



**HUMANE SOCIETY
INTERNATIONAL**

European Grey Wolf

(Canis lupus)



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IMPACTS OF TROPHY HUNTING

- Unsustainable offtake
- Social disruption
- Increases human-wolf conflict
- Ineffective at preventing livestock loss

POPULATION

The grey wolf (*Canis lupus*) is found in Europe, Asia, and North America. The broader European population is estimated to exceed 17,000 wolves and increasing as of 2018.¹ The European Union (EU) population is estimated at fewer than 13,000-14,000 wolves across all EU Member States as of 2018.¹

The grey wolf is considered Least Concern at global, European, and EU levels.¹ Within Europe, there are nine populations, each with its own IUCN status (see Table 1 below). There was a tenth population, Sierra Morena in Spain, which has been extirpated. In addition, the wolf population on the Italian pen-

QUICK FACTS:

Population Size:	Europe: 17,000; EU: 13,000-14,000 (2018)
Population Trend:	Europe: Increasing; EU: Unknown (2018)
Range:	Unknown
IUCN Red List:	Least Concern in Europe and EU (2018)
CITES:	Appendix II (since 2010)
International Trade:	73 trophies exported from the EU from 2009-2018 (69 originated in EU)
Threats:	Human intolerance, poorly regulated hunting, poaching, poor species management

insula is a distinct subspecies (*Canis lupus italicus*). The Iberian wolf (*Canis lupus signatus*) may also be a distinct subspecies.¹

Table 1. European population summary (IUCN).^{1,2}

Population	Countries	Population size (mature individuals)	Population trend	IUCN status (2018)
Baltic	Estonia, Latvia, Lithuania, Poland	1,713-2,240	Stable	Least Concern
Carpathian	Romania, Serbia, Poland, Slovakia, Czech Republic, Hungary	3,460-3,840	Stable	Least Concern
Central European	Germany, Poland	780-1,030 (480-620)	Increasing	Vulnerable
Dinaric-Balkan	Croatia, Bosnia & Herzegovina, Slovenia, Montenegro, Macedonia, Albania, Serbia, Greece, Bulgaria	3,750-4,000	Unknown	Least Concern
Iberian	Portugal, Spain	2,160-2,880	Unknown	Near Threatened
Italian Peninsula	Italy	1,070-2,400	Slightly increasing	Near Threatened
Karelian	Finland	204-234 (200)	Stable to increasing	Near Threatened
Scandinavian	Norway, Sweden	430 (260)	Increasing	Vulnerable
Western-Central Alps	France, Switzerland, Italy, Austria, Slovenia	550-700 (330-415)	Increasing	Vulnerable

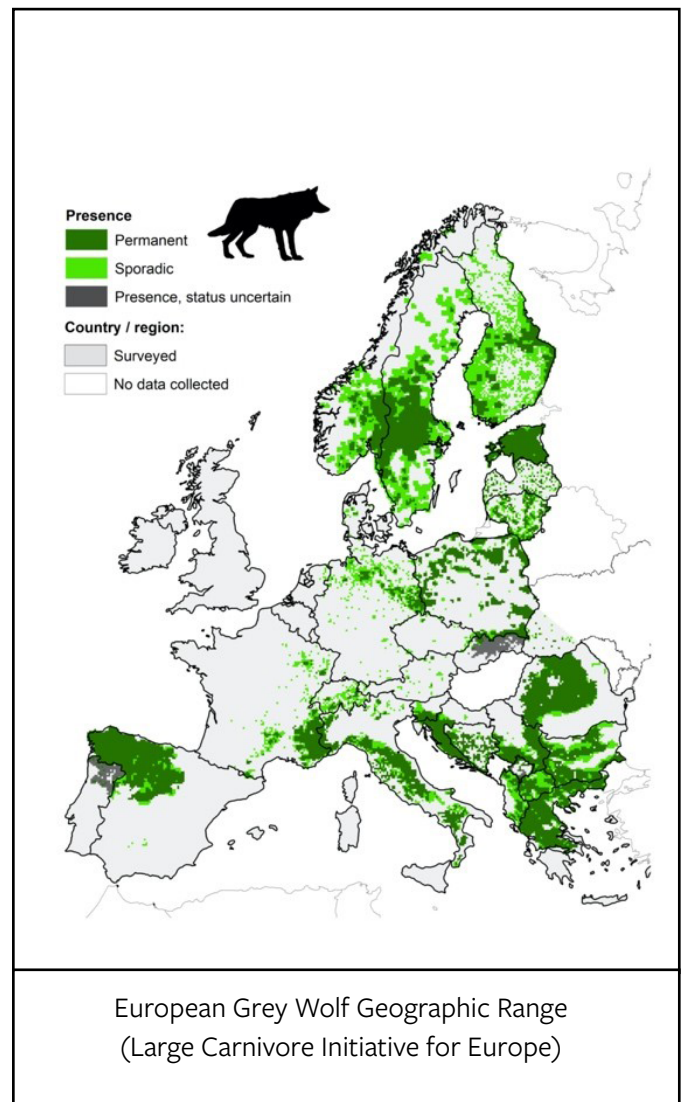
Historically wolves were present throughout most of Europe, but by the mid-20th century their range was greatly reduced.¹ Its only been in the last 50 years that their range has expanded to include nearly all continental European countries.¹

RANGE

The historical range of the grey wolf included most of the northern hemisphere, however they have since been eradicated from large portions of this range.¹ Grey wolves became extinct in much of Western Europe.³ Human persecution was the main driver in range loss for grey wolves.³ Habitat deterioration is an important predictor of range loss, however, even when suitable habitat is available, wolves are constricted by human threats such as high hunting intensity.⁴ In addition, roads through dense forest allowed hunters to easily detect and access wolves.⁴

Range-wide persecution and population declines resulted in fragmented populations and local extinctions across Europe. Despite recovery in many parts of Europe, the loss of genetic diversity resulting from these population crashes still threatens long-term survival. Following functional extinction in the 1960s, Scandinavian wolves exhibited severe inbreeding depression which continues to threaten population viability.⁵ This severe inbreeding effect had reduced population growth in Scandinavian wolves.⁵ Despite severe inbreeding, the Swedish government continued to allow hunting, risking further loss of genetic diversity.⁶ Populations in the southwest part of Europe have lower genetic diversity than those in the northeast.⁷ The largest populations have the highest genetic diversity.⁷

Following heavy persecution and recent recovery, wolf-dog hybridization has become a problem across Europe and can have negative effects on the wolf gene pool.^{8,9} European wolf populations exhibit widespread evidence of wolf-dog hybridization across their range,^{10,9} more so than North American wolf populations.⁹ For example, some wolves in Italy, especially those on the periphery of the population range, show genetic evidence of mixed ancestry with dogs along with morphological features such as black coats or dewclaws.⁸ There is evidence that strong hunting pressure may facilitate hybridization in wolves as it can lead to population declines, decreased population density, fragmentation, social disruption, and dispersal.^{11,12,13,14} Wolf-dog hybridization in Estonia and Latvia can be explained by



hunting pressure and increased abundance of stray dogs.¹¹ In Bulgaria, scientists suggest that unregulated hunting caused high levels of inbreeding and wolf-dog hybridization which threatens long-term viability of the population.¹² A study in Canada found that intense harvest of eastern wolves (*Canis lycaon*) transformed genetic composition and facilitated hybridization with coyotes; while a ban on hunting and trapping promoted genetic recovery.¹³ Wolf populations in Europe are genetically different from dogs, but greater hybridization frequency could be detrimental.⁹ Hybridization between wolves and dogs in Europe is a problem that conservation scientists say needs to be addressed in management plans. Scientists highlight the importance of grey wolves as a keystone species in their ecosystems, and the importance of understanding the impacts of wolf-dog hybridization on their conservation.⁹ The most effective way to minimize wolf-dog hybrids is to maintain wolf populations at stable densities.¹¹ In addition, wolf hunting should be prohibited in areas with low wolf population density (including the edges of healthy populations) and where stray

dogs are present.¹¹

LIFE HISTORY AND REPRODUCTION

Wolves are seasonal breeders and give birth once per year.¹⁵ The median age at first reproduction is 3 years old for females and 2 years old for males.¹⁶ Pregnancy lasts approximately 2 months.¹⁵ Litter size is approximately 5-6 pups. Females have limited mobility before and after birth and typically stay near the den.¹⁵ Young females in a pack may assist in attending to young in the den.¹⁵ Approximately 2 months after giving birth, females resume their normal movement patterns.¹⁵ At around 4 months old, juveniles are able to join packs on hunts.¹⁷

Wolf population growth density-dependent and is limited by internal population dynamics such as interactions or territoriality.¹⁸ Therefore, wolf populations will not grow exponentially, even where prey is abundant. Human offtake, from legal hunting or culling, and poaching, can also alter reproduction and population growth. Human-caused mortality can disrupt social structure and breeding pairs,¹⁹ and can increase territorial turn-overs (see *Social Structure*) which can contribute to lower age at first reproduction.¹⁶ Hunting can also slow reproduction and population growth through lowering reproductive rates and pup survival.²⁰ For example, if a breeding wolf is lost, the likelihood of reproduction the following year is cut in half and litter sizes are generally smaller.²⁰ Hunting can also reduce pack size, which is positively correlated with pup survival and breeder replacement.²⁰ Population growth has also been slowed due to inbreeding in some populations. The Scandinavian wolf population has experienced high inbreeding due to near extinction at the end of the 1960s.⁵ High inbreeding in this population also correlated with smaller litters, a measure of population growth.⁵

SOCIAL STRUCTURE

Wolf populations are highly social and live in groups (i.e., packs) that share a territory.²¹ Wolf packs comprise of a mating pair, plus their relatives and/or offspring.²¹ Within packs, only certain individuals (typically one breeding pair) are actively breeding.²¹ Offspring will typically stay with the pack for 2-3 years to help care for young before dispersing from their natal pack. In order to successfully breed,

wolves disperse from their natal pack to find a mate and establish a territory with sufficient resources.²¹

Wolves communally hunt and care for young.¹⁵ Following loss of a member of the breeding pair, pup survival was higher in larger packs (>6 wolves).²⁰ Non-breeding adult-sized wolves (also called ‘auxiliaries’ or ‘helpers’) were the most important for pup survival following breeder loss.²⁰ Auxiliaries provide food and care for pups and will also help raise the pups after the mother has died.^{18,17} Following the loss of a breeder, larger packs are more likely than smaller ones to reproduce in the following season.²⁰ Wolf packs in small recolonizing wolf populations (\leq 75 wolves) took longer to replace the lost breeder and were slower to reproduce than larger wolf populations.²⁰

While wolf packs change naturally over time, lethal removal, such as hunting or poaching, can alter the timing and frequency of dispersal and pack dissolution. Hunting can negatively affect the socio-spatial organization of wolves and the killing of breeding individuals often leads to pack dissolution.^{14,20,22,19,23} Human-caused death is the reason for dissolution of the majority of breeding pairs (when the cause was known) and pair dissolution occurs earlier when culling is the cause.²³ Legal hunting can have complex effects on genetic compositions. For example, hunting can increase relatedness between packs.²⁴ Human-caused mortality can also limit wolf recolonization and settlement through territory disruption.²⁵

Wildlife managers focus too much on the number of wolves in the population, rather than the wide-ranging impacts that hunting will have on social organization, reproduction, behavior, and genetics.²⁶ Some important effects of hunting that are often overlooked are decreased pack size and population fragmentation, less selective mating, more breeding pairs, less stable territory use.²⁶ These impacts of hunting are complex and must be considered in order to properly manage wolves.²⁶

HABITAT AND ECOLOGY

Wolf habitat use is driven by human disturbance, prey density, and range size.¹ Wolves avoid human settlements and roads.^{27,28} The largest threat to wolf habitat is human land use.¹ Human presence has fragmented wolf populations and forced wolves

into unsuitable habitat.¹ Human structures, such as roads and railways, are also associated with wolf mortality.¹ Infrastructure has also prevented recolonization and the establishment of territories in parts of Scandinavia, despite suitable habitat.²⁵ Wolves are constrained in their habitat use due to human presence and habitat fragmentation.²⁸ This means that wolves may forego optimal habitats (e.g., those with high prey density) to avoid human-associated risks. Human population density is the strongest predictor of wolf habitat suitability across Europe.²⁹ Wolves avoid areas where humans are present and establish territories away from human populations.^{30,31} Habitat suitability is negatively correlated with human population density and positively correlated with forest cover.²⁹

Wolves are generalists and opportunistically choose prey.¹ Their diet may include moose, red deer, roe deer, wild boar, small mammals, birds, invertebrates, vegetation and carcasses.¹ A study on wolves in Southern Europe (Italy, Spain, Portugal) found that wolves prefer wild prey to livestock.³²

Wolves are important predators that shape their ecosystem through prey regulation, removal of sick and injured prey, influence on prey behavior and habitat-use, and altering habitat availability for other species.^{33,34,35,36,37} They shape their ecosystem through prey regulation, removal of sick and injured prey, influence on prey behavior and habitat-use, and altering habitat availability for other species.^{34,35} Wolves control the number of ungulates in an ecosystem which allows for greater plant biomass and diversity.³⁵ The extirpation of wolves has contributed to ecosystem degradation through over browsing by ungulates.^{34,36} Removing wolves from an ecosystem can result in a trophic cascade that affects all levels of the food web. This cascade due to loss of wolves may result in simplification of the ecosystem.³⁴ In contrast, wolves can restore habitats when recolonized. After grey wolves were reintroduced to Yellowstone National Park in the United States, the degraded ecosystem restoration began due to vegetation recovery.³⁶ Wolves can also make important economic contributions through altering the behavior of their prey. A study in the United States found that wolves reduced vehicle collisions with deer by 24% which resulted in an economic benefit that was 63 times greater than the financial loss of wolf predation on livestock.³⁷ These benefits were also concentrated in rural areas, thus benefiting those who would be experiencing conflict with wolves over

livestock.

DIRECT ANTHROPOGENIC THREATS

Human intolerance is the greatest threat to wolves in Europe.¹ Persecution is largely driven by fear, misunderstanding, and conflict with livestock, even though the percentage of sheep and cattle taken is very low.¹ In addition to intolerance, poorly regulated hunting and poaching are the top threats to wolf survival.¹ According to Large Carnivore Initiative for Europe (LCIE), human caused mortality, from poaching and hunting, is the most important factor affecting wolves.² Similarly, a 2017 study found that hunting and poaching were a threat to the nearly all European wolf populations.⁷

Solutions to human-wolf conflict include using non-lethal measures to prevent livestock predation and educating the public to increase acceptance. Better preventive practices for livestock conflict implemented in the Western-Central Alps population has led to a decrease in wolf predations.¹ According to LIFE WOLFALPS EU, common misconceptions are that wolves attack people, their populations grow exponentially, and they've been reintroduced or released from captive-breeding facilities.³⁸

Despite high rates of persecution due to perceived conflict, wolves generally avoid areas populated by humans.²⁷ Hunting may increase conflict with humans by disrupting social structures, dissolving packs, and increasing dispersal rates.³⁹ Wolves avoid areas populated by humans, especially in their natal range.³⁰ However, during dispersal, wolves are bolder and less likely to avoid human-associated areas,^{30,28} unlike wolves with established territories who avoid human settlements.⁴⁰ Therefore, disruption of pack structure and territory stability can increase human-wolf conflict.

Wolves are poached, or killed illegally, for several reasons, including fear, competition with hunters for a prey species, or in retaliation for suspected livestock loss.⁷ A public opinion study in the United States found that poaching occurred mostly out of competition for hunting deer.⁴¹ High rates of poaching, which is nearly impossible to track, means that no amount of legal hunting can be sustainable. Poaching is responsible for a large percentage of wolf deaths across Europe.^{42,43} A study in Finland found that 97% of radio-collared wolves died from

human-caused mortality, primarily poaching followed by legal hunting, from 1998 to 2016.⁴³ This study also predicted that low rates of survival in collared wolves from poaching and legal hunting would lead to extinction if representative of the entire population. In the Iberian population, poaching accounts for an estimated 50% of total mortality.¹ The Italian peninsula population is protected in theory, but poaching is common and rarely prosecuted.¹ Poaching is focused on breeding adults,⁴³ which can have severe long-term consequences on population structure and growth that are not accounted for when determining hunting quotas. Therefore, it is highly probable that hunting quotas are unsustainable if taken into consideration with other threats, such as poaching.

Some managers and hunting organizations suggest that legal hunting promotes greater tolerance of wolves, however scientists caution that this is just an assumption and not supported by empirical evidence.⁴⁴ In fact, empirical evidence shows that legal hunting and culling increase wolf poaching.^{43,44,45,46} In Finland, poaching followed by hunting were the primary causes of death for wolves from 1998 to 2016.⁴³ Hunting alone does not promote tolerance of wolves.⁴³ A study published in 2021 found no evidence that hunting promotes tolerance in Mexican grey wolves (*Canis lupus baileyi*), a subspecies of the grey wolf, in the United States that face the same threats as European grey wolves.⁴⁴ In fact, their study supports the idea that legal hunting *facilitates* poaching.⁴⁴ Wolves in this study were 121% more likely to disappear under less protections, despite similar legal removal by the government.⁴⁴ A recent study from Scandinavia suggested that “legal culling may have some dampening effect” on poaching,⁴⁷ however the methods used in this study have been criticized as inappropriate.⁴⁸ Studies in the United States found that tolerance for wolves either didn’t change^{49,50} or declined as lethal control and public hunting of wolves increased.⁴¹ In fact, the desire to poach wolves was most strongly associated with the perceived competition for deer hunting, so even hunting of other species increases the desire to poach wolves.⁴¹ Although these studies are from grey wolves in the United States (*C. lupus* and *C. lupus baileyi*), the results are generalizable to the European grey wolves (*C. lupus*) given they are the same species and face the same threats. Thus, there is ample evidence that hunting does not reduce poaching or human tolerance of wolves.

European grey wolves have a long history of being overexploited and persecuted across Europe. For example, the grey wolf became functionally extinct in Norway and Sweden by the end of the 1960s.⁵ Similarly, wolves were nearly eradicated from western Poland due to high hunting intensity between 1975 and 1997.⁴ During this time two different management strategies were used in Poland, although a similar number of wolves were killed in the eradication period as the hunting management period.⁴ Unfortunately, wolves continue to be overexploited in Europe. According to the IUCN assessment: “In some countries, poorly regulated hunting of wolves poses a threat, while in others licenses for killing wolves are issued irrespective of biological understanding.”⁷¹ Excessive lethal control and poorly regulated hunting are a major threat to the Dinaric-Balkan, Carpathian, Baltic, and Scandinavian populations, due to limited protections in some countries.¹ Evaluating current hunting pressure per country can be difficult on a large scale since hunting data are not always transparent or accessible. This is especially difficult for countries that are not party to the EU Habitats Directive and wolf hunting derogations are not required to be reported to a central database. According to the IUCN assessment, poorly regulated hunting or excessive hunting pressure are especially concerning in Hungary and Slovakia.¹ Based on the IUCN assessment and the most recent data reported for derogations under the EU Habitats Directive (2018), wolf hunting occurs in Estonia, Latvia, Lithuania, Poland, Romania, Spain, and Sweden.^{1,51} Although as of January 2021, Slovakia has announced that the wolf will be protected year-long.⁵² Countries like Romania have banned trophy hunting, but killing under derogation for ‘nuisance’ wolves still exists. A study published in 2017 found that legal hunting pressure was high (>35% of the population) in Bosnia-Herzegovina, Bulgaria, Estonia, Latvia, Macedonia, and hunting pressure was medium (10-35% of the population) in Croatia, Finland, Lithuania, Romania, Slovakia.⁷ According to the International Wolf Center, the current population in Latvia is 670 wolves, and each year about 300 wolves are killed by hunters.⁵³

Across Europe, legal hunting has been used in response to wolf-livestock conflict, however studies show lethal management does not work and non-lethal solutions should be considered instead.^{7,13,54,55,56} In addition, hunting can make management more difficult because it can cause pack dissolution and dispersal.²⁰ In contrast, stable packs are easier to

manage non-lethally because wolves maintain established territories and prevent new wolves from entering.⁵⁵ Conservation professionals believe that preventive measures for livestock depredation are the most effective strategies for mitigating conflict with large carnivores.⁵⁷

Many wolf management policies assume that human-caused mortality has a compensatory effect, meaning that mortality from humans (hunting or culling) will be compensated by decreased natural mortality.⁵⁸ Instead, human offtake has an additive or super-additive effect on wolf mortality, where it acts *in addition to* other threats.⁵⁸ Indirect effects of hunting can be especially problematic in small populations.⁵⁸ The effects of hunting may not be observed until the following year or later, especially due to the indirect effects, such as social disruption and loss of dependent offspring.⁵⁸ By ignoring indirect effects of hunting and additive mortality, wolf management plans allow offtake that is greater than what is biologically sustainable.⁵⁸ This also leads to unsustainable hunting quotas. For example, a large-scale study using genetic sampling and recovered bodies in Norway and Sweden, estimated that 59% of wolf deaths go undetected based on current methods.⁵⁹ A study on Scandinavian wolves found that management plans must consider the long-term population effects of lethal offtake. Despite seemingly moderate offtake and little short-term impacts, the long-term impacts could be catastrophic, especially in small populations. Statistical models indicated that unforeseen catastrophic events could unexpectedly drive a population to extinction.⁶⁰ If populations aren't accurately censused each year, then management decisions should be based on *minimum* population counts rather than estimated population size to prevent extinction.⁶⁰

Hunting can result in direct population declines in wolves through several pathways. Offtake of a breeding wolf (male or female) results in smaller litter sizes and wolves are half as likely to reproduce in the following season.²⁰ Offtake of auxiliary wolves (non-breeding adults) can also negatively affect pup survival given that auxiliary wolves increase pup survival.²⁰ Offtake of breeding wolves can disrupt packs and cause wolves to disperse.²⁰ Reducing pack size can have negative effects on population growth since larger packs are associated with higher pup survival and faster replacement of a lost breeder.²⁰ Hunting can also result in loss of important genetic diversity and prohibits genetic recovery in popula-

tions with inbreeding.⁶ Wolves from heavily hunted populations have higher stress hormones and reproductive steroids than wolves under less hunting pressure.²² Hunting can also fragment populations, alter mate pairings, modify territories, prevent recolonization, and increase natural mortality rates.^{25,26} Unregulated hunting in Bulgaria is believed to have caused high levels of inbreeding and hybridization which threatens long-term viability of the population.¹² Despite these negative effects, scientists warn that we still don't fully understand the harmful effects of hunting.⁷

MANAGEMENT IMPLICATIONS

The legality of wolf hunting is currently being challenged in the EU.⁶¹ As of 2021, Slovakia has announced that the wolf will be protected year-long, and Spain is considering a total ban on wolf hunting. The EU Habitats Directive requires that all alternatives are exhausted before lethal control is utilized. Yet, wolf management in Europe and the EU rely on lethal predatory control, which is not based on the best available science.⁵⁶ As detailed below, non-lethal solutions are highly effective yet under-utilized for wolf management across Europe

Lethal predator control methods, which are commonly used, have not been tested to determine effectiveness at preventing livestock predation.⁵⁶ Hunting and culling are not the only ways to manage wolves; they're not even the best way. In fact, research on lethal predator control lacks scientific rigor and should be halted until more reliable research is published on the effectiveness of lethal management.⁵⁶ A survey of international conservation professionals revealed that legal hunting of large carnivores ranked as the least effective conflict mitigation strategy.⁵⁷ Targeted removal of problem animals also ranked low in terms of efficacy.⁵⁷

Lethal management decisions are often not based in science and have unintended negative consequences. A study in Spain found that culling wolves as a management strategy was positively related to the number of news stories on wolf damages rather than economic costs of damaging, indicating that media can drive negative attitudes towards wolves and the use of lethal management.⁶² This study also found that livestock damages were positively correlated with wolf culling intensity in the previous year, indicating that culling may actually have the opposite effect in increasing conflict with livestock.⁶²

This may be due to social disruption or source-sink. Similar results have been observed in cougars where increased offtake in the previous year is correlated with increased livestock depredations.⁶³ Hunting on prey species may be a better predictor of conflict, one study found a positive correlation between ungulates hunted the previous year and wolf-livestock conflict.⁶²

There are many non-lethal solutions that are highly effective.^{55,56,64} Livestock guard dogs and visual deterrents are highly effective at preventing livestock predation from carnivores, especially wolves.⁵⁶ In fact, non-lethal solutions can actually be more effective than lethal control, even at large scales.^{55,56} Over a seven-year study in the US, sheep depredation losses to wolves were 3.5 times higher in the area with lethal management and hunting than the area that used non-lethal management.⁵⁵ A study in Slovenia found that legal wolf culling did not decrease livestock depredations from 1995 to 2009.⁵⁴ In contrast, a study in the French Alps found that non-lethal methods were very successful in preventing livestock depredations.⁶⁴ The combination of confining sheep at night and employing guard dogs prevented nearly all livestock loss.⁶⁴ Many scientists advocate for using non-lethal management strategies in place of culling or lethal control.^{7,55,56,13,62} Thirteen biologists and wolf experts have signed on to an initiative to disproving of lethal control as a wolf management tool and in strong support of non-lethal coexistence methods for European wolf populations.⁶⁵

Very few international conservation professionals believe that the goal of conservation should be to merely maintain minimum viable populations of large carnivores; instead most believe that the goal should be to re-establish populations to fulfill their ecological functions.⁵⁷ The vast majority of conservation professionals think that humans and large carnivores can share the same landscape, especially with the use of measures that prevent conflict.⁵⁷ Indeed, wolves are able to persist in human-dominated habitats, and scientists believe human-wolf coexistence can be successful with protective legislation, public support, and the use of livestock protection measures to prevent conflict.⁶⁶

Wolf management must emphasize more than just population numbers.²⁶ Management plans must also consider the implications of hunting on social structure,¹⁹ require non-lethal strategies to pre-

vent wolf-livestock conflict, include transboundary management to prevent issues associated with source-sink dynamics (e.g., Sweden and Norway⁵⁹), and incorporate better genetic monitoring.^{9,60} Another problem is that management plans are not accurately taking the negative effects of hunting into consideration if they do not consider the long-term (>100 years) effects on the population.⁶⁰ Even with low levels of hunting pressure, populations can go extinct due to combined hunting pressure, inbreeding depression, and unforeseen catastrophic events.⁶⁰ Therefore, population goals must incorporate some uncertainty and err on the side of caution to account for unexpected events.⁶⁰

Public opinion of wolves is one of the most important pieces of wolf conservation.³ Artificially decreasing wolf populations by using lethal measures, including derogations under the EU Habitats Directive, is not a long-term strategy for encouraging coexistence. Public education is critical, especially on the ecological importance of wolves, as well as wolf behavior and the importance of stable wolf population dynamics. By incorporating non-lethal, preventive conflict measures, wildlife managers can improve public opinions of wolves and encourage the use of better management tools.⁵⁵ In the United States, one study found that public tolerance of wolves declined as lethal control and public hunting of wolves increased.⁴¹ Continuing to frame wolves as 'pests' and using lethal management will only weaken tolerance and invite conflict.

REFERENCES

1. Boitani, L. 2018. *Canis lupus* (errata version published in 2019). *The IUCN Red List of Threatened Species* 2018: e.T3746A144226239.
2. Large Carnivore Initiative for Europe (LCIE). Wolf - *Canis lupus*. Available at: <https://www.lcie.org/Large-carnivores/Wolf->
3. Boitani L. (1995) Ecological and cultural diversities in the evolution of wolf-human relationships. In *Ecology and conservation of wolves in a changing world* (Carbyn L.N., Fritts S.H., & Seip D.R., eds.), pp. 3–11. Canadian Circumpolar Institute., Edmonton.
4. Nowak S. & Myslajek R.W. (2017) Response of the wolf (*Canis lupus linnaeus*, 1758) population to various management regimes at the edge of its distribution range in western Poland, 1951-2012. *Appl. Ecol. Environ. Res.* 15, 187–203.
5. Liberg O. et al. (2005) Severe inbreeding depression in a wild wolf (*Canis lupus*) population. *Biol. Lett.* 1,

- 17–20.
6. Laikre L. et al. (2013) Hunting effects on favourable conservation status of highly inbred Swedish wolves. *Conserv. Biol.* 27, 248–253.
 7. Hindrikson M. et al. (2017) Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management. *Biol. Rev.* 92, 1601–1629.
 8. Randi E. (2008) Detecting hybridization between wild species and their domesticated relatives. *Mol. Ecol.* 17, 285–293.
 9. Pilot M. et al. (2018) Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for the conservation status of hybrids. *Evol. Appl.* 11, 662–680.
 10. Fan Z. et al. (2016) Worldwide patterns of genomic variation and admixture in grey wolves. *Genome Res.* 26, 163–173.
 11. Hindrikson M. et al. (2012) Bucking the trend in wolf-dog hybridization: first evidence from Europe of hybridization between female dogs and male wolves. *PLoS One* 7, 1–12.
 12. Moura A.E. et al. (2014) Unregulated hunting and genetic recovery from a severe population decline: The cautionary case of Bulgarian wolves. *Conserv. Genet.* 15, 405–417.
 13. Rutledge L.Y. et al. (2012) Intense harvesting of eastern wolves facilitated hybridization with coyotes. *Ecol. Evol.* 2, 19–33.
 14. Hindrikson M. et al. (2013) Spatial genetic analyses reveal cryptic population structure and migration patterns in a continuously harvested grey wolf (*Canis lupus*) population in north-eastern Europe. *PLoS One* 8, 1–12.
 15. Schmidt K. et al. (2008) Reproductive behaviour of wild-living wolves in Białowieża Primeval Forest (Poland). *J. Ethol.* 26, 69–78.
 16. Wikenros C. et al. (2021) Age at first reproduction in wolves: different patterns of density dependence for females and males. *Proc. R. Soc. B Biol. Sci.* 288, 20210207.
 17. Packard J.M. (2003) Wolf Behavior: Reproductive, Social, and Intelligent. In *Wolves: Behaviour, ecology and conservation* pp. 35–65.
 18. Cariappa C.A. et al. (2011) A reappraisal of the evidence for regulation of wolf populations. *J. Wildl. Manage.* 75, 726–730.
 19. Rutledge L.Y. et al. (2010) Protection from harvesting restores the natural social structure of eastern wolf packs. *Biol. Conserv.* 143, 332–339.
 20. Brainerd S.M. et al. (2008) The effects of breeder loss on wolves. *J. Wildl. Manage.* 72, 89–98.
 21. Mech L.D. & Boitani L. (2003) Wolf Social Ecology. In *Wolves: Behaviour, ecology and conservation* pp. 1–34.
 22. Bryan H.M. et al. (2015) Heavily hunted wolves have higher stress and reproductive steroids than wolves with lower hunting pressure. *Funct. Ecol.* 29, 347–356.
 23. Milleret C. et al. (2017) Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. *J. Anim. Ecol.* 86, 43–54.
 24. Ausband D.E. & Waits L. (2020) Does harvest affect genetic diversity in grey wolves? *Mol. Ecol.* 29, 3187–3195.
 25. Recio M.R. et al. (2020) Agent-based models predict patterns and identify constraints of large carnivore recolonizations, a case study of wolves in Scandinavia. *Biol. Conserv.* 251, 108752.
 26. Haber G.C. (1996) Biological, conservation, and ethical implications of exploiting and controlling wolves. *Conserv. Biol.* 10, 1068–1081.
 27. Carricondo-Sanchez D. et al. (2020) Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. *Biol. Conserv.* 244, 108514.
 28. Rio-Maior H. et al. (2019) Designing the landscape of coexistence: Integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. *Biol. Conserv.* 235, 178–188.
 29. Cimatti M. et al. (2021) Large carnivore expansion in Europe is associated with human population density and land cover changes. *Divers. Distrib.* 27, 602–617.
 30. Barry T. et al. (2020) Does dispersal make the heart grow bolder? Avoidance of anthropogenic habitat elements across wolf life history. *Anim. Behav.* 166, 219–231.
 31. Mancinelli S. et al. (2019) Social, behavioural and temporal components of wolf (*Canis lupus*) responses to anthropogenic landscape features in the central Apennines, Italy. *J. Zool.* 309, 114–124.
 32. Meriggi A. & Lovari S. (1996) A review of wolf predation in Southern Europe: does the wolf prefer wild prey to livestock? *J. Appl. Ecol.* 33, 1561–1571.
 33. Ripple W.J. et al. (2013) Widespread mesopredator effects after wolf extirpation. *Biol. Conserv.* 160, 70–79.
 34. Soulé M.E. et al. (2003) Ecological effectiveness: conservation goals for interactive species. *Conserv. Biol.* 17, 1238–1250.
 35. Licht D.S. et al. (2010) Using small populations of wolves for ecosystem restoration and stewardship. *Bioscience* 60, 147–153.
 36. Beschta R.L. & Ripple W.J. (2009) Large predators and trophic cascades in terrestrial ecosystems of

- the western United States. *Biol. Conserv.* 142, 2401–2414.
37. Raynor J.L. *et al.* (2021) Wolves make roadways safer, generating large economic returns to predator conservation. *Proc. Natl. Acad. Sci.* 118, e2023251118.
 38. LIFE WOLFALPS EU. Misconceptions about the wolf. Available at: <https://www.lifewolfalps.eu/en/misconceptions/>
 39. Borg B.L. *et al.* (2015) Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *J. Anim. Ecol.* 84, 177–187.
 40. Kojola I. *et al.* (2016) Wolf visitations close to human residences in Finland: The role of age, residence density, and time of day. *Biol. Conserv.* 198, 9–14.
 41. Treves A. *et al.* (2013) Longitudinal analysis of attitudes toward wolves. *Conserv. Biol.* 27, 315–323.
 42. Liberg O. *et al.* (2012) Shoot, shovel and shut up: Cryptic poaching slows restoration of a large carnivore in Europe. *Proc. R. Soc. B Biol. Sci.* 279, 910–915.
 43. Suutarinen J. & Kojola I. (2017) Poaching regulates the legally hunted wolf population in Finland. *Biol. Conserv.* 215, 11–18.
 44. Louchouart N.X. *et al.* (2021) Evaluating how lethal management affects poaching of Mexican wolves. *R. Soc. Open Sci.* 8, 200330.
 45. Chapron G. & Treves A. (2017) Blood does not buy goodwill: allowing culling increases poaching of a large carnivore. *Proc. R. Soc. B Biol. Sci.* 284.
 46. Santiago-Ávila F.J. *et al.* (2020) Liberalizing the killing of endangered wolves was associated with more disappearances of collared individuals in Wisconsin, USA. *Sci. Rep.* 10, 1–14.
 47. Liberg O. *et al.* (2020) Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. *Biol. Conserv.* 243, 108456.
 48. Treves A. *et al.* (2020) Modelling concerns confound evaluations of legal wolf-killing. *Biol. Conserv.* 249, 108643.
 49. Hogberg J. *et al.* (2016) Changes in attitudes toward wolves before and after an inaugural public hunting and trapping season: Early evidence from Wisconsin’s Wolf range. *Environ. Conserv.* 43, 45–55.
 50. Browne-Núñez C. *et al.* (2014) Tolerance of wolves in Wisconsin: A mixed-methods examination of policy effects on attitudes and behavioral inclinations. *Biol. Conserv.* 189, 59–71.
 51. European Environment Agency. EIONET Central Data Repository (2021) Available at: https://cdr.eionet.europa.eu/ReportekEngine/search-dataflow?dataflow_uris=http%3A%2F%2Frod.eionet.europa.eu%2Fobligations%2F268&-years%3Aint%3Aignore_empty=&partofyear=&reportingdate_start%3Adate%3Aignore_empty=&reportingdate_end%3Adate%3Aignore_empty=&country=http%3A%2F%2Frod.eionet.europa.eu%2Fspatial%2F96&release_status=released&sort_on=reportingdate&sort_order=reverse&batch_size=
 52. The wolf will become a year-long protected animal as law stops trophy-hunters (2021) *Slovak Spect.* Available at: <https://spectator.sme.sk/c/22573322/the-wolf-will-become-a-year-long-protected-animal-as-law-stops-trophy-hunters.html>
 53. International Wolf Center: Latvia at a Glance (2020) Available at: <https://wolf.org/wow/europe/latvia>
 54. Krofel M. *et al.* (2011) Effectiveness of wolf (*Canis lupus*) culling as a measure to reduce livestock depredations. *Zb. gozdarstva Lesar.*, 11–21.
 55. Stone S.A. *et al.* (2017) Adaptive use of nonlethal strategies for minimizing wolf-sheep conflict in Idaho. *J. Mammal.* 98, 33–44.
 56. Treves A. *et al.* (2016) Predator control should not be a shot in the dark. *Front. Ecol. Environ.* 14, 380–388.
 57. Lute M.L. *et al.* (2018) Conservation professionals agree on challenges to coexisting with large carnivores but not on solutions. *Biol. Conserv.* 218, 223–232.
 58. Creel S. & Rotella J.J. (2010) Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (*Canis lupus*). *PLoS One* 5.
 59. Bischof R. *et al.* (2020) Estimating and forecasting spatial population dynamics of apex predators using transnational genetic monitoring. *Proc. Natl. Acad. Sci.* 117, 30531–30538.
 60. Nilsson T. (2004) Integrating effects of hunting policy, catastrophic events, and inbreeding depression, in PVA simulation: The Scandinavian wolf population as an example. *Biol. Conserv.* 115, 227–239.
 61. Epstein Y. *et al.* (2019) EU Court: Science must justify future hunting. *Science.* 366, 961.
 62. Fernández-Gil A. *et al.* (2016) Conflict misleads large carnivore management and conservation: Brown bears and wolves in Spain. *PLoS One* 11, e0151541.
 63. Peebles K.A. *et al.* (2013) Effects of remedial sport hunting on cougar complaints and livestock depredations. *PLoS One* 8, 1–8.
 64. Espuno N. *et al.* (2004) Heterogeneous response to preventive sheep husbandry during wolf recolonization of the French Alps. *Wildl. Soc. Bull.* 32, 1195–1208.
 65. Non-Lethal Wolf Management. Available at: <https://zoological.wixsite.com/nonlethalwolfmng/signatories>

66. Chapron G. *et al.* (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*. 346, 1517-1519.