GRAY WOLF
BIOLOGICAL REPORT

Information on the Species in the Lower 48 United States

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Introduction

The purpose of this report is to provide a concise overview of the changes in the biological status (range, distribution, abundance) of the gray wolf (*Canis lupus*) in the lower 48 United States over the last several decades. While Mexican wolves are a subspecies of the gray wolf and the taxonomic position of the red wolf relative to gray wolves remains uncertain (see *Taxonomy*, below), these two taxa are not the subject of this report and are only mentioned to provide context.

Taxonomy

The gray wolf is a member of the dog family (*Canidae*) in a global genus that includes domestic dogs (*C. familiaris*), coyote (*C. latrans*), several species of jackal (*C. aureus*, *C. mesomelas*, and *C. adustus*), and the dingo (*C. dingo*, formerly *C. lupus dingo*). Among those members of the genus found in North America, the specific taxonomic relationships have been studied extensively, though with a notable lack of consensus, even on issues such as the phylogenetic history of dogs, wolves, and coyotes (Cronin et al. 2015 and references therein; Fitak et al. 2018).

There is general agreement that the gray wolf and coyote represent valid, distinct species in North America. In addition, there is general recognition of a "red wolf" and an "eastern wolf" phenotype (morphological form), even with a lack of agreement on the correct taxonomic assignment of these two entities or on their evolutionary origin (vonHoldt et al. 2016; Hohenlohe et al. 2017; vonHoldt et al. 2017; Waples et al. 2018). The U.S. Fish and Wildlife Service's (USFWS) view of the taxonomy of the red wolf (*C. rufus*) is summarized in the 2018 Species Status Assessment and will not be discussed further here (USFWS 2018; see also Waples et al. 2018). The "eastern wolf" has been the source of perhaps the most significant disagreement on North American canid taxonomy among scientists, and has been variously described as a species (Wilson et al. 2000; Wilson et al. 2003; Kyle et al. 2006; Wheeldon and White 2009; Fain et al. 2010; Chambers et al. 2012), a subspecies of gray wolf (Goldman 1944; Nowak 1995; Nowak 2002), an ecotype of gray wolf (Koblmüller et al. 2009), or the product of hybridization between gray wolves and coyotes (Lehman et al. 1991; Leonard and Wayne 2008; vonHoldt et al. 2011; vonHoldt et al. 2016). Here, because of the continuing debate and ongoing research on the subject, we simply present an overview of relevant information, while recognizing uncertainty around the evolutionary history of North American canids.

Morphologically, eastern wolves have a long history of being considered distinct from western gray wolves and coyotes (Chambers et al. 2012 and references therein; Nowak 2002). The earliest known description of the eastern wolf dates to 1775, when Schreber described it as a distinct species based on morphology (in Nowak 1995). Although scientists have differed on the resulting taxonomic assignment, many have generally found the eastern wolf to be consistently intermediate between the gray wolf and the coyote, both morphologically and genetically (Nowak 2002; Nowak 2009; references in Kyle et al. 2006; Koblmüller et al. 2009; Rutledge et al. 2010). A number of authors have also noted that the smaller size of eastern wolves is likely correlated with the different forest types found in much of eastern North America and the corresponding abundance of white-tailed deer (*Odocoileus virginianus*) instead of larger ungulates, such as moose (*Alces alces*) and elk (*Cervus elaphus*), which are the favored prey of western gray wolves (Schmitz and Lavigne 1987; Forbes and Theberge 1996; Kyle et al. 2006; Benson et al. 2012; but see Benson et al. 2017).

Regardless of viewpoint on the correct taxonomic status of the eastern wolf, there is wide recognition that hybridization has played, and continues to play, an important role among eastern wolves (Leonard and Wayne 2008; Fain et al. 2010; Koblmüller et al. 2009; Wheeldon and White 2009; Mech 2010; Mech 2011; vonHoldt et al. 2011; Benson et al. 2012; Rutledge et al. 2015; vonHoldt et al. 2016). Scientists who favor the view that eastern wolf is a distinct species suggest that hybridization between eastern wolf and coyote occurs readily in certain parts of the range while hybridization between eastern wolf and gray wolf occurs in other areas, particularly in the western Great Lakes area (Kyle et al. 2006; Fain et al. 2010; Mech 2010; Rutledge et al. 2010; Rutledge et al. 2011). Those scientists who do not view the eastern wolf as a distinct species attribute the same genetic patterns to a history of hybridization between gray wolf and coyote that is either relatively ancient (Koblmüller et al. 2009) or more recent (vonHoldt et al. 2011; vonHoldt et al. 2016). It is often noted that gray wolves and coyotes do not readily hybridize west of the Great Lakes area, even when they are sympatric or when wolf numbers have been drastically reduced (Wheeldon et al. 2010). Successful artificial breeding of a male wolf and a female coyote and the unassisted, successful reproduction of those crosses, demonstrates that no strict biological barriers exist between gray wolves and coyotes (Mech et al. 2014; vonHoldt et al. 2017). It is possible that changing habitats, intense harvesting, different prey availability, or an interaction among these or other factors has led to hybridization in a manner that does not occur in the western United States (Nowak 2002; Kyle et al. 2006; Rutledge et al. 2011).

Minnesota is often seen as the western edge of this hybrid zone, with wolves in western Minnesota appearing to be gray wolves both morphologically and genetically compared with wolves in eastern Minnesota, other Great Lakes states, or southeastern Canada (Mech and Paul 2008; Kays et al. 2010a; Kays et al. 2010b; Mech 2010). Mech and Paul (2008) looked at wolf size across Minnesota and found that there was a size cline, with larger wolves in the west and smaller wolves in the east. The authors suggested this cline was consistent with a hybrid zone in which western Minnesota wolves had greater gray wolf ancestry and eastern Minnesota wolves had greater eastern wolf ancestry (Mech and Paul 2008). Morphological differences have been similarly linked with introgression elsewhere in the range as well. Benson and colleagues noted a range of different size canids in the area surrounding Algonquin Provincial Park in Canada, with gray wolves on the large end and coyotes on the small end of the spectrum (Benson et al. 2012). Although the genetic results of their study were consistent with the existence of either 2 clusters (gray wolf and coyote) or three clusters (gray wolf, eastern wolf, and coyote), they found that genetic estimates of ancestry were consistently linked to size in predictable fashion.

Human-mediated extirpation of wolves may have played a role in the current variation seen in the area. The near-extirpation of wolves in the United States in the mid-1900s left them in only two places, Isle Royale in Lake Superior and northeastern Minnesota. As wolves continued to disperse from the Canadian provinces of Ontario and Manitoba into Minnesota, they subsequently moved into Wisconsin and Michigan (Mech et al. 1995; Mech 2010). These recolonizing wolves were more similar to eastern wolves (Mech et al. 1995; Wheeldon and White 2009). As a result, researchers have suggested that wolves currently occupying much of the Great Lakes area may not be the same as the wolves that were in the area prior to their extirpation (Leonard and Wayne 2008, but see Mech 2009). Nonetheless, it seems the eastern wolf, introgressed with gray wolf to varying degrees, is present in much of the Great Lakes area, while northwest Minnesota continues to be more genetically pure gray wolf (Mech 2010).

In the western United States, there are no species-level controversies about wolves, though there have been a variety of sub-specific designations through time. The definition and use of subspecies designations is often controversial in any taxa, since there is often a somewhat arbitrary nature to the division of intra-specific variation across which movement and breeding may occur freely. Nonetheless, the Endangered Species Act specifically addresses subspecies, and taxonomists have long defined subspecies within *Canis lupus*. In that context, the most clearly delineated subspecies of *Canis lupus* is the Mexican wolf (*Canis lupus baileyi*), which has been recognized as a distinct subspecies both morphologically and genetically (Nowak 1995; vonHoldt et al. 2011; Fredrickson et al. 2015; Fan et al. 2016). In the rest of the western United States, early canid taxonomic work included many subspecies designations (Goldman 1944, Hall 1981). More recently, Nowak (1995) conducted a comprehensive examination of taxonomy based on skull morphometrics and consolidated specimens into two distinct gray wolf subspecies in the western United States in addition to the Mexican wolf. *Canis lupus occidentalis* was said to be found in the Rocky Mountains up into northern Alaska and *C. l. nubilus* was described in the Great Plains and Pacific coastal areas through southeastern Alaska. Chambers and colleagues noted good support for both *C. l. occidentalis* and *C. l. nubilus* in their review of wolf taxonomy suggesting that the two subspecies may represent independent migration events from Eurasia, with *C. l. nubilus* arriving earlier and *C. l. occidentalis* arriving during some later period (Leonard et al. 2005; Weckworth et al. 2010, reviewed in Chambers et al. 2012).

An increasing body of genetics research has added important insight into genetic variation among wolf populations beyond a traditional taxonomic framework. This work often does not directly address the taxonomic validity of designated subspecies, and at times has shown a lack of strong support for those designations (vonHoldt 2011; Cronin et al. 2014). Nonetheless, this research has provided strong evidence that genetic differentiation among wolves is often correlated with ecological factors. Factors such as habitat type and prey specialization have been shown to influence genetic structuring, leading to measurable differentiation even between areas with no physical barriers to dispersal (Carmichael et al. 2001; Musiani et al. 2007; Pilot et al. 2006). Ecological factors have been shown to influence phenotypic factors such as cranial morphology (O'Keefe et al. 2013) and have been linked to putative functional genes that determine morphology, coat color, and metabolism (Schweizer et al. 2016). The term "ecotype" is often used to distinguish between distinct groups of wolves, with some authors proposing that a population genetic framework may be more appropriate than a traditional taxonomic approach for discussing variation among wolves (Cronin et al. 2015; Wayne and Shaffer 2016).

The concept of ecotypes has been applied in the Pacific northwest, where an inland and a coastal ecotype have been identified that are genetically and morphologically distinct, and display distinct habitat and prey preferences, despite relatively close proximity (Muñoz-Fuentes et al. 2009; Weckworth et al. 2010; Hendricks et al. 2018). Muñoz-Fuentes et al. (2009) also noted that when Nowak (1995) consolidated the previously recognized coastal subspecies *C. l. fuscus* into *C. l. nubilus*, no samples from coastal British Columbia were included in the morphological analysis. Nonetheless, the distinctiveness of the coastal ecotype has been confirmed in several genetic analyses (Leonard et al. 2005; Weckworth et al. 2005; Weckworth et al. 2010; vonHoldt et al. 2011), and samples with coastal wolf ancestry have been identified in historical samples as far south as southwestern Oregon (Hendricks et al. 2018). Genetic analysis of wolves currently occupying Washington and Oregon has shown that, while all Oregon wolves are derived from dispersers from the northern Rocky Mountains, Washington has individuals from the northern Rocky Mountains as well as wolves of the coastal ecotype, including wolves of mixed ancestry (Hendricks et al. 2018). This result indicates that there has been effective dispersal into Washington from coastal British Columbia as well as from states to the east, and that admixture between ecotypes is actively taking place there (Hendricks et al. 2018).

The connection between ecological factors and genetic differentiation has been noted in eastern wolves as well, although in that context the genetic differences are often attributed to varying levels of introgression between gray wolves, eastern wolves, and coyotes, since admixture between those groups is so ubiquitous. In a study around Algonquin Provincial Park in Canada, higher proportions of gray wolf ancestry, as opposed to eastern wolf or coyote ancestry, were found in areas with reduced human disturbance and increased moose density (Benson et al. 2012). In similar work focusing on introgression between wolves and coyotes, areas of higher deer density were associated with wolf, rather than coyote ancestry (Monzón et al. 2014) and Kays et al. (2010a) suggested that introgression with wolves conferred an adaptive advantage to coyotes in certain habitat types. These results and the evident variety of introgression throughout the Great Lakes area and southeastern Canada suggest that hybridization and introgression may act as a component of canid adaptation to environmental heterogeneity in the area (Nowak 2002; Kyle et al. 2006; Koblmüller et al. 2009).

In summary, wolf taxonomy and evolutionary history are complex and controversial in North America. The science around wolf subspecies, unique evolutionary lineages, ecotypes, and admixture of formerly isolated populations continues to develop. For example, while genetic studies have found indications that Pacific coastal wolves in southeastern Alaska and British Columbia constitute a distinctive and largely isolated group, there is now evidence of admixture of coastal and inland wolves where the two forms meet in Washington. In the eastern United States and the area around the Great Lakes, wolves appear to have a complex evolutionary history in which hybridization with coyotes likely has played a significant role, and where there is uncertainty regarding the number of valid wolf species (reviewed by Waples et al. 2018). With ongoing debates and continuing scientific efforts aimed at clarifying the taxonomic relationships among various Canid groups, we have an imperfect understanding of their evolutionary history in North America. Furthermore, even with complete knowledge of those evolutionary histories, some uncertainty over taxonomic categorizations would remain given the application of different species concepts and the fact that evolution is a dynamic process, where evolutionary units often occur on a continuum rather than fitting into discrete categories. Given the above, for the remainder of this report we use the term "eastern wolf" and "western gray wolf" to describe wolves in those specific geographic areas, whereas we will use "gray wolf" to include both eastern wolves and western gray wolves.

Biology and Ecology

The biology and ecology of the gray wolf have been widely described in the scientific literature (e.g., Mech 1970, Mech and Boitani 2003), in USFWS recovery plans (e.g., Northern Rocky Mountain Recovery Plan (USFWS 1987) and Recovery Plan for the Eastern Timber Wolf (USFWS 1992)), and in previous proposed and final rules (e.g., 68 FR 15804, April 1, 2003; 71 FR 15266, March 27, 2006; 74 FR 15123, April 2, 2009; 75 FR 46894, August 4, 2010; and 76 FR 81666, December 28, 2011). Gray wolves are the largest wild members of Canidae, or dog family, with adults ranging from 18 to 80 kilograms (kg) (40 to 175 pounds (lb)), depending on sex and geographic locale (Mech 1974). Gray wolves have a circumpolar range including North America, Europe, and Asia. In North America, wolves are primarily predators of medium and large mammals, such as moose, elk, white-tailed deer, mule deer (*Odocoileus hemionus*), caribou (*Rangifer tarandus*), muskox (*Ovibos moschatus*), bison (*Bison bison*), and beaver (*Castor canadensis*). Gray wolves have long legs that are well adapted to running, allowing them to move fast and travel far in search of food (Mech 1970), and large skulls and jaws that are well suited to catching and feeding on large mammals (Mech 1970). Wolves also have keen senses of smell, hearing, and vision, which they use to detect prey and one another (Mech 1970). Pelt color varies in wolves more than in almost any other species, from white to grizzled gray to brown to coal black (Mech 1970).

Wolves share an evolutionary history with other mammalian carnivores (Order Carnivora), or meat eaters, which are distinguished by their long, pointed canine teeth, sharp sheering fourth upper premolars and first lower molars, simple digestive system, sharp claws, and highly developed brains (Mech 1970). Divergence among the ancestral mammalian carnivores began 40 to 50 million years ago (Mech 1970), and at some point during the late Miocene Epoch (between 4.5 to 9 million years ago) the first species of the genus *Canis* arose, the forerunners of all modern wolves, coyotes, and domestic dogs (Nowak 2003). The lineage of wolves and coyotes diverged between 1.8 and 2.5 million years ago (Nowak 2003). Domestication of wolves led to all modern domestic dog breeds and probably started somewhere from 135,000 to 13,000 years ago (reviewed by Honeycutt 2010).

Gray wolves are highly territorial, social animals and group hunters, normally living in packs of 7 or less but sometimes attaining pack sizes of 20 or more wolves (Mech 1970; Mech and Boitani 2003). Though pack composition can vary, packs are typically family groups consisting of a breeding pair, their pups from the current year, offspring from previous years that have not yet dispersed, and occasionally an unrelated wolf (Mech 1970; Mech and Boitani 2003). Normally, only the top-ranking male and female in each pack breed and produce pups, although sometimes maturing wolves within a pack will also breed with members of the pack or through liaisons with members of other packs (Mech and Boitani 2003). Wolves of both sexes reach sexual maturity between 1 and 3 years of age and, once paired with a mate, may produce young annually until they are over 10 years old. Litters are born from early April into May and can range from 1 to 11 pups but generally include 5 to 6 pups (Mech 1970; Fuller et al. 2003). Normally a pack has a single litter annually, but 2 litters from different females in a single pack have been reported, and in one instance 3 litters in a single pack were documented (reviewed by Fuller et al. 2003). Offspring usually remain with their parents for 10–54 months before dispersing (reviewed by Mech and Boitani 2003; Jimenez et al. 2017).

Packs typically occupy and defend a territory of 33 to more than 2,600 square kilometers (sq km) (13 to more than 1,016 square miles (sq mi)), with territories tending to be smaller at lower latitudes (Mech and Boitani 2003; Fuller et al. 2003). The large variability in territory size is likely due to differences in pack size; prey size, distribution, and availability; population lags in response to changes in prey abundance; and variation in prey vulnerability (e.g., seasonal age structure in ungulates) (Mech and Boitani 2003).

Pack social structure is very adaptable and resilient. Breeding members can be quickly replaced from either within or outside the pack, and pups can be reared by another pack member should their parents die (Packard 2003; Brainerd et al. 2008; Mech 2006; Borg et al. 2014). Consequently, wolf populations can rapidly overcome severe disruptions, such as pervasive human–caused mortality or disease. Wolf populations have been shown to increase rapidly if the source of mortality is reduced after severe declines (Fuller et al. 2003; USFWS et al. 2012).

A wolf pack will generally maintain its territory as long as the breeding pair is not killed, and even if one member of the breeding pair is killed, the pack may hold its territory until a new mate arrives (Mech and Boitani 2003). If both members of the breeding pair are killed, the remaining members of the pack may disperse, starve, or remain in the territory until an unrelated dispersing wolf arrives and mates with one of the remaining pack members (Brainerd et al. 2008; Mech and Boitani 2003).

Wolves of all ages may disperse, but in general, by the age of 3 years, most wolves will have dispersed from their natal pack to locate social openings in existing packs or find a mate and form a new pack (Mech and Boitani 2003; Jimenez et al. 2017). Dispersers may become nomadic and cover large areas as lone animals, or they may locate unoccupied habitats and members of the opposite sex to establish their own territorial pack (Mech and Boitani 2003). Dispersal distances in North America typically range from 65 to 154 km (40 to 96 miles) (Boyd and Pletscher 1999; Jimenez et al. 2017), although dispersal distances of several hundred kilometers are occasionally reported (Boyd and Pletscher 1999; Mech and Boitani 2003; Oregon Department of Fish and Wildlife (ODFW) 2011; ODFW 2016; Jimenez et al. 2017). These dispersal movements allow a wolf population to quickly expand and colonize nearby areas or even those that are separated by a broad area of unsuitable habitat.

Wolf populations are remarkably resilient as long as food supply (a function of both prey density and prey vulnerability), habitat, and regulation of human-caused mortality (Fuller et al. 2003; Creel and Rotella 2010) are adequate. It is generally believed that, in the absence of high levels of anthropogenic influences, wolf populations are regulated by the distribution and abundance of prey on the landscape (Fuller et al. 2003; McRoberts and Mech 2014; Mech and Barber-Meyer 2015). However, there is some evidence to suggest that wolves may be regulated by density-dependent, intrinsic mechanisms (e.g., social strife, territoriality, disease) when ungulate densities are high but are limited by prey availability when ungulate densities are low (Carriappa et al. 2011; Cubaynes et al. 2014). Where harvest occurs, high levels of reproduction and immigration can compensate for mortality rates of 17% to 48% (Fuller et al. 2003 [+/– 8%]; Adams et al. 2008 [29%]; Creel and Rotella 2010 [22%]; Sparkman et al. 2011 [25%]; Gude et al. 2012 [48%]; Vucetich and Carroll 2012 [17%]). Some studies suggest that the sustainable mortality rate may be lower, and that harvest may have a partially additive or even super-additive effect (harvest increases total mortality beyond the effect of direct killing itself through social disruption or the loss of dependent offspring) on wolf mortality (Murray et al. 2010; Creel and Rotella 2010), but there is substantial debate on this issue (Gude et al. 2012). When populations are maintained below carrying capacity and natural mortality rates and self–regulation of the population remain low, human-caused mortality can replace up to 70% of natural mortality (Fuller et al. 2003).

Suitable Habitat

Wolves can successfully occupy a wide range of habitats, and they are not dependent on wilderness for their survival. In the past, gray wolf populations occupied nearly every type of habitat north of mid-Mexico that contained large ungulate prey species, including bison, elk, white-tailed deer, mule deer, moose, and caribou. Inadequate prey densities and high levels of human persecution limit wolf distribution (Mech 1995). Virtually any area that has sufficient prey and adequate protection from human-caused mortality could be considered potential gray wolf habitat.

Various researchers have investigated habitat suitability for wolves in the central and eastern portions of the United States (Mladenoff et al. 1995, 1997, 1998, 1999 and 2009; Harrison and Chapin 1997 and 1998; Wydeven et al. 2001; Erb and Benson 2004; Potvin et al. 2005). Suitable habitat for wolves in the Great Lakes area can be determined by considering four factors: road density, human density, prey base, and size. In much of the Great Lakes area the white-tailed deer density is well above adequate levels, causing the other factors to become the determinants of suitable habitat. Prey base is primarily of concern in the UP where severe winter conditions cause deer to move away from some lakeshore areas, making otherwise suitable areas locally and seasonally unsuitable. Road density and human density can be highly correlated; therefore, road density is often used as a predictor of habitat suitability. However, areas with higher road density may still be suitable if the human density is very low, so a consideration of both factors is sometimes useful (Erb and Benson 2004). Finally, although the territory of individual wolf packs can be relatively small, packs are not likely to establish territories in areas of small, isolated patches of suitable habitat.

Several modeling efforts have also been conducted for suitable wolf habitat in the western United States (Oakleaf et al. 2006; Carroll et al. 2001, 2006 and 2010; Larsen and Ripple 2006; Houts 2003; and Ratti et al. 2004). Despite difference in modeling approaches and assumptions, suitable wolf habitat in these modeling efforts was typically characterized by large-blocks of public land, mountainous forested habitat, abundant wild ungulate populations (or areas of higher productivity), lower road densities, lower human population densities, and lower livestock densities. There are exceptions, however, in northeastern Oregon where a large remnant prairie is remote and supports large elk herds in a non-forested environment (ODFW 2015). In general, suitable wolf habitat in California is described similarly as for other western states; however, reoccupancy of wolves in California is just beginning and more information on actual habitat use will be collected as additional packs become established.

Historical Distribution and Abundance

The range of the gray wolf prior to European settlement was generally believed to include most of North America. In the lower 48 United States, wolves were reportedly absent from coastal and interior portions of California, the arid deserts and mountaintops of the western United States, and parts of the eastern and southeastern United States (Young and Goldman 1944; Hall 1981; Mech 1974; and Nowak 1995). However, some authorities have questioned the reported historical absence of gray wolves in parts of California (Carbyn in litt. 2000; Mech in litt. 2000). In addition, there are long-held differences of opinion regarding the precise boundary of the gray wolf's historical range (at the time of European settlement) in the eastern and southeastern United States, largely due to disputes over Canid taxonomy. As discussed under *Taxonomy* above, the evolutionary history of the eastern wolf has been the source of perhaps the most significant disagreement on North American canid taxonomy among scientists. The various positions include that the eastern wolf is a distinct species, a subspecies of the gray wolf, an ecotype of the gray wolf, or result of hybridization between gray wolves and coyotes. In the Southeast, some scientists regarded Georgia's southeastern corner as the southern extent of gray wolf range (Young and Goldman 1944, Mech 1974); others believed gray wolves did not extend into the Southeast at all (Hall 1981) or did so to a limited extent, primarily at somewhat higher elevations (Nowak 1995). The southeastern and mid-Atlantic States, however, are generally recognized as being within the historical range of the red wolf, but it is not known how much range overlap historically occurred between gray wolves (inclusive of the area of uncertainty) and red wolves. Because of these various scientific positions, the historical extent of gray wolf range in much of the East remains uncertain (Figure 1).

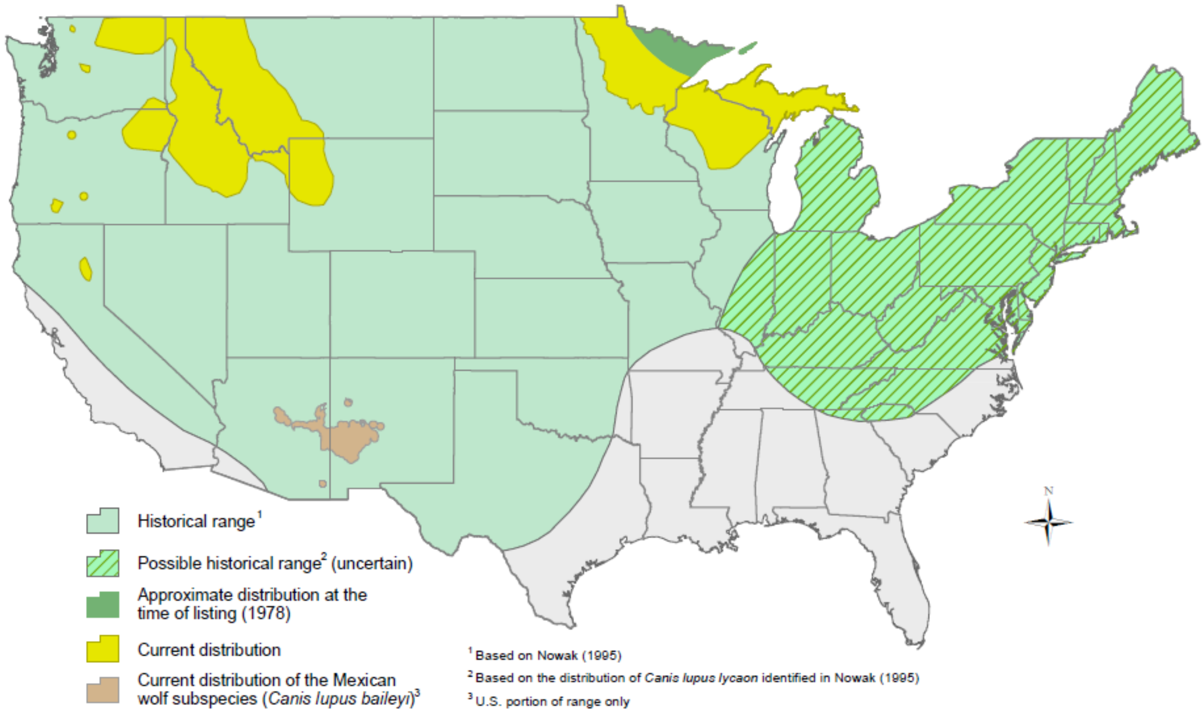

Figure 1. Historical range and distribution of the gray wolf (*Canis lupus*) in the lower 48 United States.

<u>Western U.S.</u>

In the western United States wolves were historically common and widely distributed prior to major Euro-American settlement of the West (Suckley 1859; Suckley and Gibbs 1859; Conard 1905; Bailey 1936; Dalquest 1948). Estimates of historical populations are notoriously difficult to verify, but genetic data suggest that there were likely hundreds of thousands of gray wolves once occupying the western U.S. (Leonard et al. 2005). As a result of poisoning, unregulated trapping and shooting, and the public funding of wolf extermination efforts, gray wolf populations were essentially eliminated from Oregon, Washington, and the northern Rocky mountain states of Montana, Idaho, Wyoming, Utah, and Colorado by the 1930s (Young and Goldman 1944); although there was some evidence of wolf occupancy in the Cascade Mountains of Oregon and in the remote parts of central Idaho into the 1940s (Young and Goldman 1944, USFWS 1987). After human-caused mortality of wolves in southwestern Canada was regulated in the 1960s, populations expanded southward (Carbyn 1983). Dispersing individuals occasionally reached the northern Rocky Mountains of the United States (Ream and Mattson 1982; Nowak 1983), but lacked legal protection there until 1974 when they were first listed under the Act as the subspecies *C. l. occidentalis*.

Historical range maps show considerable variation in the gray wolf's former range in California (Shelton and Weckerly 2007). There are only two known recent museum records of gray wolves from California, one in the Providence Mountains in San Bernardino County (Jurek 1994) and one in the Cascade Mountains of Lassen County (Jurek 1994). Despite limited preserved physical evidence for wolves in California, there were many reports of wolves from around the state in the 1800s and early 1900s (e.g., Sage 1846; Price 1894; Dunn 1904; Dixon 1916; Young and Goldman 1944; Sumner and Dixon 1953; Schmidt 1991), with the earliest reports noting that they were ''numerous and troublesome'' and ''a source of great annoyance to the inhabitants by destroying their sheep, calves, colts, and even full-grown cattle and horses'' (Sage 1846). Cronise (1868) described gray wolves in the mid-1800s as ''common in the northern and higher districts of the state [of California],'' In 1904, Stephens (1906) stated, ''A very few Gray Wolves live in the high Sierras and in the mountains of northeastern California.'' In the 1920s, five wolves were confirmed and one was shot in Modoc County on the Oregon-California border (Young and Goldman 1944). In 1939, the U.S. Forest Service estimated that wolves were present in small numbers in Lassen (16 wolves), Tahoe (4), Eldorado (12), Stanislaus (6), and Angeles (5) National Forests in California, although the basis for these estimates is not given (Young and Goldman 1944). The paucity of physical evidence of wolves occupying California is likely an artifact of targeted elimination associated with the Spanish missions and their extensive livestock interests (Schmidt 1991) prior to the era of collecting specimens for natural-history museums. The adaptability of wolves and the early firsthand accounts of wolves in California suggest that wolves likely occurred in northern California, the Sierra Nevada, and southern California mountains.

In Nevada, wolves may have always been scarce (Young and Goldman 1944), but probably occurred in the forested regions of the state (Young and Goldman 1944). During 20 years of predator control campaigns of the early 1900s, six wolves were taken, only one of which was from the western half of the state, near the ghost town of Leadville, NV (Young and Goldman 1944; Hall 1946). In addition to this record, there is one record of early-recent gray wolf bone remains, near Fallon, Nevada (Churchill County) (Morrison 1964; Nowak 1979). Several wolf observations from western Nevada were also reported in 1852 from around the Humboldt River, Humboldt Sink, and Carson Valley (Turnbull 1913; Young and Goldman 1944).

Historically, wolves were numerous and widely distributed across most of Colorado and Utah, with the primary exception being the Great Salt Lake desert in western Utah (Young and Goldman 1944). During the mid to late 1800s, market hunters decimated native ungulate populations throughout the west and, consequently, wolves began to prey upon livestock brought west by settlers with increased frequency (Young and Goldman 1944). As a result, wolves and other large predators were targeted for extermination through government (state and federal) sponsored eradication programs. Due to the success of these programs, wolves were functionally extirpated from Colorado in 1943 (E. Odell, personal communication, February 13, 2018) and from Utah in 1930 (Utah Division of Wildlife Resources and Utah Wolf Working Group 2005).

<u>Great Lakes Area</u>

Wolves likely occurred throughout Minnesota prior to European settlement and may have numbered 4,000-8,000 at that time (Mech 2000). By 1900, wolves were rare in the southern and western portions of the state. During the pre-1965 period of wolf bounties and legal public trapping, wolves persisted in the remote northeastern portion of Minnesota, but were eliminated from the rest of the state. Estimated numbers of Minnesota wolves before were first listed under the Act as the subspecies *C. l. lycaon* in 1974 include 450 to 700 wolves in 1950–53 (Fuller et al. 1992, based on data in Stenlund 1955), 350 to 700 wolves in 1963 (Cahalane 1964), 750 wolves in 1970 (Leirfallom 1970), 736 to 950 wolves in 1971–72 (Fuller et al. 1992), and 500 to 1,000 wolves in 1973 (Mech and Rausch 1975). Although these estimates were based on different methodologies and are not directly comparable, each puts the prelisting abundance of wolves in Minnesota at 1,000 or less. This was the only significant wolf population in the United States outside Alaska during those time periods.

In Wisconsin, 3,000-5,000 wolves are speculated to have occupied the area prior to European settlement (Wydeven et al. 2009). A bounty operated in the area from 1839-1847 and again (nearly continuously) from 1865-1957, which effectively eliminated wolves from the state. Wolves had declined to approximately 200 individuals by the early 1920s, and only a few scattered individuals persisted by the late 1950s (Wydeven et al. 2009). Wolves were considered extirpated in the state by 1960 (Thiel 1993).

Prior to European settlement, wolves occupied both the upper and lower peninsulas of Michigan and likely occurred in every county in the state. Although no estimates of wolf abundance were recorded at that time, Beyer et al. calculated an estimated abundance (based on maximum wolf densities from recent times) of fewer than 6,000 wolves in the state. As in other areas, European settlers held a negative view of wolves, and targeted wolves in an attempt to eliminate them. A bounty was first established in Michigan in 1817 and continued in multiple forms (including a state-funded trapping program) until 1960 (Beyer et al. 2009), by which time the population in the state had crashed. Wolves were state-listed in 1965. By 1973, only about 6 wolves may have existed in the upper peninsula and an attempt in 1974 to release 4 wolves from Minnesota into the Michigan's upper peninsula failed, as all 4 were killed within 8 months.

Northeast U.S.

Although historical abundance data are unavailable, gray wolves are known to have ranged in suitable habitats throughout the Northeast, where they may have hybridized with the eastern Canadian wolf (*Canis lycaon*) (Rutledge et al. 2010), until extirpated from this region in the 1890s (Krohn and Hoving 2010). Mitochondrial DNA extracted from a wolf killed in Maine in the 1880s and the last wolf reportedly killed in New York State dating to the 1890s indicated these animals represented a distinct eastern genotype (Wilson et al. 2003). These specimens are significant as they were taken well before the expansion of western coyotes (*Canis latrans*) into the northeastern United States (Thiel and Wydeven 2012).

Wolves are known to have occurred historically in the states of Maine, New Hampshire, Vermont, New York, Massachusetts, and Connecticut. They were extirpated from Maine by the end of the 1800s, and from New Hampshire and Vermont by the middle to late 1800s (Thiel and Wydeven 2012). Reports of wolves occurred in Connecticut into the early 1800s (Goldman 1944), while they may have persisted in the western mountains of Massachusetts to the end of the 1800s (Goldman 1944).

Wolves persisted in portions of northern New York until the late 1800s (Goldman 1944). Between 1871 and 1897, 98 wolves were submitted for bounty in New York, mainly in northern counties (Goldman 1944). The bounty ended in 1898, and wolves were considered extirpated in the state thereafter.

Southwestern U.S. and Mexico (Mexican Wolf)

The Mexican wolf was common throughout portions of the southwestern United States (southern Arizona and southwestern New Mexico) and Mexico (the Sierra Madre of Mexico south at least to southern Durango) through the mid-1800s. As human settlements expanded across in that area, wolves increasingly came into conflict with livestock operations and other human activities. Due to predator eradication efforts, Mexican wolves were effectively eliminated from the wild in the U.S. and numbers in Mexico had been severely reduced by the 1970s.

Distribution and Abundance at the Time of Listing

In 1978, when several gray wolf subspecies were consolidated into a single lower 48 U.S./Mexico listing and a separate Minnesota listing under the ESA, the gray wolf occurred in only a small fraction of its historical range (Figure 1) and was very rare in most places where it existed. Fewer than 200 wolves survived in Mexico, and those were widely scattered and subject to intensive human pressure. In the Southwest United States, the wolf was present only as an occasional wanderer near the Mexico border. Although the 1978 listing rule indicated that wolves in the northwestern United States were restricted mainly to remote parts of the Rocky Mountains, there were occasional unconfirmed sightings. There is no information to indicate that there were reproducing packs in those areas at that time, however. Wolves had been eliminated in much of the eastern half of the United States with the exception of northeast Minnesota and a small group of approximately 40 wolves on Isle Royale, Michigan. Although it was suspected that wolves inhabited Wisconsin at this time, it was not until 1979 that wolf presence was confirmed in the state.

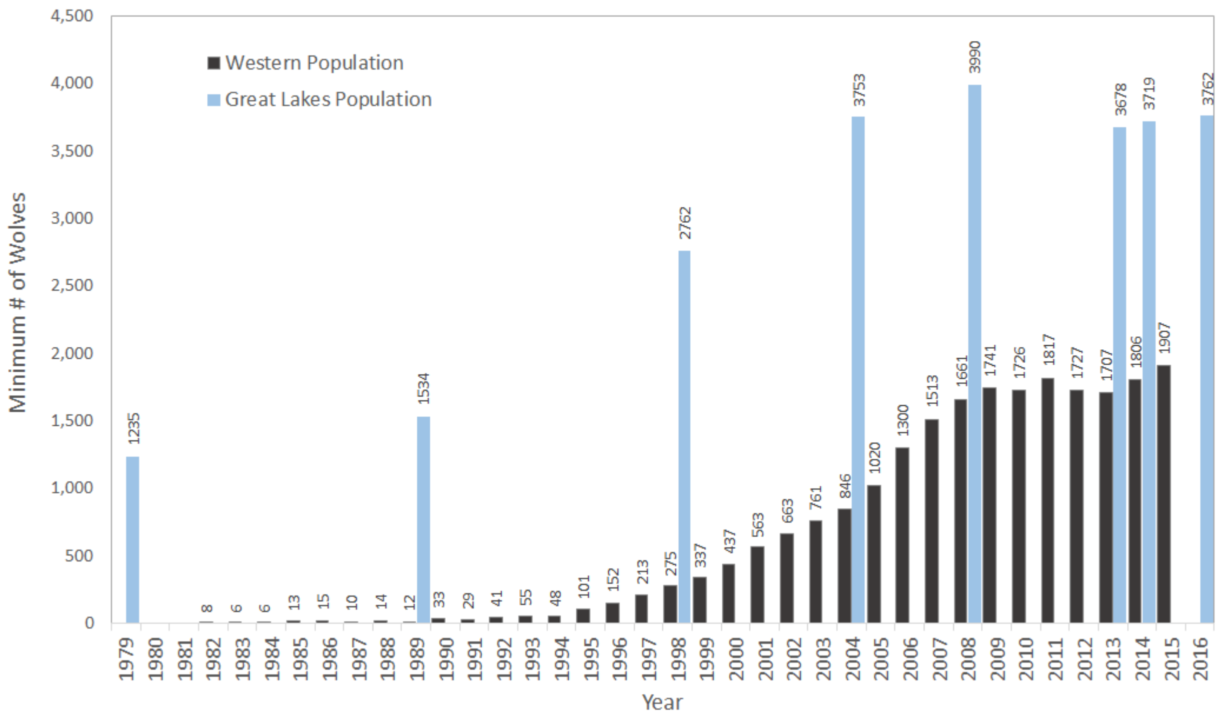

Figure 2. Minimum number of gray wolves (*Canis lupus*) counted in the lower 48 United States, 1979-2016. Does not include Mexican wolves. Great Lakes Population counts are only given for years when consistent data were available for all States in that region. Western population minimum counts were not available in 2016 due to changes in State monitoring strategies (see text for more details).

<u>Western Population</u>

Idaho, Montana, and Wyoming

In 1974, an interagency wolf recovery team was formed, and it completed the Northern Rocky Mountain Wolf Recovery Plan in 1980 (USFWS 1980). The Rocky Mountain Plan focused wolf recovery efforts on the large contiguous blocks of public land from western Wyoming and central Idaho through Montana to the Canadian border.

In 1982, a wolf pack from Canada began to occupy Glacier National Park along the United States-Canada border. In 1986, the first litter of pups documented in over 50 years was born in the Park (Ream et al. 1989). In recognition of the ongoing natural recovery of wolves arising from these Canadian dispersers, the Rocky Mountain Plan was revised in 1987 (USFWS 1987). The revised Rocky Mountain Plan recommended that recovery be focused in areas with large blocks of public land, abundant native ungulates, and minimal livestock. Three recovery areas were identified— northwestern Montana, central Idaho, and the Greater Yellowstone Area.

In 1995 and 1996, the USFWS reintroduced a total of 66 wolves from southwestern Canada to remote public lands in central Idaho and Yellowstone National Park (Bangs and Fritts

1996; Fritts et al. 1997; Bangs et al. 1998). The USFWS designated these wolves as nonessential experimental populations to increase management flexibility and address local and State concerns (59 FR 60252 and 60266; November 22, 1994). Wolves that were naturally recolonizing northwestern Montana remained listed as endangered, the most protective category under the Act.

The reintroduction of wolves to Yellowstone National Park and central Idaho in 1995 and 1996 greatly expanded the numbers and distribution of wolves in the northern Rocky Mountains of the United States. Because of the reintroduction, wolves soon became established throughout central Idaho and the Greater Yellowstone Area. In 1995, an estimated 8 breeding pairs (using the Environmental Impact Statement (EIS) definition of a male and female successfully raising 2 pups until December 31 of the year of their birth), within a total population of about 101 individual wolves, produced pups in the northern Rocky Mountains (USFWS et al. 2016, Table 6a and 6b). By 1996, a total population of 152 wolves contained 14 breeding pairs (USFWS et al. 2016, Table 6a and 6b).

At the end of calendar year 2000, the northern Rocky Mountain (NRM) population had 30 breeding pairs and more than 300 wolves that were well-distributed among Montana, Idaho, and Wyoming (68 FR 15804, April 1, 2003; USFWS et al. 2016, Table 6a and 6b). Three years later (by the end of 2002), at least 663 wolves and at least 49 breeding pairs were present (USFWS et al. 2016, Table 6a and 6b). By the end of 2015, the final year of a combined NRM annual report, the NRM gray wolf population (excluding Oregon and Washington) included a minimum estimate of 1,704 wolves (including at least: 536 in Montana; 786 in Idaho; and 382 in Wyoming) and 95 breeding pairs (including at least: 32 in Montana; 33 in Idaho; and 30 in Wyoming; USFWS et al. 2016, Table 6a and 6b, Figure 7a and 7b).

The five-year federal oversight period for Idaho and Montana ended in 2015, and since that time, wolf monitoring in these states has begun to transition from obtaining minimum counts of the total number of wolves, packs, and breeding pairs on the landscape to developing other techniques that are just as, if not more, accurate and are more cost efficient. Post-2015, Idaho transitioned from analyzing wolf data based on a calendar year to a biological year (BY; May 1–April 30) which more closely coincides with wolf birth pulses (Idaho Department of Fish and Game [IDFG] 2018). Idaho also conducts systematic camera surveys in suitable wolf habitat to estimate distribution and a minimum number of packs present in the state following techniques described by Ausband et al. (2014; IDFG 2018). Furthermore, genetic samples are collected from harvested wolves and analyzed to estimate a minimum number of confirmed litters in the state for that specific year (IDFG 2018). Idaho estimated a minimum of 81 packs present during summer 2016 and estimated a minimum of 63 litters during the summer of BY 2015 (IDFG 2018).

Montana no longer attempts to document every wolf, pack, or breeding pair in the state, but continues to conduct minimum counts to ensure wolf estimates remain above the minimum federal recovery requirements of 150 wolves and 15 breeding pairs. At the end of 2017, Montana estimated a minimum of 633 wolves in 124 packs with 63 breeding pairs (Montana Fish, Wildlife, and Parks [MFWP] 2018). At present, Montana primarily relies on Patch Occupancy Modeling (POM) to estimate wolf numbers, distribution, and trends over time. This method incorporates information from annual hunter surveys, known wolf locations, habitat covariates, and estimates of territory and pack size to estimate wolf distribution and number across the state (MFWP 2018). Statewide estimates using POM have been completed through 2016 and POM estimates tend to be higher than minimum counts.

Wyoming, where wolves were delisted in 2017 (82 FR 20284, May 1, 2017), continues to conduct minimum counts of wolves, packs, and breeding pairs to meet minimum federal recovery requirements. At the end of 2017, a minimum of 347 wolves in 53 packs with 23 breeding pairs were documented in Wyoming (Wyoming Game and Fish Department et al. 2018).

Washington and Oregon

In Washington, sporadic reports of wolves were received in the latter half of the twentieth century, and these reports increased during the 1990s to early 2000s, but no resident packs were documented during this time. Dispersing wolves from increasing populations in Idaho, Montana, and British Columbia, Canada, were likely responsible for the increased reports of wolves in northern Washington during the 1990s to early 2000. The first account of breeding by wolves since the 1930s was documented in the north-central Washington in 2008. Since that time wolves have continued to expand their distribution and abundance rapidly. From 2013 to 2017, WDFW reported minimum population counts increased between 2 and 32% per year (mean = 19.8%) (Becker et al. 2014, Becker et al. 2015, Becker et al. 2016, WDFW et al. 2017, WDFW et al. 2018). At the end of 2017, there were at least 122 wolves in 22 packs in Washington, most of which were located in the eastern one-third of the state where wolves are managed under state authority (WDFW et al. 2018). Three wolf packs (totalling at least 14 wolves and 1 breeding pair) were known to occur in the western two-thirds of the State where wolves are managed under federal authority. In 2017, a single male wolf was also captured and collared in Skagit County on the west side of the North Cascade Mountains.

In Oregon, the first evidence of multiple wolves and wolf reproduction since wolves were extirpated from the state in the mid-1940s occurred in July 2008, when a wolf pack including both adults and pups was confirmed in a forested area in northeastern Oregon. Since that time, the Oregon wolf population has grown rapidly and expanded westward. From 2013 to 2017, ODFW reported minimum population counts increased between 2 and 36% per year (mean = 20.4%) (ODFW 2014, ODFW 2015, ODFW 2016, ODFW 2017, ODFW 2018). At the end of 2017, there were at least 124 wolves in 12 packs (Oregon defines a pack as four or more wolves traveling together in winter), plus an additional 9 groups of two to three wolves, in Oregon, most of which were located in the eastern one-third of the State where wolves are exclusively managed under state authority (ODFW 2018). In Oregon, a single wolf pack (the Rogue Pack, which included a breeding pair and consisted of at least 7 wolves) and several dispersing wolves were reported in the western two-thirds of Oregon where wolves remain federally listed (ODFW 2018). Since wolves were first documented in Oregon, a minimum of six radio-collared and three uncollared wolves dispersed from areas under state management in northeast Oregon to southwest Oregon and northern California (OR-3, OR-7, OR-25, OR-28, OR-33, OR-44, Rogue Pack breeding female, and the breeding male and female of California's Shasta Pack) where they are federally listed. Other uncollared wolves have been detected in Klamath, Lake, and Wasco counties since 2013. In southwestern Oregon, a single wolf was known from the Silver Lake area of Lake County, with other individual wolves were recently photographed in southern Crater Lake National Park and in the vicinity of Gearhart Mountain in Klamath County. In north-central Oregon, two wolves are known from the vicinity of White River Wildlife Area, Mt. Hood National Forest, and the Warm Springs Indian Reservation in Wasco County (ODFW 2018) and were recently documented to have produced at least two pups in 2018.

California

Wolves are beginning to expand their range into California, with numerous confirmed detections of dispersers and breeding wolves over the past several years. The first was OR-7 in 2011, who eventually settled in southern Oregon as the breeding male of the Rogue Pack (California Department of Fish and Wildlife [CDFW] 2018a). In August of 2014, trail cameras photographed a wolf in northern Siskiyou County. Additional trail camera photographs of two wolves were taken in early 2015 in Siskiyou County, with five pups discovered in August of 2015 (CDFW 2018a). These animals became known as the Shasta Pack. The breeding male and female were descendants of the Imnaha Pack in northeast Oregon. However, regular detections of wolves in the Shasta Pack territory stopped in fall of 2015. Since then, the only detections were of a male yearling (from the 2015 Shasta Pack litter) in May 2016 within the territory and unconfirmed evidence of at least one wolf near the territory in summer and fall of 2017 (CDFW 2018a).

In August of 2015, a female wolf was photographed on a trail camera in Lassen County. In February of 2016, tracks of at least two wolves were detected in the same area. The second animal was later determined to be a male born into the Rogue Pack in 2014. In 2017, the pair produced at least four pups; three of which were known to be alive in March 2018 (CDFW 2018a). These animals became known as the Lassen Pack and occupy portions of Lassen and Plumas counties. The Lassen Pack also denned in 2018, producing at least two pups (CDFW 2018a).

Other individual wolves are also known to have travelled into California. Multiple observations of a black wolf in the vicinity of the Lassen Pack have been reported (CDFW 2018b); all Lassen Pack wolves are gray-phase. At this time it does not appear that the animal is part of the pack, but may be "shadowing" the Lassen Pack. Scat samples were collected from areas where this animal was observed; the results of genetic analyses of the scat are not yet available. A single set of wolf tracks were observed in northern Siskiyou County (north of the historical Shasta Pack territory) in early 2017. Genetic analysis of scat determined the wolf was a female born into the Rogue Pack in 2014 (CDFW 2018a). This animal has not been re-detected.

Two wolves collared in Oregon are also dispersing in California. A female wolf, OR-54, from the Rogue Pack entered California in January of 2018 and returned to Oregon three weeks later. She re-entered California in April of 2018. She has travelled through six northern California counties, as far south as Nevada County, California (CDFW 2018a). A male wolf, OR-44, from the Chesnimnus Pack in northeastern Oregon entered California in March of 2018 (CDFW 2018a). The majority of his time in California has been in Siskiyou County; however, his GPS collar stopped functioning in May of 2018 (CDFW 2018b).

Great Lakes Area

Minnesota

After several subspecies of gray wolf were first listed under the Act in 1974, the Minnesota population estimates increased (see Appendix 1). Mech estimated the population to be 1,000 to 1,200 wolves in 1976 (USFWS 1978), and Berg and Kuehn (1982) estimated that there were 1,235 wolves in 138 packs in the winter of 1978–79. In 1988–89, the Minnesota Department of Natural Resources (MN DNR) repeated the 1978–79 survey and also used a second method to estimate wolf numbers in Minnesota. The resulting independent estimates were 1,500 and 1,750 wolves in at least 233 packs; the lower number was derived by a method comparable to the 1978–79 survey (Fuller et al. 1992).

During the winter of 1997–98, the MN DNR repeated a statewide wolf population and distribution survey, using methods similar to those of the two previous surveys. Field staff of Federal, State, tribal, and county land management agencies and wood products companies were queried to identify occupied wolf range in Minnesota. Data from 5 concurrent radio telemetry studies tracking 36 packs, representative of the entire Minnesota wolf range, were used to determine average pack size and territory area. Those figures were then used to calculate a statewide estimate of wolf and pack numbers in the occupied range, with single (nonpack) wolves factored into the estimate (Berg and Benson 1999).

The 1997–98 survey concluded that approximately 2,445 wolves existed in about 385 packs in Minnesota during that winter period (90 percent confidence interval from 1,995 to 2,905 wolves) (Berg and Benson 1999). This figure indicated the continued growth of the Minnesota wolf population at an average rate of about 3.7% annually from 1970 through 1997–98. Between 1979 and 1989 the annual growth rate was approximately 3%, and it increased to between 4 and 5% in the next decade (Berg and Benson 1999; Fuller et al. 1992). Minnesota DNR conducted another survey of the State's wolf population and range during the winter of 2003–04, again using methodology similar to the previous surveys. That survey concluded that an estimated 3,020 wolves in 485 packs occurred in Minnesota (90 percent confidence interval for this estimate is 2,301 to 3,708 wolves) (Erb and Benson 2004). The MN DNR conducted its next survey of wolf population and range during the winter of 2007–08. That survey concluded that an estimated 2,921 wolves in 503 packs occurred in Minnesota (90 percent confidence interval for this estimate is 2,192 to 3,525 wolves) (Erb 2008). Beginning in winter 2012-2013 (following federal delisting), the MN DNR conducted annual surveys to better inform wolf management decisions under a changing management regime. Those surveys estimated a stable population of wolves in the State at 2,211 in 2012-2013, 2,423 in 2013-2014, 2,221 in 2014-2015, and 2,278 in 2015-2016 (Erb et al. 2017). Wolf harvest seasons were conducted for three seasons (2012-2014), and ended in December 2014 when wolves were returned to the list as a federally threatened species. The most recent survey with available results was conducted in winter 2016-2017. That survey concluded that an estimated 2, 856 wolves in 508 packs lived in Minnesota (90 percent confidence interval of 2,371 to 3,328) (Erb et al. 2017).

As wolves increased in abundance in Minnesota, they also expanded their distribution. During 1948–53, the primary wolf range was estimated at 31,080 sq km (11,954 sq miles) (Stenlund 1955). A 1970 questionnaire survey in Minnesota resulted in an estimated wolf range of 38,400 sq km (14,769 sq miles) (calculated by Fuller et al. 1992, from Leirfallom 1970). Fuller et al. (1992), using data from Berg and Kuehn (1982), estimated that Minnesota primary wolf range encompassed 36,500 sq km (14,038 sq miles) during the winter of 1978-79. By 1982–83, pairs or breeding packs of wolves were estimated to occupy an area of 57,050 sq km (22,000 sq miles) in northern Minnesota (Mech et al. 1988). That study also identified an additional 40,500 sq km (15,577 sq miles) of peripheral range, where habitat appeared suitable but no wolves or only lone wolves existed. The 1988-89 study produced an estimate of 60,200 sq km (23,165 sq miles) as the contiguous wolf range at that time in Minnesota (Fuller et al.

1992; Berg and Benson 1999), an increase of 65% over the primary range calculated for 1978–79.

The 1997-98 study concluded that the contiguous wolf range had expanded to 88,325 sq km (33,971 sq miles), a 47% increase in 9 years (Berg and Benson 1999). By that time the Minnesota wolf population was using most of the available primary and peripheral range identified by Mech et al. (1988). The wolf population in Minnesota had increased in abundance and distribution to the point that its contiguous range covered approximately 40% of the State during 1997–98. In contrast, the 2003–04 and 2007–08 surveys failed to show a continuing expansion of wolf range in Minnesota, and any actual increase in wolf numbers since 1997–98 was attributed to increased wolf density within a stabilized range (Erb and Benson 2004; Erb 2008). In 2013, the MN DNR collected data that indicated that the wolf range in the State had expanded along the southern and western periphery, the first extension since the 1997–98 survey. The contiguous wolf range in the State was estimated to be 95,098 sq km (36,718 sq mi) (Erb and Sampson 2013). The estimated range has not changed since that time.

The Minnesota wolf population has increased from an estimated 1,000 individuals in 1976 to over 2,000 today, and the estimated wolf range in the State has expanded by approximately 225% (from approximately 38,850 sq km (15,000 sq miles) to approximately 95,000 sq km (36,700 sq miles)) since 1970. Over the past 15 or more years, the population size and range have remained stable, as most of the suitable habitat has been occupied.

Wisconsin

Wolves were considered to have been extirpated from Wisconsin by 1960. No formal attempts were made to monitor the State's wolf population from 1960 through 1978. Although individual wolves and an occasional wolf pair were reported during that time (Thiel 1978, Thiel 1993), no reproduction was documented in Wisconsin, and the wolves that were reported may have been dispersing animals from Minnesota.

Wolves are believed to have naturally recolonized Wisconsin in the winter of 1975–76, and by 1979, 5 wolf packs were established in the state. The recolonizing wolves in Wisconsin most likely came from the increasing and expanding wolf population in Minnesota (Wydeven et al. 2009).

The Wisconsin Department of Natural Resources (WI DNR) began wolf population monitoring in 1979 and, since then, has intensively surveyed its wolf population on an annual basis using a combination of aerial, ground, and satellite radio telemetry complemented by snow tracking, summer howl surveys, recovery of dead wolves, depredation investigations, and collection of public observation reports (Wydeven et al. 2006; Wydeven et al. 2009b; Wiedenhoeft et al. 2017). Wolves are trapped from May through September and fitted with radio collars, with a goal of having at least one radio-collared wolf in approximately half of the wolf packs in Wisconsin. Aerial locations are obtained from each functioning radio-collar about once per week, and pack territories are estimated and mapped from the movements of the individuals who exhibit localized patterns. From December through March, the pilots make special efforts to visually locate and count the individual wolves in each radio-tracked pack.

Snow tracking is used to supplement the information gained from aerial sightings and to provide pack size estimates for packs lacking a radio-collared wolf. Tracking is done by assigning survey blocks to trained trackers, who then drive snow-covered roads in their blocks and document all wolf tracks they encounter. Snowmobiles, skis, or snowshoes are used to conduct surveys in more remote areas with few roads. The results of the aerial and ground surveys are carefully compared to properly separate packs and to avoid overcounting (Wydeven et al. 2006). The estimated number of wolves in each pack is based on the aerial and ground observations made of the individual wolves in each pack over the winter.

Because the monitoring methods focus on wolf packs, lone wolves are likely undercounted in Wisconsin. As a result, the annual population estimates are probably slight underestimates of the actual wolf population within the State during the late-winter period. Fuller (1989) noted that lone wolves are estimated to comprise from 2 to 29% of the total population in the area. Wisconsin DNR surveys have estimated 2–15% of the winter population as loners (Wydeven et al. 2009b). These surveys, however, are focused on heavily forested portions of northern and central Wisconsin; therefore, dispersing wolves traveling in other portions of the State are less likely to be detected, and often such wolves are only documented after vehicle collisions or accidental shootings. Broader use of trail cameras by members of the public is improving the WI DNR's ability to detect lone wolves across the State.

At the time the WI DNR began their wolf population monitoring in 1979, they estimated a statewide population of 25 wolves (Wydeven and Wiedenhoeft 2000; Wydeven et al. 2009b). This population remained relatively stable for several years, and then declined to approximately 14 to 19 wolves in the mid-1980s. In the late 1980s, the Wisconsin wolf population began an increase that continued into 2012, when the estimated population was 815 wolves (Wiedenhoeft et al. 2017; see Table 1). Following Federal delisting of wolves in January 2012, Wisconsin held its first regulated wolf hunting and trapping season in 2012-2013. One hundred and seventeen wolves were legally harvested during that first season, and the population estimate in the State remained relatively stable, falling slightly to 809 wolves. During the 2013-2014 hunting and trapping season, 257 were legally harvested. In 2014, the estimated minimum population count declined by 18% to 660 wolves, marking the first significant decline in the State since the late 1980s (Wiedenhoeft et al. 2014). In response to the decline, the Wisconsin Natural Resources Board reduced the wolf quota from 275 during 2013-2014 to 156 for the 2014-2015 hunting and trapping season. Following the 2014-2015 season, in which 154 wolves were legally harvested, wolves in the Great Lakes area were re-listed as endangered due to a successful court challenge to the 2012 Federal delisting (Humane Society of the U.S. v. Jewell, 76 F. Supp. 3d 69, 110 (D.D.C. 2014). The Wisconsin wolf population again began to increase in 2015, to an estimated 746 wolves (a 13% increase over the previous year). That population growth continued into 2016, with an estimated 866 wolves (in 222 packs), and 2017, with an estimated 925 wolves (in 232 packs). An estimated 905 wolves in 238 packs were in Wisconsin in early 2018 (https://dnr.wi.gov/topic/Wildlifehabitat/wolf/documents/2017-18wolfcountbrief.pdf).

Michigan

Except for Isle Royale, wolves were extirpated from Michigan as a reproducing species long before they were first listed as the subspecies *C. l. lycaon* under the Act in 1974. Prior to 1989, the last known breeding population of wild Michigan wolves outside Isle Royale occurred in the mid-1950s. However, as wolves began to reoccupy northern Wisconsin, the Michigan Department of Natural Resources (MI DNR) began noting single wolves at various locations in the Upper Peninsula (UP) of Michigan. Wolf recovery in Michigan began with the documentation of three wolves traveling together and making territorial marks in the central UP during the fall of 1988; and the subsequent birth of pups in this territory during spring 1989

(Beyer et al. 2009). Since that time, wolf packs have spread throughout the UP, with immigration occurring from Wisconsin on the west and possibly from Ontario on the east. Wolves now are found in every county of the UP.

The MI DNR annually monitors the wolf population in the UP by conducting a winter survey. Roads and trails are searched intensively and extensively for wolf tracks and other wolf sign using trucks and snowmobiles (Potvin et al. 2005). Complete surveys conducted from 1999 to 2006 provided an opportunity to evaluate multiple sampling approaches (MI DNR 2008). Based on these evaluations, it was determined that a geographically stratified sampling protocol produced unbiased, precise estimates of wolf abundance (Potvin et al. 2005; Drummer, unpublished data). The sampling protocol implemented beginning in 2007 allows trackers to spend more time in smaller areas (MI DNR 2008).

The UP is divided into 21 survey units from which a stratified random sample is drawn, covering roughly 50% of the UP every year (MI DNR 2008). Pack locations are derived from previous surveys, citizen reports, and extensive ground and aerial tracking of radio-collared wolves. Surveys along the border of adjacent survey units are coordinated to avoid double counting of wolves and packs occupying those border areas. In areas with a high density of wolves, ground surveys by four to six surveyors with concurrent aerial tracking are used to accurately delineate territories of adjacent packs and count their members (Beyer et al. 2004; Huntzinger et al. 2005; Potvin et al. 2005). As with Wisconsin, the Michigan surveys likely miss lone wolves, thus underestimating the actual population.

Based on annual surveys in late winter, estimates of wolves in the UP increased from 10 wolves in late winter 1989-90 to 116 wolves in 1995-96 and to 557 wolves in 2009-10. In 2010-11, the last year the MI DNR conducted annual surveys before switching to an every-other year cycle, there were an estimated 687 wolves in the UP (see Table 1 above). There appear to be two distinct phases of population growth, with relatively rapid growth (25.8% average) from 1995 through 2000 and slower growth (10.1% average) from 2001 through 2010. Since then, the annualized rate of change has fluctuated slightly year-to-year (with some decreases and some increases), but overall the population grew by 19% over the 8 years. During the winter of 2017-2018, the UP had an estimated 662 wolves in 139 resident packs.

In 2004, a coyote trapper mistakenly captured and killed a wolf in Presque Isle County in the northern Lower Peninsula (LP) of Michigan. This was the first verification of a wolf in the northern LP since 1910 (Roell et al. 2010). This wolf had been trapped and radio-collared by the MI DNR the previous year (2003) while it was a member of an eastern UP pack. Since 2004, Michigan has surveyed the northern LP to determine whether wolves have successfully colonized the area. From 2005 through 2007, the survey had two components: a prioritized area search and a targeted area search based on citizen reports of wolves or wolf sign. USDA Wildlife Services, Little Traverse Bay Band of Odawa Indians, and Central Michigan University worked cooperatively on the surveys. Nine units ranging in size from 322–644 sq km (200–400 sq miles) were surveyed; however, no wolf sign was found (Roell et al. 2010). Beginning in 2008, a targeted search approach was used; again, no wolves were detected in winters of 2008–10 (Roell et al. 2009; Roell 2010, pers. comm.). However, in the summer of 2009, video images of single wolves were recorded in two of the three northern LP counties nearest to the UP (Emmet and Presque Isle) (Roell et al. 2010).

In 2010, USDA Wildlife Services and MI DNR staff reported a presumed breeding pair of wolves with three pups in Cheboygan County in the northern LP (MI DNR 2010). That 2010 report was based on an assessment of the physical features of three pups that were captured and handled, observations of adult wolf-sized tracks, and remote camera photographs of large wolf-like canids. Subsequent DNA analysis assigned all three pups as eastern coyotes (Wheeldon et al. 2012). In 2014, biologists with the Little Traverse Bay Band (LTBB) of Odawa Indians discovered tracks and collected scat of what was presumed to be wolves in the LP's Emmet County. They submitted the scat for DNA analysis, which confirmed it was from a male gray wolf. Furthermore, the nuclear DNA assigned very closely to samples collected from wolves in northeast Ontario, which indicates that the wolf was likely not an escaped captive. During the winter of 2015, MI DNR staff investigated tracks characteristic of wolves in Cheboygan and Emmet Counties. Because no scat or hair was present for DNA analysis, a definite genetic confirmation could not be made. To date, a breeding population has not been confirmed in the northern LP.

The wolf population of Isle Royale National Park, Michigan is small and isolated and lacks genetic uniqueness (Wayne et al. 1991). For genetic reasons and constraints on expansion due to the island's small size, this wolf population does not contribute significantly towards meeting numerical recovery criteria; however, long-term research on this wolf population has added a great deal to our knowledge of the species. The wolf population on Isle Royale has typically varied from 18-27 wolves in 3 packs, but has been down to just 2 wolves (a father-daughter pair) since the winter of 2015-2016 (Peterson et al. 2018). The National Park Service recently announced plans to move additional wolves to Isle Royale in an effort to restore a viable wolf population (83 FR 11787; March 16, 2018).

Northeast U.S.

It is widely accepted that wolves became extirpated from the northeastern United States by the year 1900 (Young and Goldman 1944; Nowak 2002; Villemure and Jolicoeur 2004). The lack of reliable evidence of breeding pairs or wolves with established territories has been reaffirmed in subsequent analyses of the existing status of the wolf in the northeastern United States, including a 2003 final reclassification rule (68 FR 15804, April 1, 2003), a 90-day finding on a petition to list a DPS of gray wolves in the northeastern U.S. (75 FR 32869, June 10, 2010), a status assessment of eastern wolves conducted in 2011 (Thiel and Wydeven 2012), and a finding on an October 9, 2012, petition to continue to protect all wolves in the Northeast and develop a Northeast wolf recovery plan (78 FR 35664, June 13, 2013).

Although potential source populations of the eastern wolf phenotype (as discussed in *Taxonomy*, above) occur north of the St. Lawrence River in Quebec and Ontario, Canada, within the recorded dispersal capability of a wolf (Thiel and Wydeven 2012), and eastern wolf-coyote hybrids do occasionally disperse southward into the Northeast from Canada, we currently have no information indicating that wolves have formed breeding pairs in the Northeast U.S.

Southwest U.S. and Mexico (Mexican Wolf)

Prior to the early 1900s, the Mexican wolf (*Canis lupus baileyi*) was distributed over a large geographic area that included portions of the Southwest and much of Mexico. The Mexican wolf was nearly eliminated in the wild by the mid-1900's due to predator eradication efforts. The establishment and success of a captive-breeding program temporarily prevented immediate absolute extinction of the Mexican wolf and, by producing surplus animals, enabled the reestablishment of Mexican wolves in the wild by releasing captive animals into the experimental population areas in Arizona and New Mexico.

The Mexican wolves that currently occupy the Mexican Wolf Experimental Population Area (MWEPA) can be characterized as a relatively small but growing population. After exhibiting moderate growth in the initial years of the reintroduction (1998-2003), followed by a period of relative stagnation from 2003-2009, the population has exhibited sustained growth for the last seven years (with the exception of 2014-2015) with relatively high adult survival. The 2016 annual minimum population count in the MWEPA was 113 wolves, the largest population size reached by this population in its 19 years (USFWS files). Population growth in 2017 was relatively flat with the addition of at least one wolf to the minimum count.

The Mexican wolves that occupy northern Sierra Madre Occidental in Mexico can be characterized as an extremely small, establishing population. In October 2011, Mexico initiated the establishment of a wild Mexican wolf population in the Sierra San Luis Complex of northern Sonora and Chihuahua, Mexico, with the release of five Mexican wolves from captivity into the San Luis Mountains in Sonora just south of the U.S.-Mexico border (SEMARNAT e-press release, 2011). Since that time, from 2012 to 2016, 41 Mexican wolves have been released into the state of Chihuahua, 18 of which died within a year after release (Garcia Chavez et al. 2017). Out of 14 adults released from 2011 to 2014, 11 died or were believed dead, and 1 was removed for veterinary care. As of July 2017, approximately 31 wolves inhabit the northern portion of the Sierra Madre Occidental in the state of Chihuahua (CONANP 2017; Garcia Chavez et al. 2017). See the Biological Report for the Mexican Wolf (USFWS 2017) for a detailed description of the status of the Mexican wolf.

Confirmed Wolf Reports Elsewhere in the U.S.

There are confirmed records of a few lone gray wolves elsewhere within the lower 48 United States. These lone individuals are believed to be dispersing away from the more saturated habitat in the primary range of the West, Great Lakes area, or Canada populations into peripheral areas where wolves are scarce or absent (Licht and Fritts 1994; Licht and Huffman 1996; 76 FR 26100, May 5, 2011; Jimenez et al. 2017). Since the early 2000s, there have been ten confirmed records of individual wolves in South Dakota, nine in Utah, and five in Colorado (Jimenez et al. 2017; USFWS 2018, unpublished data). A gray wolf was observed in the northwest corner of the state of Nevada in the fall of 2016. Genetic analysis of scat was used to verify the animal as a male from the 2015 Shasta Pack litter from California (CDFW 2018a). This animal has not been re-detected, nor are there further reports of wolves in Nevada. A few individual dispersing gray wolves have been reported in areas of the Midwest as well, including a gray wolf that dispersed from Michigan to north-central Missouri (Mech and Boitani 2003; Treves et al. 2009) and another that dispersed from Wisconsin to eastern Indiana (Thiel 2009; Treves et al. 2009). At least 10 wolves have been reported in Illinois since 2000 (https://m.extension.illinois.edu/wildlife/directory_show.cfm?species=wolf). Two individual wolves were also reported (on different occasions) in Nebraska (Anschutz in litt. 2003, Anschutz in litt. 2006, Jobman in litt. 1995) and two in Kansas (USFWS 2018, unpublished data). Of the areas outside the more established western U.S. and Great Lakes area populations, North Dakota has the most records of individual dispersing wolves, with at least 27 verified records and an additional 45 probable but unverified reports since 2000 (North Dakota Game and Fish Department 2018, unpublished data).

Current Distribution and Abundance

Gray wolves currently exist in large, growing or stable meta-populations[1] in two disparate geographic areas in the lower 48 States—the western U.S. and the Great Lakes area —and there is a small, growing population of Mexican gray wolves in Arizona and New Mexico with an establishing population in Mexico (Figure 1).

As discussed above under *Population Trends Since Listing*, wolves in the Great Lakes area number over 4,400 individuals and occupy areas across 3 states. Wolves have successfully colonized most, perhaps all, suitable habitat in Minnesota. Since 1997-98, wolf numbers and density in Minnesota have stabilized and occupied range in the State has remained unchanged (see Appendix 1). Wisconsin wolves now occupy most habitat areas believed to have a high probability of wolf occurrence (except, perhaps, some areas of northeastern Wisconsin), and the State's wolf population continues to annually increase in numbers (except for 2013-14). The upper peninsula of Michigan has wolf packs throughout the peninsula and the wolf population in the State grew nearly every year from 1988 through 2010, and has stabilized since then, consistent with any population expanding into and then filling available habitat. The wolves in these three states occupy areas of high quality habitat with abundant prey.

Additionally, gray wolves in the Great Lakes area are connected to the large and expansive population of wolves in Canada. Ontario and Manitoba, the two Canadian Provinces that boarder the states of Minnesota, Wisconsin, and Michigan have an estimated 8,000-10,000 wolves (https://www.ontario.ca/document/state-resource-wolves) and an estimated 4,000 wolves (http://www.gov.mb.ca/sd/wildlife/mbsp/fs/grwolf.html), respectively. Wolves have been documented to disperse from the Great Lakes area to at least 3 Canadian provinces (Treves et al. 2009) and from Canada to the Great Lakes area (Thiel and Hammill 1988). Thus, gray wolves in the Great Lakes area do not function as an isolated population of around 4,400 individuals, but serve as part of a much larger metapopulation due to its connectivity with Canada. Furthermore, although the populations of gray wolves in Minnesota, Wisconsin, and Michigan are interconnected, they are broadly distributed across the northern portions of the three states.

Similarly, at the end of 2015, the final year minimum counts are available for gray wolves in the western U.S. indicated that there was a population of >1,900 wolves. Wolf populations in the Northern Rocky Mountain states of Idaho, Wyoming, and Montana grew by an average of 22% per year through 2008 then appeared to stabilize as wolves colonized most of the available suitable habitat in the area (USFWS et al. 2016, Table 6a and 6b, Figure 7a and 7b). At the end of 2015, there were more than 1,700 wolves in these three states alone. Suitable wolf habitat in these areas is generally characterized as public land with mountainous, forested habitat that contains abundant year round wild ungulate populations, low road density, low numbers of

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[1] A metapopulation is a concept whereby the spatial distribution of a population has a major influence on its viability. In nature, many populations exist as partially isolated sets of subpopulations termed ''metapopulations.' A metapopulation is widely recognized as being more secure over the long-term than are several isolated populations that contain the same total number of packs and individuals (USFWS 1994, Appendix 9). This is because adverse effects experienced by one of its subpopulations resulting from genetic drift, demographic shifts, and local environmental fluctuations can be countered by occasional influxes of individuals and their genetic diversity from the other components of the metapopulation.

domestic livestock that are only present seasonally, few domestic sheep, low agricultural use, and few people (Carroll et al. 2003; Oakleaf et al. 2006; Carroll et al. 2006). As suitable habitat became more saturated in the core ranges of Idaho, Montana, and Wyoming, wolves have begun to recolonize portions of Oregon, Washington, and, more recently, northern California. At the end of 2017, there were at least 122 wolves in 22 packs in Washington, 124 wolves in Oregon in 12 packs, and at least 6 wolves in California with one confirmed pack. Most of the wolves in these three States occurred in eastern Washington and eastern Oregon; although as packs fill the suitable habitat in those areas there are an increasing number of wolves dispersing to western Washington, western Oregon, and northern California. There are also several wolf packs that are now established in these areas.

Wolf populations in the western United States are interconnected with a large metapopulation of wolves that occur throughout western Canada. British Columbia and Alberta have an estimated 8,500 (B.C. Ministry of Forests, Lands and Natural Resource Operations 2014) and 7,000 wolves (P. Frame, personal communication, June 14, 2018), respectively. Wolves in Washington, from both NRM and non-NRM portions of the state have dispersed into Canada (WDFW 2018).

The two large, growing or stable meta-populations discussed above (the Great Lakes area and the western U.S.) are distributed in two disperse areas of the lower 48 states, with the core of one occurring in the Great Lakes states of Minnesota, Wisconsin, and Michigan, and the core of the other in the western states of Idaho, Montana, and Wyoming (and includes wolves in the Pacific Northwest states of Washington, Oregon, and California).

Although there is some debate about the degree of genetic difference between the wolves that occupy the West versus the Great Lakes area, it is generally agreed that wolves in those two areas, at minimum, represent different ecotypes (see *Taxonomy* above). Wolves in the Great Lakes area are generally morphologically smaller, they occupy habitat dominated by mixed deciduous-coniferous forests with relatively little elevation change, and their primary prey is white-tailed deer; whereas wolves in the western United States occupy montane forests and prey on larger ungulates like elk, moose, and bison. Having robust populations of these different ecotypes improves the species' ability to adapt to changing environmental conditions over time.

In addition to the populations of gray wolves in the Great Lakes area and the western U.S., the Mexican wolf inhabits the Southwest U.S. (Arizona and New Mexico) and Mexico. The population in Arizona and New Mexico is small, but growing and there is an establishing population in Mexico.

Appendix 1

Minimum winter wolf populations in Minnesota, Wisconsin, and Michigan (excluding Isle Royale) from 1976 through winter 2017-2018. (Note that there are several years between the first three estimates.)

Year	**Number of Wolves**		
	Minnesota	**Wisconsin**	**Michigan**
1976	1,000–1,200		
1978–79	1,235		
1988–89	1,500–1,750	31	3
1989–90	(no survey)	34	10
1990–91	(no survey)	39	17
1991–92	(no survey)	45	21
1992–93	(no survey)	40	30
1993–94	(no survey)	54	57
1994–95	(no survey)	83	80
1995–96	(no survey)	99	116
1996–97	(no survey)	148	113
1997–98	2,445	178	139
1998–99	(no survey)	204	169
1999–2000	(no survey)	248	216
2000–01	(no survey)	257	249
2001–02	(no survey)	327	278
2002–03	(no survey)	335	321
2003–04	3,020	373	360
2004–05	(no survey)	435	405
2005–06	(no survey)	467	434
2006–07	(no survey)	546	509
2007–08	2,921	549	520
2008–09	(no survey)	637	577
2009–10	(no survey)	704	557
2010–11	(no survey)	782	687
2011–12	(no survey)	815	(no survey)
2012–13	2,211	809	658
2013–14	2,423	660	636
2014–15	2,221	746	(no survey)
2015–16	2,278	866	618
2016-17	2,858	925	(no survey)
2017-18		905	662

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