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Perspective

Where can wolves live and how can we live with them?



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ABSTRACT

In the contiguous 48 United States, southern Canada, and in Europe, wolves (*Canis lupus*) have greatly increased and expanded their range during the past few decades. They are prolific, disperse long distances, readily recolonize new areas where humans allow them, and are difficult to control when populations become established. Because wolves originally lived nearly everywhere throughout North America and Eurasia, and food in the form of wild and domestic prey is abundant there, many conservation-minded people favor wolves inhabiting even more areas. On the other hand, wolves conflict in several ways with rural residents who prefer fewer wolves. This article discusses the recovery of wolves, their benefits and values, the ways in which they conflict with humans, and the potential for their expansion into new areas. It concludes that wolf conservation will best be accomplished by each responsible political entity adaptively prescribing different management strategies for different zones within its purview. Some zones for some periods can support total protection, whereas in others, wolf numbers will have to be reduced to various degrees or removed.

1. Introduction: wolves are showing up in many new places

On August 26, 2015, Illinois passed a law protecting gray wolves (*Canis lupus*) in that state. Wolves in Illinois? Although no wolf pack resides there yet, several wolves dispersing from Minnesota, Wisconsin, or Michigan have made it there before reaching their demise, so Illinois is preparing for when wolves start breeding there.

Besides spreading from the U. S. upper Midwest, wolves have been rapidly expanding their range in the West. Natural dispersers from Canada recolonized northwestern Montana in the 1980s (Ream et al., 1991). Wolves reintroduced into Wyoming and Idaho (Bangs and Fritts, 1996) mixed with them, and the population proliferated into Oregon and Washington, and from Oregon to California (Jimenez et al., 2017) (Fig. 1). Another reintroduction has been underway in Arizona and New Mexico (Harding et al., 2016). Wolves were once the most widely distributed, non-human, land mammal worldwide (Young and Goldman, 1944) living everywhere from Mexico City to northernmost Canada, and southern India to northern Greenland and Russia. Even today they inhabit most of Canada and Eurasia, including India and the Mideast (Boitani, 2003.)

Wolves are highly prolific. Annual litter sizes average six (Mech, 1970), winter densities sometimes reach 182/1000 km² (Fuller et al., 2003; McRoberts and Mech, 2014), and established populations increase at mean rates of up to 20% per year (Fuller et al., 2003). In northern Michigan, for example, the population increased from 30 in 1993 to 434 in 2016 (Beyer et al., 2009). Maturing 1–4-year-old wolves

of both sexes often disperse hundreds of kilometers (Mech and Boitani, 2003). A wolf from the upper Midwest turned up at least 870 km away, in Kentucky, (McSpadden, 2013); a wolf in southeastern Norway dispersed to northeastern Finland 1092 km away (Wabakken et al., 2007).

Although once exterminated from all of the contiguous U.S. except Minnesota and Isle Royale National Park, Michigan, primarily by government poisoning (Young and Goldman, 1944), wolves from the current lower U. S. reservoir of 6000 could reach just about any state. Similarly, although wolves were eradicated long ago from much of western and northern Europe, they have recently been recolonizing parts of France, Germany, Switzerland, Denmark, and Scandinavia (Fig. 1B) from large populations in Spain, Italy, Russia, and eastern Europe (Chapron et al., 2014). In Canada, wolves have been returning to southern and eastern areas from their vast northern reservoir. Because wolves thrive on various species of deer and other ungulates as well as livestock, which inhabit every U.S. state and most countries, there is plenty of food for wolves throughout their former range.

2. Legal status of wolves in the United States

Thus the question arises as to why wolves cannot again live almost everywhere in their original range (Durkin, 2014). This article describes the current biological and legal status of gray wolves in the contiguous 48 United States and Europe, and their increasing conflict with humans and explores the question of where and how they can live sustainably.

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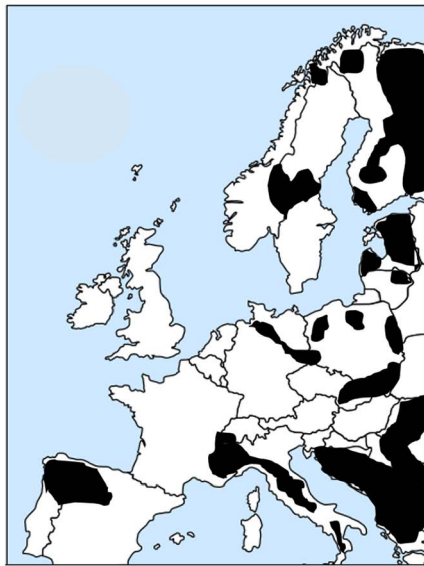
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A



B

Fig. 1. A. Current distribution of the gray wolf (*Canis lupus*) in the contiguous United States. Original distribution was the entire area except possibly the Southeast, where the red wolf (*Canis rufus*) lived. B. Current distribution of the gray wolf (*Canis lupus*) in western and central Europe. Original distribution was the entire area.

Currently U.S. wolves are protected by the federal Endangered Species Act throughout the 48 contiguous states except for a few western states where Congress delisted them: Montana, Idaho, northern Utah (where no breeding population is known to exist), eastern Oregon and eastern Washington (Mech, 2013). In the latter two states and California they are also protected by state law and are increasing. Even in Montana and Idaho, where regulated annual harvesting has occurred since 2011, the populations have held their own or increased (USFWS et al., 2016). Although the U.S. Fish and Wildlife Service (USFWS) has removed (delisted) the wolf in the West and in the Upper Midwest several times from the Endangered Species List, courts have relisted them each time based on legal technicalities (Mech, 2013). The latest ruling, on December 19, 2014, held that the USFWS cannot separately delist individual wolf populations such as the 3700 wolves in the Upper Midwest but must base its delisting on the entire gray wolf population in the 48 contiguous states. At this writing, an appeal of that decision is underway by the USFWS.

Even if the gray wolf is delisted in part or all of its current U.S. range, the population will almost certainly continue to increase and recolonize new areas. When delisted, wolves would be managed by individual states. States usually try to balance the need to maintain viable wolf populations with the needs and desires of their human

populations, which vary from folks who want no wolves to those who believe wolves should be totally protected. Most state wildlife-management agencies try to cater to wolf advocates through closed hunting and trapping seasons for much of the year and to people favoring fewer wolves by allowing regulated taking for livestock-depredation control and to try to limit conflict. The USFWS closely monitors each state's wolf management and population trajectory to make sure the population is not threatened with falling below recovery levels. If such a situation should arise, the USFWS can immediately relist the wolf. After at least 5 years of post-delisting monitoring, the USFWS can still relist whenever conditions warrant, although that requires a lengthier process.

However, the USFWS would likely never have to relist the wolf. Wolves have been off the federal Endangered Species List during some years in Minnesota, Wisconsin, and Michigan (2007–2008, part of 2009, and 2012–2014), Montana, Idaho and eastern Oregon and eastern Washington (2009, and 2011 to the present) and managed by those states. The populations, nevertheless, have maintained themselves or increased. Dispersers from these populations continue to show up in other states (Treves et al., 2009; Jimenez et al., 2017).

The states where wolves were delisted did allow livestock-depredation control, and most allowed regulated public wolf harvesting. Some states tried to reduce their wolf populations through public take. However, most took fewer wolves than the annual increment from reproduction, so some even liberalized their regulations. Still, as anticipated (Mech, 1998, 2010), the states found it very difficult to reduce their wolf populations. Montana's population of at least 497 wolves in 2008, for example, included at least 536 in 2015 after 8 years of increasingly liberal harvesting regulations and a public take of more than 750 wolves plus more than 590 killed for depredation control (Table 1).

3. Wolf population control

A common belief among the public is that wolves control their own numbers by social factors such as territoriality. That view was held by most scientists (Pimlott, 1967; Mech, 1970) until evidence mounted that wolf numbers were determined by food supply (Packard and Mech, 1980; Keith, 1983; Fuller, 1989; Fuller et al., 2003; Hatton et al., 2015). The social-factor hypothesis was raised again as a possible wolf-population-control factor in systems with unusually high prey densities (Cariappa et al., 2011; Cubaynes et al., 2014), but that hypothesis was challenged (McRoberts and Mech, 2014). Even with the highest prey density studied in any wolf-prey system, wolf density was still predicted by prey density (Mech and Barber-Meyer, 2015).

The only other way most wolf populations have been limited is by human control. Occasionally in the Arctic, rabies limits wolves temporarily (Weiler et al., 1995; Ballard and Krausman, 1997), and when canine parvovirus first appeared, it limited wolf numbers for a few

Table 1
Wolf population and public harvest information for Montana (U.S. Fish and Wildlife Service et al., 2016).

Year	Minimum Population	Next year harvest	
		Quota	Killed ^a
2008	497	75	72
2009	524	^b	^b
2010	566	220	211
2011	653	No quota	225
2012	625	No quota	230
2013	627	No quota	206
2014	554	No quota	^c
2015	536	No quota	205

^a Plus 590 killed for depredation control, 2009–2014.

^b Wolves were restored to the federal Endangered Species List for this year.

^c 94 in 2013–2014 season and 119 in the 2014–2015 season.

years (Kreeger, 2003). When a wolf population is low in numbers or distribution, human limitations by hunting, trapping, poaching, or livestock-depredation control can be effective. However, once a wolf population becomes well established and widely distributed, such techniques have limited impact.

Historically most wolf populations that were reduced or eliminated in North America and Eurasia were controlled mainly by systematic and intensive poisoning by government agencies (Young and Goldman, 1944). Poison is still used in at least one area of Canada to control wolf numbers (Hervieux et al., 2014; Parr and Genovali, 2015) and is also legal in parts of Europe (Guitart et al., 2010) and used illegally to kill wolves elsewhere there (Berglund, 2016). However, in the U.S. most types of poisoning are illegal. Thus there is no impediment there to wolf recolonization now that reservoirs of wolves are established from which dispersers can colonize new areas. The rapid recolonization of the Upper Midwest, the northern Rocky Mountains and northwestern U.S. are cases in point.

The reason wolves were originally exterminated from most of the 48 contiguous states, parts of southern Canada, and several European countries was primarily because of their depredations on livestock, although fear of wolf predation on humans, both by rabid and non-rabid wolves, also fostered general public intolerance. To a growing extent, the same factors are causing public intolerance today, along with concern by hunters and guides who consider wolves competitors for big game animals. As wolf numbers and distribution increase, so do livestock depredations (Mech, 1998; Bradley et al., 2015; Olson et al., 2015a). Although fewer than 300 wolves inhabit Oregon and Washington, local public intolerance is high. The Washington Department of Fish and Wildlife recently spent \$119,500 to kill seven wolves (Jenkins, 2016a), and Washington has paid up to \$8000 per day for a counselor to mediate a Wolf Advisory Group with opposing views on how wolves should be managed (Jenkins, 2016b). The first pack of wolves in almost a century recently recolonized California from Oregon, and within a few months began depredating on livestock (Ortiz, 2015).

4. Wolf conflicts with humans

Attacks on humans by healthy, non-rabid wolves, despite earlier contrary claims when wolf populations were low (Mech, 1970), have been increasingly documented (Shahi, 1983; Linnell et al., 2002; McNay, 2002a, 2002b; Butler et al., 2011; Behdarvand and Kaboli, 2015), although they are nowhere near as prevalent as some thought they would be (Geist, 2008). Still, wolves have chased bicyclists and motorcyclists (Associated Press, 2009a; Hopper, 2013), and in several areas, people have fed wolves, habituating them (Heilhecker et al., 2007) and ultimately promoting attacks (McNay, 2002a, 2002b). Even close encounters foster the widespread and exaggerated perception (Linnell et al., 2003) that wolves are far more dangerous to humans than they are (Bjerke et al., 2001; Roskaft et al., 2007). Such issues feed public intolerance by folks living in or near wolf range. Thus, it can be expected that as wolf populations and distributions expand, so too will human conflicts and intolerances (Ruid et al., 2009; Olson et al., 2015a, 2015b).

Some reports imply that wolves could live in currently wolf-free areas because people there are more tolerant (Bruskotter et al., 2014). However, this view overlooks the logic and findings that human attitudes change when confronted with wolves (Olson et al., 2015b) and that the closer humans live to wolves, the less tolerant they are (Williams et al., 2002; Karlsson and Sjöstrom, 2007). It also ignores the fact that in some areas with only lone dispersers, human intolerance is so great that it has prevented or retarded wolf recolonization.

Examples of areas in the U.S. with sufficient prey and a nearby reservoir of wolves that have not yet been colonized are (1) southern, central, and extreme western MN and eastern North and South Dakota and (2) Utah, Colorado, eastern Wyoming and eastern Montana. Minnesota has recently hosted some 2000–3600 wolves (Erb

et al., 2016), but central and extreme western Minnesota support high densities of livestock, and government depredation controllers have been taking large numbers of wolves, including pregnant breeding females or those with new pups on the edges of this area for years (Harper et al., 2005, 2008, J. Hart, pers. comm.). Wolf distribution has been expanding there but slowly (cf. Fuller et al., 1992; Erb and Sampson, 2013). When wolf density is low, as it would be along the leading edge of this area, then such depredation control along with accidental or illegal wolf killing help check populations. Such types of mortality are common in non-forested areas adjacent to wolf populations (Licht and Fritts, 1994; Smith et al., 2010).

A second example is the Utah and Colorado area south of eastern Wyoming and eastern Montana, east of the current northern Rocky Mountain wolf population of at least 1900 wolves (USFWS et al., 2016). Wolves have dispersed into those areas but have been killed illegally or accidentally (Reuters, 2015), supporting Smith et al. (2010) but counter to Bruskotter et al. (2014:403) that “illegal killing has not generally prevented range expansion.” Even Carroll et al. (2003) who found parts of Colorado suitable for wolves, warned that depredation on livestock (a common motive for both agency and illegal wolf killing) could hinder dispersal to Colorado.

This is especially a problem for wolves in prairies and other open areas. Such areas are hazardous to wolves for two reasons: (1) livestock are usually raised there, so wolves prey on them and are subject to depredation control and (2) the lack of cover makes wolves more vulnerable to humans. It is all too easy for violators to kill wolves with impunity because of the remoteness of wolf-occupied areas and because people who poison or shoot wolves do not even need to approach the animal. Thus little evidence is left for the very limited number of conservation agents in most areas. A prime example is the Mexican wolf recovery program in which poaching greatly attenuated the population for several years (Harding et al., 2016).

In Scandinavia, more than two-thirds of wolf poaching went undetected, and this illegal kill was estimated to have limited this population to only one quarter of what it would have been without poaching (Liberg et al., 2012). Similarly, poachers in Finland (Pohja-Mykra, 2016) are thought to have reduced the wolf population from 250 to 300 in 2007 to 120–135 by 2015 (The Guardian, 2016). In Italy, estimates are that 15–20% of wolves are killed illegally or accidentally (Ciucci, 2015), and in Germany most of the known wolf mortality was caused by poaching and vehicle strikes (Von Rushkowsky, 2016).

5. Wolf recolonization issues

When a wolf population numbers in the thousands, however, such as in the Upper Midwest or the western U.S., that population can sustain high levels of poaching and other human-caused mortality. Even the Mexican wolf population, once it reached more than a minimum of 60 wolves, was able to begin increasing almost every year (Fig. 2), demonstrating that once a wolf population becomes large enough, it can outgrow mortality factors that retard a lower population. This finding has relevance to recent efforts to reintroduce wolves into Mexico (Lopez Gonzalez and Lara Diaz, 2016).

The net result of 4 decades of wolf protection, the wolf's high reproductive potential and long dispersal ability, the rural public's general intolerance, and the ease with which small populations can be stymied by anthropogenic mortality is that wolves in the 48 contiguous U.S. have only been able to recolonize certain types of areas. These areas include primarily forested land where for most of the year (spring, summer, and fall) and most of the daylight hours, they can find refuge.

If an area with some cover supports a high prey density, then wolves can at least settle and raise pups in as small an area as 20 km² (Mech and Tracy, 2004). Although wolves prefer to den in areas remote from human activities (Sazatornil et al., 2016) they will raise pups unusually close to humans (Fritts et al., 2003; Heilhecker et al., 2007). Eventually, however, if pets or livestock are nearby, those wolves or dispersers from

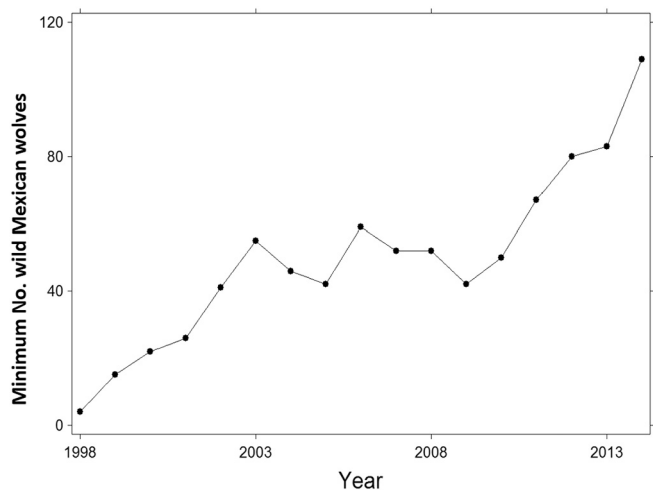


Fig. 2. Trajectory of Mexican wolf population reintroduced into Arizona and New Mexico. <http://www.fws.gov/southwest/es/mexicanwolf/MWPS.cfm> accessed Feb. 26, 2016.

their packs will conflict with humans, and many will be killed, legally or illegally.

The wolf situation in Europe provides an excellent example, with that continent hosting a wide variety of wild lands, although limited in size. Wolf recolonization of several European countries is currently underway as a result of the combination of decreased rural human density, restoration of wild prey, greater environmental awareness, and protective legislation (Boitani, 2003; Chapron et al., 2014). In fact, Europe, although half the size of the 48 contiguous United States and with twice the average human density, now hosts twice as many wolves, and European biologists have cited this fact to support the idea that wolves and high human densities can coexist (Chapron et al., 2014). The strong implication is that these two species can coexist compatibly.

Several qualifications are necessary, however, to properly understand the European situation and how that relates to wolf recolonization of the 48 contiguous United States (Mech, 2016). First, the high human densities in Europe are mostly in cities, so any wolf conflict is borne by the sparse populations in the countryside. Most European wolves inhabit Spain, Italy and such countries as Greece, Romania, Bulgaria, whereas wolves have only recently begun to recolonize the wealthier nations such as Germany (Fechter and Storch, 2014). Thus the average European human density as cited by Chapron et al. (2014) is not a suitable metric by which to gauge wolf compatibility with humans. Second, several of the countries supporting the highest number of wolves attempt to control them by hunting (Boitani, 2003), including Sweden, which is in open violation (Castle, 2015) of the European Union's Habitat Directive (Epstein et al., 2016). Third, in every country, whether wolves are legally protected or not, there is a high rate of human taking by vehicle strikes, livestock depredation control and poaching (Boitani, 2003; Liberg et al., 2012; Ciucci, 2015; Von Rushkowsky, 2016). Even in the European Union, wolf protection is weakly enforced (Sazatornil et al., 2016).

Fourth, although wolves are compatible with most European urban residents, they conflict with interests of many rural dwellers. Because of these conflicts, wolves tend to promote rural-urban polarization and civil unrest. In France, for example, shepherds were so irate over wolf depredations that a group of about 50 shepherds kidnapped both the president of the National Park of Vanoise in the French Alps and the director, demanding that five wolves in the middle of the park be killed (Samuel, 2015). As mentioned, Sweden with about 400 wolves has established a wolf hunting season in violation of European Union Law (Castle, 2015). Switzerland recently spent \$44,000 to kill a single wolf (Swissinfo.ch, 2016).

Last, and possibly most important, the fact that wolf recolonization of the wealthiest European nations has just begun belies the ultimate conflicts that can result when more wolves continue to proliferate in numbers and distribution and occupy more areas. Boitani (2003:326) forecast this reality when he stated: “the return of the wolf to areas from which it had been absent for more than a century will undoubtedly cause serious management problems,” and Chapron et al. (2014) conceded that. Castle (2015) evinced that this prediction was accurate: “Once hunted remorselessly, the wolf is now a protected species, and its return has provoked unease across Europe, from Finland to France.”

Thus Europe is currently experiencing the same type of wolf population resurgence as the U.S. and southern Canada along with the same public relations and management issues, greatly qualifying the conclusion that “The European situation reveals that large carnivores and people can share the same landscape” (Chapron et al., 2014:1517). From a cultural viewpoint, Europe is responding more diversely, given the diverse cultures as indicated above. Nevertheless, among some of the public, sentiment is strong for wolf protection and range expansion in Europe, as it also is in the U.S., with lawsuits by animal-protection groups attempting to maintain or strengthen legal wolf protection.

6. Where will humans tolerate wolves?

If wolves are increasingly protected, only illegal and accidental mortality by humans, then, will limit their number and range expansion. Wolves might then inhabit suburbs, where, at least in the U.S., white-tailed deer (*Odocoileus virginianus*) often abound. From suburbs, dispersing wolves could then end up in cities. Although wolves in cities might seem absurd, thousands of the wolf's smaller cousin, the coyote (*Canis latrans*), as well as coyote x wolf hybrids already inhabit many U.S. and Canadian cities (Way, 2007; Monzon et al., 2014; Burke, 2012; Fig. 3). Although generally coyotes are of little threat to humans, there are over 150 records of them attacking people (Carbyn, 1989; Timm et al., 2004; White and Gehrt, 2009; Associated Press, 2009b).

Fear and dislike of wolves, however, is much greater (Kellert, 1985), and it is increasing in rural areas (Treves et al., 2013). As with coyotes, wolves generally are afraid of humans. Canada, for example, which has long hosted 50,000–60,000 wolves (Boitani, 2003), has reported only a single wolf-killed human in the last 50 years (McNay, 2002a, 2002b; Linnell et al., 2002; Mowry, 2007). However, there are enough records of wolves attacking and killing humans in several areas of the world to maintain the general public's fear of wolves. Wolves also regularly attack domestic dogs which greatly angers people (Kojola and Kuittinen, 2002; Ruid et al., 2009; Edge et al., 2011).

Both because of public fear of wolves and because of wolf depredations on dogs, there is a reason to believe that the public would show little tolerance of wolves in suburban or urban areas (Bruskotter and Wilson, 2014) contrary to its acceptance of coyotes. The fact that wolves usually travel in packs during most of the year and kill large animals, leaving scattered bones, blood, and hide, no doubt would also intimidate urbanites.

Nevertheless, as wolf populations increase and expand their ranges, they are moving closer to suburbs and cities every year. As wolves encounter more people, some wolves become habituated to them and cause public concern (Heilhecker et al., 2007). Wolves now live within a few km of Rome (Conniff, 2015) and have walked through the city streets in Romania (BBC, 2008), although with no reported conflicts yet. In 2016, wolves attacked a mare and her foal in Katzrin, Israel, the capital of the Golan Heights (Poch, 2016), and earlier rabid wolves attacked children in Katzrin (The Times of Israel, 2015). Similarly, in North America, wolves are becoming more habituated to humans. A pack of five recently killed a deer in the middle of Banff, Alberta, Canada (population 9300) and dragged it down Cougar Street (Derworiz, 2015). In Wisconsin, a pack regularly headquartered along and on a state highway, and a wolf jumped into the back of a truck that



Fig. 3. Coyote on roof in New York City, USA, thought to have come from exploring nearby buildings as part of a larger urban coyote population (Bittel 2015).

had stopped to watch them (Heilhecker et al., 2007). In 2012, authorities had to kill eight wolves in Ironwood, Michigan (population 5000) (Kovarik, 2012). A few Wisconsin wolves also had to be destroyed because of their regular proximity to people (Olson et al., 2015a).

Thus, if wolves continue to increase, they could live almost anywhere. The real question society must face is where will people tolerate them? Will many folks want to live in fear, valid or not, while out for walks at night? How many will be willing to risk their dogs and cats being killed? Their livestock? Will many folks tolerate large numbers of wolves killed legally and/or illegally around their suburbs and cities? A Wisconsin attitude survey in spring 2014 showed that only 8% of state residents outside of wolf range wanted wolves living in rural areas adjacent to suburban developments despite most of these people generally being very favorable toward wolves (Holsman et al., 2014).

7. The challenges of wolf conservation

To many citizens, experiencing wildlife provides considerable pleasure (Mech, 1996). On the other hand, wildlife also conflicts with humans to varying degrees. Thus State and Federal agencies strive to manage wildlife such as to balance the costs and benefits of each species and to cater to constituencies that may have opposite opinions about how wildlife should be managed (Clark and Rutherford, 2014). Two disparate types of U.S. wildlife might illustrate the issue with wolves. On the one hand giant Canada geese (*Branta canadensis*) have rebounded in many areas and are common in some cities. Their feces, however, mar trails, lawns, and sidewalks. Thus in some areas, authorities break their eggs or oil them, along with promoting liberal harvest in nearby areas to help counter their numbers. Such management helps the public tolerate geese.

On the other hand, bison (*Bison bison*), which once teemed in much of the Midwestern U.S., are not allowed to roam through the wheat and cornfields of their former range. They are kept in parks and fenced pastures, which the public generally accepts.

Wolves are more like bison in that respect: they can inhabit parks and wild areas with little conflict with humans. However, when they live outside wild lands, conflicts with humans greatly increase. Like Canada geese, wolves can be managed. However, unlike geese, they are not easy to control once a population is well established, as discussed above. That is why poison was used to control and eradicate wolves in the late 1800s and early 1900s (Young and Goldman, 1944), why at least one Canadian province still resorts to it (Hervieux et al., 2014; Parr and Genovali, 2015) and why it is used illegally in both Europe (Berglund, 2016) and the U.S. (Tsai, 2011).

If the only place wolves can live with minimal conflict with humans is in wild lands, where are there sufficient wild lands that are still wolf-free? Wild lands can be considered any extensive area undeveloped and relatively uninhabited by humans. There is necessarily some variation and subjectivity in considering where such areas suitable for wolves exist because the region surrounding many suitable wild lands would sustain conflict from wolves dispersing from them. The degree of conflict and the tolerance of local citizens will vary by locale. In Europe, that will depend considerably on the culture of each individual nation. How many of the 10,000 wolves Germany might be capable of supporting (Fechter and Storch, 2014) will it tolerate? In the U.S., estimates are that part of the southern Rocky Mountains could sustain a population of more than 1000 wolves (Carroll et al., 2003). In the Central U.S., a habitat-suitability study suggested that about 42% of the region (primarily Texas north through North Dakota) was suitable for wolves (Smith et al., 2015). However, those studies did not explicitly consider such negative factors as potential for depredation on livestock and other conflicts with humans, as well as local public attitudes toward wolves. The importance of these factors can be seen in the latter study's conclusion that substantial parts of North and South Dakota were deemed suitable even though wolves have been unable to recolonize them from Minnesota for decades because of poaching (Licht and Fritts, 1994).

8. Potential new U.S. wolf range

Nevertheless, both the Carroll et al. (2003) and the Smith et al. (2015) assessments suggest regions that could be examined for livestock-free areas and areas of positive, or least-negative, public attitudes toward wolves. Individual states, then, could decide whether to reintroduce wolf populations there. Prime states for that approach would be parts of Colorado, Utah, Nevada, South Dakota, and Nebraska. Conceivably improvements in two relevant issues would allow wolves to inhabit more areas: (1) objective education about wolves, although a recent analysis is discouraging (Houston et al., 2010), and (2) non-lethal means of reducing wolf depredations on livestock, again an

improvement not yet reached despite many millions of dollars spent trying.

The animosity toward wolves, especially by rural folks who have to live with them, that originally caused the extirpation of the species from large areas has not abated (Williams et al., 2002; Kaczensky et al., 2013). Even though positive attitudes toward wolves generally predominates, primarily by urbanites (Williams et al., 2002; George et al., 2016), the animosity is personal and strong enough that it can often

prevail. In some cases, that strength is reflected in unusual legal maneuverings, such as Sweden's and Finland's attempts at bypassing the European Union's directive referred to earlier and the U.S. Congress' legislative removal of the wolf in Montana and Idaho bypassing the Endangered Species Act (Mech, 2013). When such maneuvers aren't possible or aren't used, the minority anti-wolf residents resort to poaching. Finland recently authorized a hunt to take about 20% of its wolf population to reduce illegal killing (The Guardian, 2016), although whether this will work is not clear (cf. Treves et al., 2013; Hogberg et al., 2015; Olson et al., 2015b; Pohja-Mykra, 2016).

In Europe, such a large proportion of rural people have vacated the countryside that, in many areas, wolf poaching has not been able to stem the expansion of wolf range (Chapron et al., 2014). In others, such as Austria, poaching appears to have retarded recolonization (Kaczensky et al., 2013).

9. Wolf recovery in Europe and the U.S.

Although Europe and the U.S. share many of the issues surrounding re-establishment of wolves, one critical aspect of wolf recovery differs between the two areas. Whereas Europe contains almost no extensive block of wild lands where wolves can live with minimal conflict with humans (Chapron et al., 2014), the contiguous U.S. possesses many such regions. Thus the type of wolf recovery and conservation the U.S. Fish and Wildlife Service has settled on to implement the Endangered Species Act is the separation model (Packer et al., 2013), whereas Europe has been forced to rely on the coexistence model.

Now that wolves have recovered in the U.S. Midwest and been reintroduced to the West and Southwest and the red wolf (*Canis rufus*) in the Southeast under the Endangered Species Act, the current U.S. wolf population that inhabits primarily wild lands has been demonstrating a practical way of determining which areas are suitable for long-term viability. As indicated earlier, in the upper Midwest during several decades of legal protection Minnesota wolves have proliferated into adjacent Wisconsin and Michigan but not adjacent North Dakota, South Dakota, or Iowa. In the northern Rockies over 20 years they have proliferated from Montana, Idaho, and Wyoming into neighboring Washington, Oregon, and California but not into adjacent Colorado or Utah. Even within each of the above states wolves have been unable to recolonize some areas where there are sufficient prey but where conflict is too great. In other words, the natural progression of the wolf-human relationship itself has determined where wolves can live and where they cannot. This same process is playing out in Europe, and in the long run, that is what almost certainly will determine where wolves will live.

In the U.S. outside of national parks and other extensive wild lands, if wolves are to survive, that will require considerable attitude adjustment by humans toward them. Recently, some have proposed that in many non-wilderness areas large carnivores and humans can coexist through humans adapting to the carnivores (Carter and Linnell, 2016; Chapron and Lopez-Bao, 2016). However, even assuming that human attitudes will change (George et al., 2016, but see Houston et al., 2010; Holsman et al., 2014), and better techniques to reduce conflict are developed, this proposition overlooks the high reproductive potential of wolves. Increased tolerance will merely allow populations to increase and proliferate to many new areas until they do conflict and cause agencies to control them (Mech, 1996). Even such control can bring further public animosity (Linnell et al., 2011). Thus wolf management in human-dominated areas would have to be highly prescriptive to each local area to sustainably minimize both wolf conflict with humans and conflict by humans with each other.

10. Wolf conservation: adaptive management and zoning

The precise nature of wolf-human interactions will vary considerably throughout actual and potential wolf range, and over time (Linnell and Boitani, 2012). One of the most useful ways of promoting wolf

conservation is via the preservation of wild lands, where wolves will conflict least with humans. In addition, wolf conservation and management approaches will vary according to local situations. These approaches will include total protection in national parks, nature reserves, and other wild lands where conflict with humans is minimal, elimination where conflict is too great, and every type of management in between, especially in human-dominated landscapes. This means that ultimately different management agencies will have to prescribe different types of wolf conservation for each area. Large political entities such as states in the U.S. or large countries like Germany, might need several types of management in different zones.

Zoning has been used in wildlife conservation for many decades, and the first wolf management plan, The Eastern Timber Wolf Recovery Plan (USFWS, 1978), featured it. Currently the only three states in the U.S. where public wolf taking is legal (Alaska, Idaho, and Montana) all employ zoning to prescribe various open seasons and take quotas. Zoning has also been recommended for wolf conservation in Europe (Linnell et al., 2005). The U.S. hosts enough wild land and semi-wild land that wolves can be totally protected in some zones without conflicting with humans. Such land also provides corridors over which wolves can disperse more successfully to recolonize new areas.

However, Europe lacks such areas (Chapron et al., 2014), so, there, some emphasis will have to be put on zones in which protection of undeveloped areas is maintained in order to facilitate more successful wolf dispersal (Boitani et al., 2007). The dynamic and variable nature of wolf-human conflicts and the wide spectrum of human attitudes toward wolves will continue to make wolf-conservation zoning necessary in both Europe and the U.S. In the U.S., such prescriptive management must await wolf delisting from the Endangered Species List, and in the European Union, it must await modification of the Bern Convention and the European Habitat Directive, all of which were promulgated to recover wolf populations.

11. Benefits of wolves

Many people in both the U.S. and Europe revere wolves (Mech, 1996; Fritts et al., 2003), and that is the main value of wolves to society. Wolves also tend to reduce the number of their prey (Mech and Peterson 2003, Ripple and Beschta, 2012), which can lower such conflicts with humans as vehicle collisions and crop damage. Fewer prey can then bring cascading effects via decreasing plant herbivory (Estes et al., 2011). However, despite the exaggerated claims of a YouTube video (accessed 10 April 2017).

https://www.youtube.com/results?search_query=wolves+change+rivers, viewed more than 35 million times, the degree, extent, and importance of such wolf-caused trophic cascades have been challenged (Mech, 2012; Allen et al., 2017) and are unclear (Peterson et al., 2014; Smith et al., 2016).

Still, the aesthetic and cultural value of wolves is substantial and greatly helps compensate for the animal's conflicts with humans. Although the conflict between wolves and humans and the controversy around wolves will continue, government policies in the U.S. and the European Union currently allow the animals to recolonize as many areas as possible. Biologically, wolves can and will live almost any place where people will tolerate them, and that will vary with the local culture and politics, as will conservation policies when wolf numbers and distribution become too problematic. As Linnell et al. (2005:175) wrote over a decade ago, "There are no magic formulas or perfect solutions in large carnivore conservation, just a lot of more or less acceptable, and often controversial compromises."

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