (see results for justification of this threshold). We removed briefer ETMs from further analysis, assuming these are less informative about habitat use by dispersing and colonizing wolves. Combined with the radio locations of unambiguous dispersers, our sample then comprised 60 movements by 49 wolves, with 609 radio locations (OBSERVED). Of these, 455 OBSERVED locations were from Wisconsin, 138 from Minnesota, and 16 from the UP of Michigan.

To test if habitat used during long-term movements was random relative to available habitat, we defined a comparison area for analysis around those 609 OBSERVED

locations. The comparison area was derived by buffering the OBSERVED locations with a 29.6-km radius (dark gray region in Fig. 12.1). The buffer's radius was derived from sequential radio locations of the 60 movements of 49 wolves, and represented a mean straight-line distance of 14.3 km (SD = 15.3) between consecutive radio locations. We used this mean distance + 1 SD as a buffer around OBSERVED locations, which produced two discrete regions (Fig. 12.1). We randomly selected points in the comparison area where wolves had not been detected as our EXPECTED sample in proportion to the numbers observed in the two regions and each state.

We placed two restrictions on EXPECTED locations to avoid pseudoreplication. EXPECTED locations had to be >1.8 km apart (see below) and could not lie on any body of water ≥ 9.8 km^2, the largest body of water on which wolves were radio located. We then collected data from an area of 908 m-radius around each OBSERVED and EXPECTED location. This area equals one section in the Public Land Survey System (PLSS, 2.59 km^2), and allowed for measurement error in aerial radio telemetry (Martin 2007). This scale also provided a simple way to map probabilities of long-range movement across the state, was visible on commercially available atlases, and was amenable to management decisions (Turner et al. 1995).
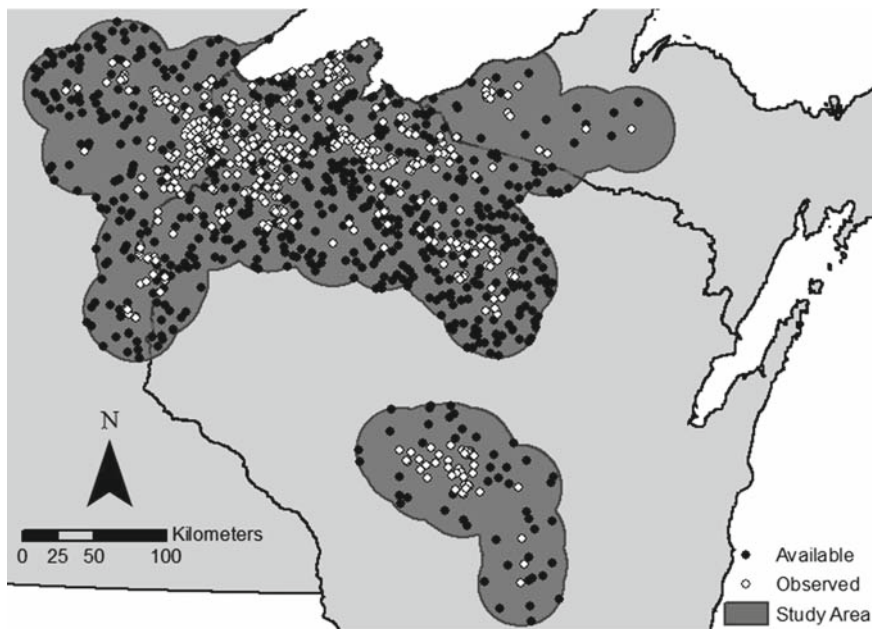

Fig. 12.1 The northern and southern sections of our analysis area, with *open circles* being OBSERVED locations of long-range movements and *closed circles* being an equal number of randomly placed EXPECTED locations

We measured spatial variation in landscape factors in four ways (Mladenoff et al. 1995; Wydeven et al. 1998; Treves et al. 2004; Potvin et al. 2005):

1. We estimated land cover composition using the 1992 National Land Cover Dataset (NLCD). NLCD divides cover into 21 classes at 30-m resolution (Vogelmann et al. 2001). We aggregated these 21 classes into 7 [water, urban, barren, forest, grasslands (generally pastures or hayfields), row crops, and wetlands] based on accuracy assessments for Wisconsin (Thogmartin et al. 2004; Wickham et al. 2004; Martin 2007).
2. We estimated white-tailed deer density as deer per km^2 averaged over the period 1995–2004 in discrete deer management units (DMUs) which generally cover 400–1,800 km^2 (WDNR 1998).
3. We estimated human population characteristics using the 2000 US Census Bureau TIGER/line files and included people and houses per km^2 at the scale of the census block (U.S. Census Bureau 2001), and road density (km/km^2).
4. We estimated agricultural characteristics using census data by county to quantify farms per km^2 and cattle per km^2 (U.S. Department of Agriculture 1997). We created and manipulated all data layers with ArcGIS 9.1 (ESRI 2005).

We used JMP 6.0.3 statistical software (SAS Institute Inc. Cary, NC) to compare habitat variables around OBSERVED and EXPECTED locations. We evaluated differences in movements with Student's t-tests, assuming unequal variances and evaluated differences in habitat variables with Welch ANOVA t-tests (Welch 1951).

12.3.2   Results and Discussion

Dispersing wolves from Wisconsin averaged 55.1 km (SD = 49.6 km) between original and final territories, with no difference between males and females in distances moved (Student's t = 1.56; P = 0.13). The 295 ETMs detected for Wisconsin wolves lasted 1–214 days ([x̄] = 19.3, SD = 31.2), with a median of 7.5 days. The distribution of ETMs was bimodal, with none in the interval 29–35 days (Fig. 12.2). This pattern generated our operational definition of long-range movements >29 days.

OBSERVED locations differed significantly from EXPECTED for 10 of 12 landscape variables (Table 12.3). Only wetland cover did not differ and farm density showed only a slight tendency. All five variables associated with the presence of humans (houses, humans, roads, farms, and cattle densities) were higher in EXPECTED locations, consistent with humans causing most wolf mortality (Woodroffe and Ginsburg 1998; Wydeven et al. 2001). EXPECTED locations had fourfold higher human and house densities than OBSERVED locations. Mean road density of OBSERVED locations was 0.93 km/km^2, compared with a maximum of 0.88 km/km^2 found previously in wolf territories in Wisconsin (Wydeven et al. 2001). Five land cover variables differed significantly between OBSERVED and EXPECTED habitat. Wolves undertaking long-range movements selected forest but avoided grassland, row crops, water, and urban areas. Deer density was significantly
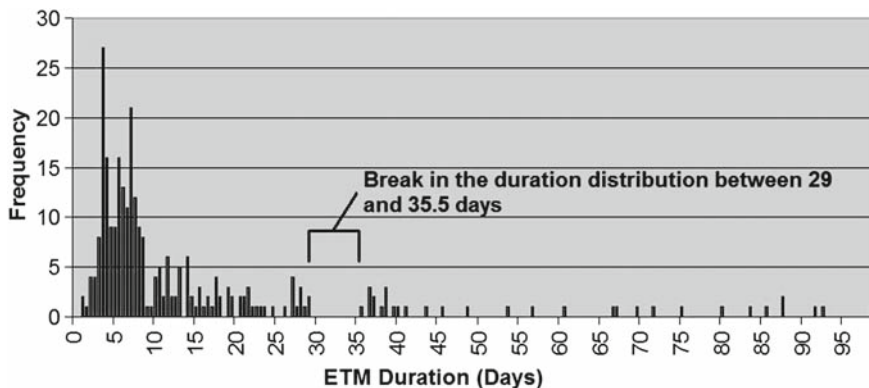
Fig. 12.2 The duration in days (*x-axis*) of extraterritorial movements (*ETMs*) by Wisconsin wolves, and the frequency (*y-axis*) with which these durations were observed

Table 12.3 Comparing landscape features of 609 OBSERVED and 609 EXPECTED locations for long-range movements

Land cover or use	EXPECTED Mean (SD)	OBSERVED Mean (SD)	Observed for females Mean (SD)	Observed for males Mean (SD)	Observed for adults Mean (SD)	Observed for sub-adults Mean (SD)
Water (% Cover)	3.9 (9.7)	1.9 (4.4)[a]	2.0 (4.6)	1.2 (3.0)	1.5 (3.9)	2.2 (4.7)
Urban (% Cover)	1.5 (8.3)	0.2 (0.8)[a]	0.2 (0.8)	0.2 (0.7)	0.2 (0.8)	0.2 (0.7)
Forest (% Cover)	54.7 (27.8)	68.9 (24.6)[a]	70.3 (24.0)	61.6 (25.9)[a]	70.7 (24.6)	67.3 (24.5)
Grassland (% Cover)	11.0 (15.0)	3.8 (7.8)[a]	4.0 (7.8)	3.2 (7.7)	2.8 (6.0)	4.7 (9.0)[a]
Row Crops (% Cover)	9.6 (14.8)	4.9 (9.0)[a]	5.0 (9.0)	4.4 (9.3)	3.2 (6.3)	6.3 (10.7)[a]
Wetlands (% Cover)	19.2 (22.5)	20.3 (22.5)	18.6 (21.5)	29.4 (25.2)[a]	21.6 (23.2)	19.3 (21.8)
Roads (km/ km²)	1.3 (1.2)	0.9 (0.8)[a]	1.0 (0.8)	0.7 (0.6)[a]	0.8 (0.7)	1.0 (0.9)[a]
Humans (per km²)	24.0 (157.5)	3.1 (7.9)[a]	3.4 (8.5)	1.2 (2.2)[a]	2.1 (6.5)	3.9 (8.8)[a]
Houses (per km²)	11.2 (70.9)[a]	2.8 (15.3)[a]	3.1 (16.8)	0.8 (1.0)[a]	1.3 (3.0)	4.0 (20.7)
Farms (per km²)	0.3 (0.2)	0.2 (0.2)	0.2 (0.2)	0.3 (0.2)[a]	0.2 (0.1)	0.3 (0.2)[a]
Cattle (per km²)	7.6 (9.0)	5.9 (5.6)[a]	5.1 (4.5)	10.0 (8.4)[a]	5.3 (5.6)	6.4 (5.7)
Deer (per km²)	10.7 (2.5)	9.9 (1.7)[a]	9.8 (1.5)	10.5 (2.5)	9.6 (1.9)	10.2 (1.5)[a]

See Fig. 12.1 for study area
[a]Indicates difference for Welch ANOVA, $P < 0.01$ values between paired means (comparisons are EXPECTED vs OBSERVED, male vs female, adult vs subadult)

lower in OBSERVED locations, in contrast with studies suggesting wolves follow deer (Poszig and Theberge 2000), and wolves prey on livestock in areas with higher deer density (Treves et al. 2004). However, the coarse resolution of information on deer density necessitates caution. Moreover, deer density increases in agricultural areas, hence apparent avoidance of areas with high density of deer may simply reflect avoidance of human-use areas.

Habitats used by female wolves during long-range movements differed significantly from those used by males in 7 of 12 variables (Table 12.3). Females used habitats with more forest cover, and higher densities of roads, humans, and houses, but lower densities of farms and cattle. Differences between adult and subadult (<2 year) wolves were clearer. Locations of adults differed significantly from those of subadults for 6 of the 12 variables (Table 12.3), with adults using less land cover associated with humans and less grassland cover.

12.4   Summary and Conclusions

Our analysis suggests that wolves undertaking long-range movements did not use habitat randomly. They selected wildland areas, while avoiding exposed habitats and areas modified by humans, including grasslands (pastures and hayfields), row crops, roads, houses, and farms. Preservation and restoration of forest and wetlands would help maintain suitable habitat for dispersal of wolves. Although dispersing wolves occasionally used more marginal habitat during movements, the most highly selected areas seemed similar to habitats selected by wolf packs (Mladenoff et al., this volume).

The observed differences between the sexes and ages are difficult to explain, although theory based on risk-taking, foraging strategies, and conspecific avoidance might prove useful (Linnell et al. 1999; Treves 2000). Females seemed to use habitats with a lower risk of encounter with agriculture and open habitats than did males, whereas males seemed to avoid people and houses. Further resolution of the timing or locations of long-range movements may resolve observed sex differences. Subadults seemed to use habitats with a higher risk than did adults. Subadults may have been avoiding adults or even pack territories because subordinate status may make them particularly vulnerable to attack from conspecifics. Alternatively, inexperienced subadults might be less aware of the hazards posed by people.

Wolves have successfully recolonized much of the forest areas of northern Minnesota, Wisconsin, and the UP of Michigan during the last 30 years. Dispersal movements of up to 886 km have been detected in this region, and have dispersed into at least five neighboring states and three Canadian provinces. Despite the extensive capacity of wolves to disperse over large areas, actual colonization and pack formation has occurred mainly in the northern portions of the region and more recently in central forest blocks and interstitial areas (Mladenoff et al. 1995; Mladenoff et al., this volume).

As wolves moved long distances, they used areas with relatively high forest cover, low road densities, wilder features, and lower human presence, similar to

other habitat models for wolves. Ongoing multivariate analyses suggest that Wisconsin wolves have been relaxing their habitat criteria when moving and when establishing pack territories (Martin et al., unpublished data). Thus, current results about subadults relaxing criteria for long-range movements may indicate wolf populations in the western Great Lakes are saturating prime habitat and dispersers will now accept lower quality habitat when seeking new territories. Indeed, the behavior of subadults in our study suggests that young animals may choose or be forced into lower-quality habitat and thereby recolonize areas previously thought unsuitable. Although young dispersing wolves are willing to travel through more marginal habitat, it remains unclear whether survival will be high enough for persistence, territories can be established and maintained, and pups can be raised in these less suitable areas.

Given the long distances wolves can disperse and their broad habitat tolerances, we anticipate that regions and states beyond the three western Great Lakes states should expect occasional wolves to appear. The lessons learned in Michigan, Minnesota, and Wisconsin will undoubtedly help states manage recolonization by a federally protected species that can damage property and engender strong feelings in diverse stakeholders.

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