

Wild Furbearer Management and Conservation in North America



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CHAPTER 32: NORTH AMERICAN WOLVES



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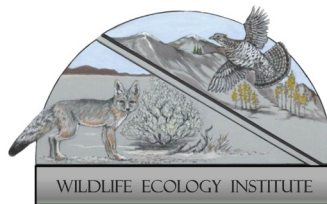
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Wild Furbearer Management and Conservation in North America
Chapter 32: North American Wolves

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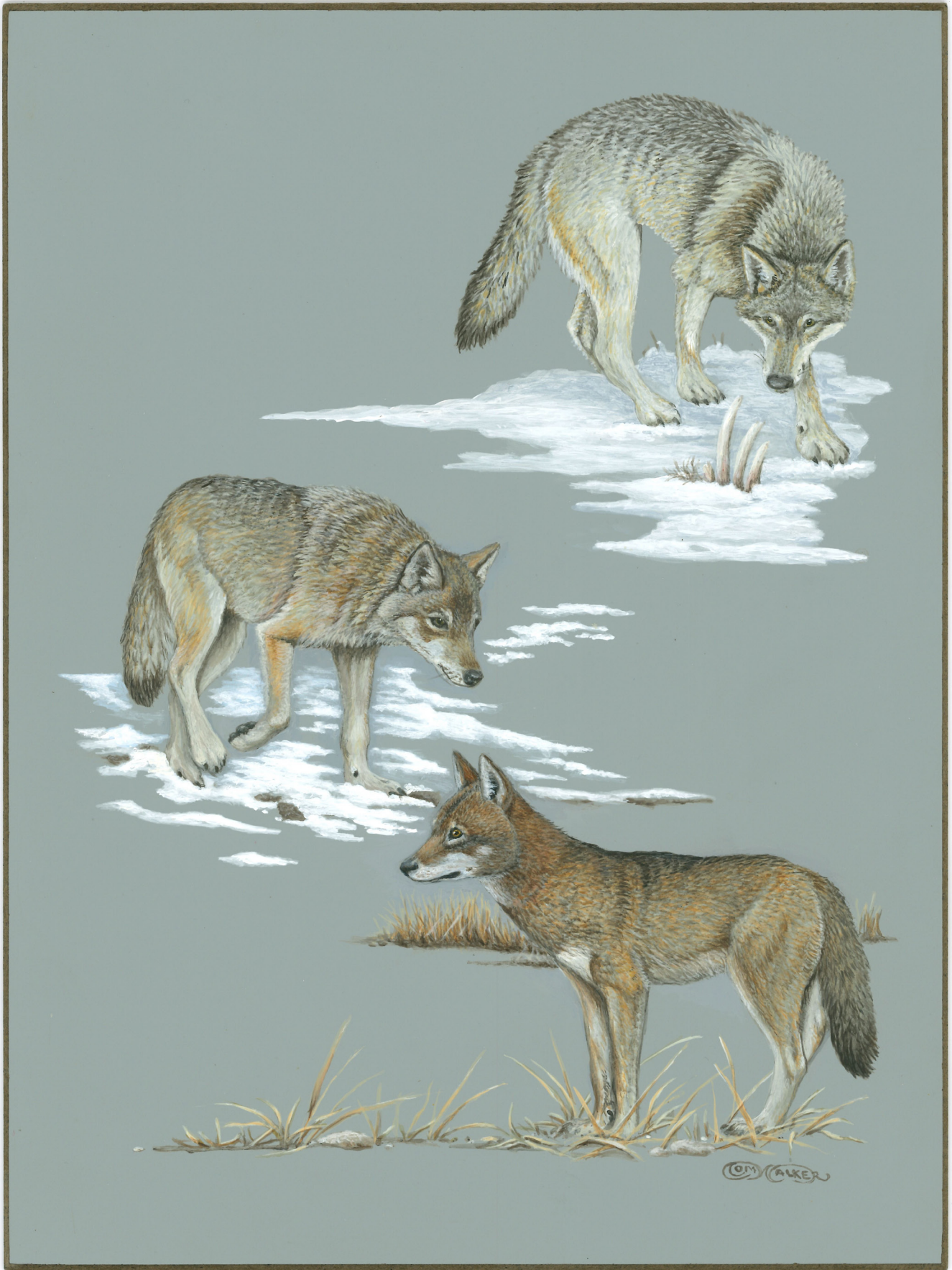
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NORTH AMERICAN WOLVES

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Since publication of the chapter on North American wolves (Carbyn 1987) in *Wild Furbearer Management and Conservation in North America* (Novak et al. 1987), there has been a substantial expansion in the distribution of wolf populations in North America and Europe, as well as advances in our understanding of wolf ecology. Mech and Boitani (2003) and Paquet and Carbyn (2003) provided important compendiums in the interim. Our objective was to provide a comprehensive update on the ecology, behavior, genetics, and population recovery of North American wolf species, as well as ongoing monitoring and management of existing populations.

Approximately two-thirds of the current distribution of North American wolves occurs in areas of low densities of human populations and almost no presence of livestock (e.g., Alaska, northern Canada). In these regions, wolf abundance is governed primarily by the abundance of their prey, with localized effects of killing by humans. In this chapter, we focus on recent wolf recovery in southern populations with higher population densities of humans, where human-wolf conflicts are relatively common and actively managed. We present historical information and new discoveries, and we reference scientific literature so that readers may find more information. In this chapter, we recognize the gray wolf (*Canis lupus*), which includes the Mexican gray wolf (*Canis lupus baileyi*; informally, Mexican wolf) as a subspecies; eastern wolves (*Canis sp. cf. lycaon*); and red wolves (*Canis rufus*) as separate species, but we also recognize that some consider these as variations of gray wolves, eastern wolves, or the product of hybridization between gray wolves and coyotes (*Canis latrans*; Kyle et al. 2006, Chambers et al. 2012, vonHoldt et al. 2016, Hohenlohe et al. 2017, Sacks et al. 2021). We use the general reference of wolf for all 3 species, but use adjectives (gray, eastern, or red) when referring to individual species.

DESCRIPTION

Wolves are large carnivores with relatively long legs, medium-sized footpads, and broad muzzles (Mech 1970, Carbyn 1987, Wang and Tedford 2008, Tedford et al. 2009). Sizes and color phases vary considerably across North America. White, gray, and black are the most common color phases, but variations include tan, cream, brown, buff, red, silver-gray, and bronze, with occasional variations of patches or stripes on the head, flanks, legs, or neck (Mech 1970, Carbyn 1987; Figs. 32.1 and 32.2). Light-colored or white wolves predominate in Arctic regions of Canada and Greenland, and are rare south of the subarctic, whereas the black and gray phases are common in subarctic and boreal forest regions, and gray phases prevail farther south (Banfield 1974, Carbyn 1987, Gipson et al. 2002, Musiani et al. 2007, Anderson et al. 2009).

Mexican wolves are gray overall, but tend to be a mix of black, dark gray, cinnamon, and buff over light underparts (Brown 1983; National Academies of Sciences, Engineering, and Medicine [NAS] 2019; Fig. 32.3). No black- or white-phase Mexican wolves have been documented. Eastern and red wolves typically have more reddish-brown or tawny coloration compared to gray wolves or coyotes, with reddish coloration on the lateral surface of their legs, behind their ears, and on their heads (Pimlott et al. 1969, Paradiso and Nowak 1972, Gipson 1976, Theberge and Theberge 2004; Fig. 32.4). The black phase in red wolves was once common in the southeastern U.S., but this trait is now absent in the extant population (Nowak 1979, Hinton et al. 2022).

Seasonal body mass of wolves is typically highest during winter and lowest during summer (Seal and Mech 1983, Butler et al. 2006, Benson et al. 2012, Mech and Buhl 2020). In Yellowstone National Park (YNP), USA, body weights of gray wolves ($n =$



Fig. 32.1. Pelage coloration among wolves varies, including within this pack of gray wolves (*Canis lupus*) in the Rocky Mountains, USA. Image courtesy of D. Smith, National Park Service, USA.



Fig. 32.2. Pelage coloration varies substantially among gray wolves, including (left to right) black, charcoal (blue), white, gray, and variations of gray (e.g., tawny; Novak et al. 1987). Image © Queen's Printer for Ontario, 1987; modified and reproduced with permission.

300) trended upward from June, peaked in January, and tapered off beginning in February (D. W. Smith, YNP, unpublished data). Increasing weights during winter may reflect the period when their ungulate prey tends to be most vulnerable to predation. Butler et al. (2006) reported that female gray wolves in south-central Alaska, USA, achieved peak body mass in early spring. Seasonal weight changes of ≤ 7 kg (15 lb) have been documented for adult wolves (Seal and Mech 1983; Benson et al. 2012; Mech and Buhl 2020; D. W. Smith, unpublished data).

The largest-bodied North American gray wolves occur in the boreal forests of Alaska, Canada, and the Rocky Mountains of western North America, where weights of adults are typically 30–50 kg (66–110 lb) for females and 40–65 kg (88–143 lb) for males (Skeel and Carbyn 1977, Gunson and Nowak 1979, Ream et al. 1991, Ballard et al. 1997, Mech et al. 1998, Butler et al. 2006, Adams et al. 2008, MacNulty et al. 2009a, Wiwchar and Mallory 2012). Both gray wolves in the Great Lakes region and Mexican wolves are smaller than wolves in northern and western North America. Adult Mexican wolves weigh 25–34 kg (55–75 lb) for females and 31–41 kg (68–90 lb) for males (McBride 1980). Adult gray wolves in northern Minnesota, USA, averaged 26–30 kg (57–66 lb) and 30–36 kg (66–79 lb) for females and males, respectively (Mech and Paul 2008). Mean weights of female and male wolves in Minnesota peaked at 5–6 years old and were 31 kg (69 lb) and 41 kg (90 lb), respectively (Mech 2006).

Eastern and red wolves are of similar size and are the smallest of the North American wolves. Hinton and Chamberlain (2014) reported an average weight of 25 kg (55 lb) and 29 kg (64 lb) for adult female and adult male red wolves, respectively. These values are similar to the weights of 24 kg (53 lb) and 30 kg (66 lb) for adult female and adult male eastern wolves, respectively (Theberge and Theberge 2004).

In gray wolves, total body length ranged 130–150 cm (51–59 in) for adult females and 140–160 cm (55–63 in) for adult males; in most cases, the tail is less than one-half of the body length (Banfield

1974, Carbyn 1987, Wheeldon and Patterson 2012). Shoulder height for Mexican wolves ranges from 72 to 81 cm (29–32 in; Brown 1983), and averages 81 cm (32 in) for males and 77 cm (30 in) for females. For eastern wolves, average body length is 109 cm (43 in) for females and 113 cm (45 in) for males (Benson et al. 2012). Average shoulder height for adult eastern wolves is 64 cm (25 in) for females and 70 cm (28 in) for males (B. R. Patterson, Ontario Ministry of Natural Resources and Forestry, unpublished data, cited in Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2015). For red wolves, mean body length is 108 cm (42 in) for adult females and 112 cm (44 in) for adult males (Hinton and Chamberlain 2014, Hinton et al. 2018). Mean shoulder height for red wolves is 66 cm (26 in) for females and 70 cm (28 in) for males (Hinton and Chamberlain 2014, Hinton et al. 2018).

The skulls of all wolves are characterized by the elongated rostrum and heavily ossified braincase (Nowak 1979, Wang and Tedford 2008; Fig. 32.5). The extended rostrum provides space and surface area for an effective olfactory organ. A broadly spreading zygomatic arch and pronounced sagittal crest provide space and attachment for massive masseter muscles, which are used to deliver powerful bites (Peterson and Ciucci 2003). Wolves have 42 teeth and a dental formula of $I = 3/3, C = 1/1, P = 4/4, M = 2/3$. The largest teeth are the canines, used in gripping and holding prey. The carnassials are formed by the last upper premolar and the first lower molar, and they function in cutting and shearing flesh, whereas massive molars aid in crushing food. The incisors are relatively small. The combination of massive skull, heavy muscles, and massive teeth results in a powerful tool for tearing and crushing (Mech 1970, Peterson and Ciucci 2003, Mech et al. 2015). Gray wolves have large, heavy skulls, widely spaced premolars, and relatively massive and proportionately shorter canines compared to most other canids (Banfield 1974; Fig. 32.5A). Eastern and red wolves have narrow-looking, less-massive skulls, and have relatively longer, but less-massive, canines compared to gray wolves (Pimlott et al. 1969; Nowak 1979, 2002; Fig. 32.5B,C).



Fig. 32.3. Typical pelage coloration of Mexican gray wolves (*Canis lupus baileyi*) is gray with some combination of black, dark gray, cinnamon, and buff over light underparts. Image courtesy of G. Andrejko, Arizona Game and Fish Department, USA.



Fig. 32.4. Eastern wolves (*Canis lycaon*) typically exhibit pelage coloration that is more reddish compared to gray wolves (*Canis lupus*) or coyotes (*Canis latrans*). Image courtesy of M. Runtz, Carlton University, Canada.

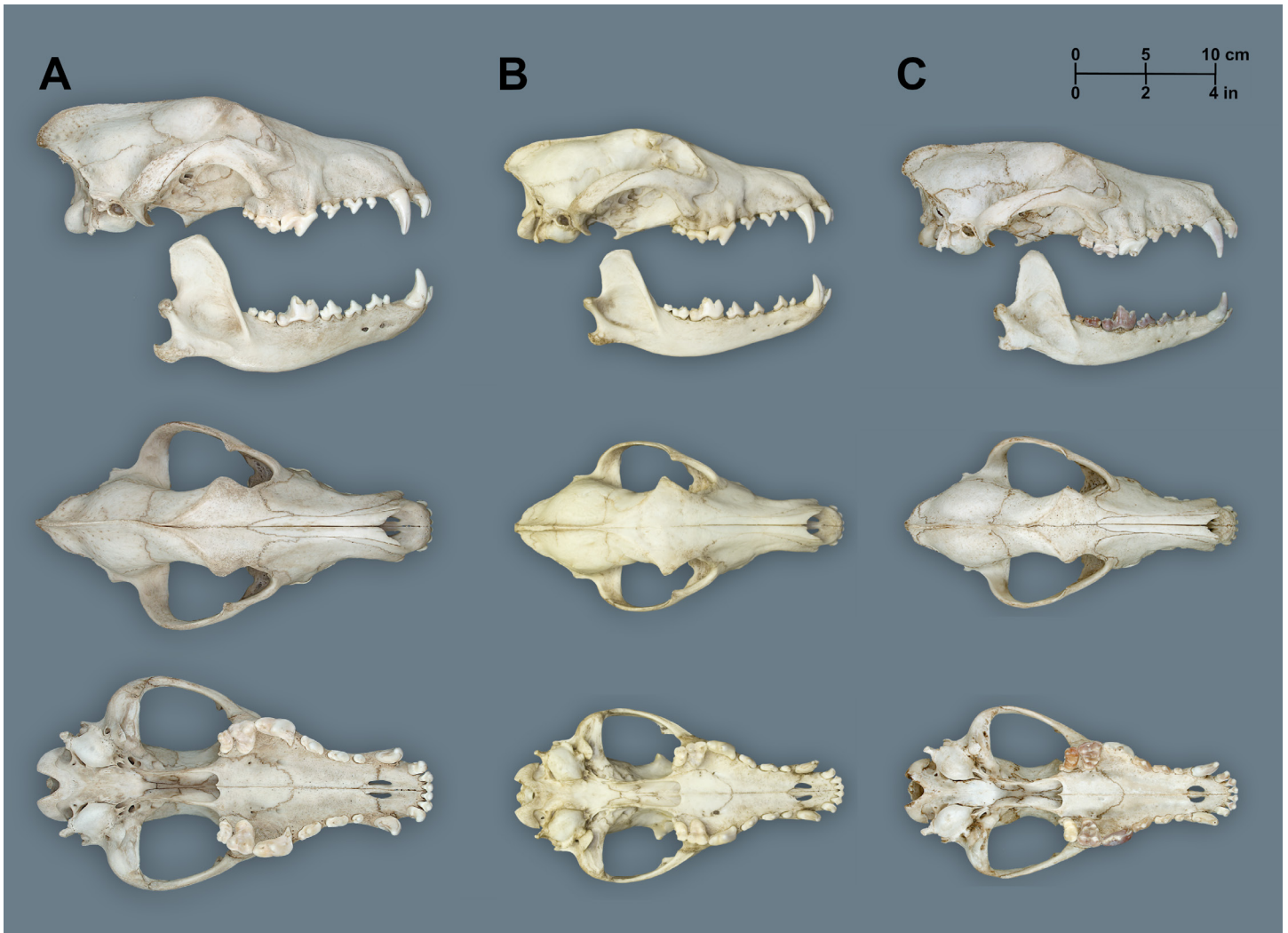


Fig. 32.5. Skull characteristics of A) gray (*Canis lupus*), B) eastern (*Canis lycaon*), and C) red (*Canis rufus*) wolves in North America. Images courtesy of Skulls Unlimited International, USA.

The postcranial skeleton of the wolf is strongly linked to locomotor behaviors and, therefore, their hunting strategies. Wolves are coursing predators that obtain their food by chasing prey. It can sometimes take days or even weeks to locate suitable prey (Mech et al. 2015, Johnson et al. 2017). Their maximum running speed is 55–70 km/hr (35–44 mi/hr; Mech 1974a), but typical travel speeds are 4–9 km/hr (3–6 mi/hr; Mech 1994, Musiani et al. 1998). Vander Vennen et al. (2016) demonstrated that much of the variation in killing rates of moose (*Alces alces*) by wolves was explained by movement rates of wolves. Wolves have excellent senses of smell, vision, and hearing, and use any or all of these senses to locate prey, depending on the circumstances (Asa and Mech 1995, Harrington and Asa 2003, Mech 2007a, Mech et al. 2015). Use of observation by wolves is an important stage of their hunting behavior, especially when pursuing large prey such as bison (*Bison bison*; MacNulty et al. 2007).

TAXONOMY AND LEGAL STATUS

The taxonomy of wolves in North America has long been complicated and controversial (Chambers et al. 2012). Taxonomic assessments of wolves were historically based on descriptive assessments of morphological characteristics (Pocock 1935, Goldman 1944). With the advent of multivariate statistical analyses in the mid-twentieth century, taxonomic assessments of wolves became based largely on statistical assessment of skull measurements (Kolenosky and Standfield 1975; Skeel and Carbyn 1977; Nowak 1979, 2002, 2003; Bogan and Mehlhop 1983). With the arrival of molecular genetic techniques in the latter part of the twentieth century, taxonomic assessments of wolves have relied increasingly on genetic data, including mitochondrial DNA (mtDNA) sequences and nuclear microsatellite loci (Wayne and Jenks 1991, Roy et al. 1994, Hedrick et al. 1997, Vilà et al. 1999, Wilson et al. 2000, Sacks et al. 2021).

Recent genetic investigations based on whole-genome sequencing continue to yield further taxonomic insights (vonHoldt et al. 2011, 2016; Rutledge et al. 2015; Fitak et al. 2018; Heppenheimer et al. 2018a; Sinding et al. 2018; Bergström et al. 2022; Vilaça et al. 2023), but as discussed below, substantial debate continues. Several reviews of the taxonomy of North American wolves have been published (e.g., Nowak 1995, 2002, 2003, 2009; Kyle et al. 2006; Chambers et al. 2012; Waples et al. 2018; NAS 2019; Loog et al. 2020; Schweizer and Wayne 2020; Sacks et al. 2021). A bibliography of interbreeding among *Canis* species in North America was recently updated (vonHoldt and Aardema 2020), which builds on gaining a better understanding of the evolutionary history of *Canis* in North America. Currently, 4 taxa of the wolf are recognized in North America for the purposes of management and conservation, including the gray wolf, Mexican wolf, eastern wolf, and red wolf.

Gray Wolf

The gray wolf is recognized as a distinct species that evolved in Eurasia during the Pleistocene and entered North America south of the ice sheets around the time of the last glacial maximum, possibly via multiple invasions (Vilà et al. 1999, Weckworth et al. 2010,

Chambers et al. 2012). More recent studies of genomics (Fan et al. 2016) and whole-mtDNA sequences, including ancient DNA (Loog et al. 2020), suggest extant gray wolves of North America may trace common ancestry with Eurasian wolves no earlier than 40,000 years ago. Earlier hypotheses suggested an early wave of gray wolves persisted south of the ice sheets in North America >100,000 years ago, and there is now genomic evidence to suggest all extant wolf-like canids in North America have at least 10–20% coyote ancestry (Bergström et al. 2022), resulting from wolf-coyote hybridization events 80,000–100,000 years ago.

The number of recognized subspecies of gray wolf has decreased from 24 (Hall and Kelson 1959, Hall 1981) to 5 (Nowak 1995, 2003). Chambers et al. (2012) concluded that morphological and genetic data supported the recognition of 3 subspecies of the gray wolf in North America, including *Canis lupus baileyi* (Mexican wolf), *Canis lupus occidentalis* (northwestern wolf), and *Canis lupus nubilus* (plains wolf); notably, *Canis lupus arctos* (Arctic wolf) was not clearly supported, but this conclusion was tentative because of limited data. Indeed, COSEWIC has considered *Canis lupus arctos* in Canada as Data Deficient since 1999, meaning there is insufficient information to assess its eligibility for a status designation or its risk of extinction (Government of Canada 2014). Chambers et al. (2012) also failed to consider the Alexander Archipelago wolf in southeastern Alaska as a distinct subspecies from the wolves of coastal British Columbia, but distinction of coastal wolves also remains controversial (Cronin et al. 2015a, 2015b; Weckworth et al. 2015; Schweizer et al. 2016; Hendricks et al. 2019). There remains no consensus regarding whether the wolf in southeastern Canada is *Canis lupus lycaon* (eastern timber wolf, a subspecies of gray wolf) or a distinct species *Canis lycaon* (eastern wolf). As such, and the conclusions of Chambers et al. (2012) notwithstanding, some researchers continue to recognize 5 gray wolf subspecies, including *Canis lupus arctos*. Chambers et al. (2012) considered eastern wolves (*Canis lycaon*) as a separate species, whereas Nowak (1995, 2003, 2009) and vonHoldt et al. (2011) have suggested it as a subspecies of gray wolf (*Canis lupus lycaon*).

We acknowledge that the species status continues to be unsettled in the scientific community, so herein we refer to this taxon as the eastern wolf, without implying acceptance of one taxonomic view over the other. González-Bernal et al. (2022) proposed designation of gray wolves in North America into 5 bioclimatic groups, including Coastal, Eastern, Northern, Southern (i.e., Mexican wolf), and Western. Schweizer et al. (2016) and Hendricks et al. (2019) recommended designation of ecotypes based on genetics and environmental factors and suggested 6 ecotypes for Alaska and Canada, including Arctic, Atlantic, Boreal Forest, British Columbia, High Arctic, and West Forest. Coastal or British Columbian wolves are recognized within both the ecotypes and bioclimatic groups, but the bioclimatic groups do not distinguish between Arctic and Boreal Forests types.

Historically, the gray wolf occurred across most of North America, including Canada, the conterminous U.S. and Alaska, and Mexico, with the possible exception of eastern deciduous forests, where an endemic North American wolf species, and

likely precursor to the eastern wolf and red wolf, is thought to have occurred (Martin 1989; Nowak 1979, 2002; Chambers et al. 2012). Currently, the gray wolf occurs across most of Canada, including portions of all provinces and territories (except the Maritime Provinces); Chihuahua Mexico; and portions of the U.S., including the Northern Rocky Mountains (NRM), western Great Lakes states, Alaska, Arizona, California, Colorado, New Mexico, Oregon, and Washington (Fig. 32.6, Tables 32.1 and 32.2).

In the U.S., the gray wolf is managed as 2 taxonomic entities: gray wolf (*Canis lupus occidentalis*, *Canis lupus nubilus*) and Mexican wolf (*Canis lupus baileyi*); it had been listed as endangered under the Endangered Species Act of 1973 (ESA) in 39 states and portions of 5 states, and as threatened in Minnesota (since 1978), but is not federally listed in Alaska. The NRM, including Idaho, Montana, Wyoming, eastern Oregon, eastern Washington, and north-central Utah were delisted from the ESA in 2009 and later (U.S. Fish and Wildlife Service [USFWS] 2019). However, on 3 November 2020, USFWS published a rule delisting gray wolves across all of the U.S. in those states with populations of gray wolves, effective 4 January 2021 (USFWS 2020), except Mexican wolves, which remained listed as federally endangered. On 10 February 2022, the U.S. District Court for the District of Northern California vacated the final rule, resulting in the reinstatement of endangered status for gray wolves in 44 states and threatened in Minnesota (Defenders of Wildlife et al. v. U.S. Fish and Wildlife Service et al., Case No. 21-CV-00344-JSW, U.S. District Court, Northern District of California, 2022). In Canada, 2 subspecies of gray wolf are recognized for conservation status, including the northern gray wolf (*Canis lupus occidentalis*) and the southern gray wolf (*Canis lupus nubilus*), the latter often referred to as the plains wolf in the U.S. Neither subspecies is considered at risk in Canada (Government of Canada 2014, COSEWIC 2015). For the purposes of this chapter, we are pooling these 2 subspecies into simply the gray wolf.

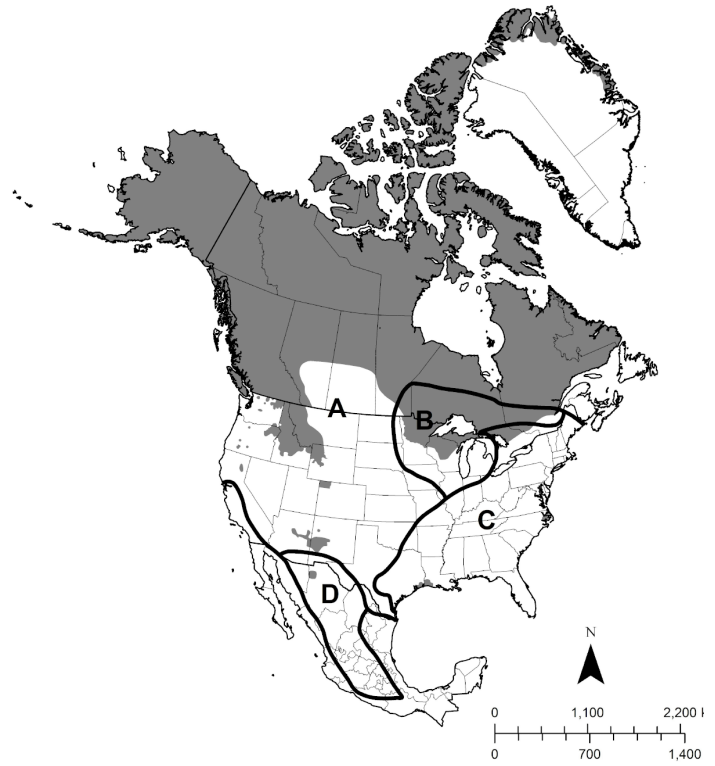


Fig. 32.6. Estimated current (shaded) and historical (polygons A–D) geographic distribution of North American wolves (*Canis* spp.). The historical distribution included: A) gray wolves (*Canis lupus*), B) Great Lakes gray wolves (*Canis lupus* × *Canis lycaon*), C) red wolves (*Canis rufus*) and eastern wolves (*Canis lycaon*), and D) Mexican gray wolves (*Canis lupus baileyi*). The current distribution of eastern wolves is limited to the shaded area in C in Canada, and the current distribution of red wolves is limited to the shaded area in C in USA. Based on information modified from Nowak 2003; Marquard–Petersen 2011; Montana Fish, Wildlife, and Parks 2018; M. Hurley, Idaho Department of Fish and Game, unpublished data.

Table 32.1. Current status of gray wolves (*Canis lupus*) in Mexico and the U.S. during 2020.

Country	State	Reintroduction (yr)	First known reproduction (yr)	Estimated population size	Population trend	Legal classification	
						State	Federal
Mexico ^a		2011	2014	40–45 ^b	Increasing	Endangered	Endangered
U.S.							
	Alaska ^c	Always extant	Always extant	7,000–10,000	Stable	Big game, furbearer	None
	Arizona ^d	1998		84	Increasing	Endangered	Endangered
	Colorado ^e		2019	3	Increasing	Endangered	Endangered
	California ^f		2015	8	Increasing	Endangered	Endangered
	Idaho ^g	1995		900	Stable	Big game	Delisted
	Michigan ^h		1989	695	Stable	Game	Endangered
	Minnesota ⁱ	Always extant	Always extant	2,696	Stable	Game	Threatened
	Montana ^j		1986	1,177	Slightly decreasing	Species in need of management	Delisted
	New Mexico ^d		1998	112	Increasing	Endangered	Endangered
	Oregon ^k	N/A	2008	173	Increasing	Special game	Endangered (west only)
	Washington ^l	N/A	2008	178	Increasing	Endangered	Endangered (west only)
	Wisconsin ^m	N/A	1976	1,034	Stable	Big game	Endangered
	Wyoming ⁿ	1995		327	Slightly decreasing	Big game, predator	Delisted

^aU.S. Fish and Wildlife Service 2017a, 2017b.

^b2017.

^cAlaska Department of Fish and Game 2019.

^dU.S. Fish and Wildlife Service 2021.

^eE. Odell, Colorado Parks and Wildlife, personal communication.

^fCalifornia Department of Fish and Wildlife 2020.

^gIdaho Department of Fish and Game 2021.

^hMichigan Department of Natural Resources 2022b.

ⁱErb and Humpal 2020.

^jParks et al. 2022.

^kOregon Department of Fish and Wildlife 2021.

^lWashington Department of Fish and Wildlife et al. 2021.

^mWiedenhoef et al. 2020.

ⁿWyoming Game and Fish Department et al. 2021.

Table 32.2. Estimated population abundance of gray wolves (*Canis lupus*), population trends (2015–2018), and method used for estimates for each Canadian jurisdiction during 2018. Estimates were based on a survey administered to jurisdictional representatives during summer 2018 (B. R. Patterson, Ontario Ministry of Natural Resources and Forestry, unpublished data).

Country Province or territory	Population		Estimation method(s)
	Abundance	Trend	
Canada	51,665–56,765		
Alberta	7,000	Stable to increasing	Model based (area of occupancy × habitat-specific average density)
British Columbia	8,500	Stable	Model based (ungulate biomass)
Manitoba	4,000–6,000	Stable to increasing	Expert based, aerial surveys
New Brunswick	0		
Newfoundland Island	Few	Possibly establishing	
Labrador	200–300	Substantially declining	Aerial surveys, expert based, territory mapping
Northwest Territories	4,000–5,000	Stable (west), declining (east)	Harvest trends, aerial surveys, expert-based modelling
Nova Scotia	0		
Nunavut	5,000–6,000	Declining (Arctic islands), increasing (mainland)	Expert based
Ontario	9,000	Stable to declining	Hunter surveys, territory mapping, aerial surveys
Prince Edward Island	0		
Québec	6,965	Unknown	Expert based, hunter surveys
Saskatchewan	3,000	Stable	Expert based (area of occupancy × habitat-specific average density)
Yukon	4,000–5,000	Stable	Aerial surveys, expert-based modelling

Mexican Gray Wolf

The Mexican gray wolf, or informally, Mexican wolf, is currently recognized as a subspecies of gray wolf based on morphological, genetic, and ecological evidence (Wayne et al. 1992; Vilà et al. 1999; vonHoldt et al. 2011, 2016; Fan et al. 2016; Heffelfinger et al. 2017a, 2017b; NAS 2019). The ancestors of the Mexican wolf are thought to have been part of an early immigration of wolves into North America from Eurasia (Chambers et al. 2012, but see Loog et al. 2020). Historically, the Mexican wolf occurred in northern Mexico and southwestern U.S., including Arizona, New Mexico, and possibly western Texas (Bogan and Mehlhop 1983; Brown 1983; Heffelfinger et al. 2017a, 2017b; USFWS 2017a, 2017b; NAS 2019), but was extirpated from the wild by the early 1980s (McBride 1980). To begin recovery efforts in the wild, that historical range was expanded 320 km (200 mi) northward by USFWS (1996) to encompass the potential zone of interchange with larger plains wolves in central Arizona and New Mexico (Leonard et al. 2005; Hendricks et al. 2016, 2017; Zander 2004; Heffelfinger et al. 2017a, 2017b). In the U.S., the Mexican wolf is federally listed as endangered, except in portions of Arizona and New Mexico, where it is listed as a nonessential experimental population to contribute to recovery efforts (USFWS 2019).

Eastern Wolf

The gray wolf was extirpated from southern Ontario and southern Québec, Canada, between 1850 and 1900 (Pimlott 1961, Kolenosky and Standfield 1975). Concurrently, a wolf smaller than the gray wolf but larger than a coyote, and putatively the ancestor of eastern wolves and red wolves, occupied areas east of the Mississippi River from the Gulf Coast to the St. Lawrence and Great Lakes and extreme southeastern Ontario (Wilson et al. 2000, Nowak 2002, Kyle et al. 2006). This smaller wolf is thought to have followed a northward expansion of its primary prey, the white-tailed deer (*Odocoileus virginianus*), into central Ontario during the late 1800s (Kyle et al. 2006, Wilson et al. 2009). A similar process may have occurred in northeastern Minnesota, where a similar population

of wolves occurred until the 1960s when they began to interbreed with larger-bodied gray wolves (Mech and Paul 2008; Mech 2010, 2011a, 2011b; Mech et al. 2011). Most remaining eastern wolves inhabit Ontario and parts of southern Québec (Fig. 32.6).

There remains much debate about the genetic origins of the eastern wolf, with leading hypotheses suggesting it is either a hybrid of the gray wolf and coyote (Lehman et al. 1991; Roy et al. 1994; Koblmüller et al. 2009; vonHoldt et al. 2011, 2016), or a distinct endemic North American species (Wilson et al. 2000; Chambers et al. 2012; Rutledge et al. 2012, 2015; Heppenheimer et al. 2018a). Early studies of canid genetics based on both mtDNA haplotypes (Lehman et al. 1991, Wayne and Jenks 1991) and nuclear microsatellites (Roy et al. 1994) suggested the possible role of coyotes in the ancestry of the red wolf, the eastern wolf, and the Great Lakes wolf (i.e., wolves occupying the entire western Great Lakes region; Fig. 32.7). In contrast, and based on both 8 microsatellite loci and unique mtDNA haplotypes, Wilson et al. (2000) suggested both the red wolf and the eastern Canadian wolf were not hybrids, but rather that both evolved in North America and shared a common lineage with the coyote until 150,000–300,000 years ago. Koblmüller et al. (2009) and vonHoldt et al. (2011, 2016) contested this view and concluded that canid genomes from the Great Lakes region showed little taxonomic distinction and that only 2 distinct North American species of *Canis* (coyote and gray wolf) occurred in the region. Rutledge et al. (2012) and Hohenlohe et al. (2017) argued that the analyses of vonHoldt et al. (2011, 2016) was negatively affected by a lack of representative samples and that the observed proportions of unique alleles revealed a higher degree of evolutionary distinctiveness in red wolves and eastern wolves relative to other North American canids. vonHoldt et al. (2017) responded to the criticisms of Hohenlohe et al. (2017) and reaffirmed their conclusions, arguing the observed fractions of novel alleles in genomes of the red wolf and the eastern wolf were comparable to, or less than, that expected for a recent wolf-coyote hybrid, and concluded there is no evidence for an independent ancestry for any of the New World wolves (i.e., red wolves and eastern wolves).



Fig. 32.7. Wolves in the western Great Lakes region are an admixture of mostly eastern wolves (*Canis lycaon*) to the east of this geographical area, transitioning to mostly gray wolves (*Canis lupus*) on the western areas. Image courtesy of J. Vucetich, Michigan Technological University, USA.

A more recent genome-wide examination of single nucleotide polymorphism of a large data set from central Ontario and the Great Lakes region ($n = 281$ canids, including $n = 30$ eastern wolves) demonstrated support for eastern wolves as a discrete genotype cluster (Heppenheimer et al. 2018a), leading to greater acceptance of eastern wolves as likely a distinct species (vonHoldt and Aardema 2020). Based on mtDNA from historical samples, Sacks et al. (2021) postulated that the endemic North American wolf may have been the red wolf. Analysis of these mtDNA data further support that red wolves diverged from coyotes about 60,000 years ago, with their purest descendants now confined to the greater Algonquin Provincial Park (APP) region of southeastern Ontario, where they are commonly referred to as eastern wolves (Sacks et al. 2021).

Hohenlohe et al. (2017) also stated that the hypothesis of a recent hybrid origin for red wolves and eastern wolves requires interbreeding between gray wolves and coyotes. Although gray wolves and coyotes have produced fertile offspring in captivity through artificial insemination (Mech et al. 2014), evidence for interbreeding in the wild is absent. Lehman et al. (1991), Roy et al. (1994), Koblmüller et al. (2009), and vonHoldt et al. (2016) suggested gray wolves might breed naturally with coyotes when the population density of wolves becomes very low. However, there is no evidence of ongoing or recent hybridization between these 2 species in the western Great Lakes (Wheeldon et al. 2010; Mech 2011a, 2011b; vonHoldt and Aardema 2020), despite gray wolves and coyotes having coexisted there since before European settlement (Wydeven and Pils 2008). Similarly, there is little evidence for hybridization between coyotes and Mexican wolves, the latter of which are smaller in stature than other gray wolves, exist at very low population densities, and are sympatric with coyotes (Hailer and Leonard 2008, vonHoldt and Aardema 2020). In contrast, hybridization between coyotes and both red wolves

and eastern wolves remains common (Kolenosky 1971, Nowak 2002, Hailer and Leonard 2008, Wilson et al. 2009, Benson et al. 2012, Bohling et al. 2016, Hinton et al. 2018, vonHoldt and Aardema 2020).

Two other important issues which have clouded this debate include the use of inconsistent and often ambiguous nomenclature and the lack of representativeness of samples. Specifically, some researchers have considered eastern wolves and Great Lakes wolves synonymous irrespective of context (vonHoldt et al. 2011, 2016; Monzón et al. 2014), implying that such wolves belonged to the same population. This inappropriate sample pooling is likely the result of misinterpretation of early accounts of the distribution of genetic material of eastern wolves in admixed *Canis* populations (e.g., Kyle et al. 2006, Wilson et al. 2009). Regardless, considering Great Lakes wolves and eastern wolves to be synonymous has biased results and led to erroneous inferences. In fact, the assertion that the eastern wolf is a hybrid of the gray wolf and the coyote is based largely on analyses that have inappropriately grouped together wolves from different populations and did not adequately sample representative eastern wolves (Koblmüller et al. 2009; vonHoldt et al. 2011, 2016, 2017).

The first genome-wide single-nucleotide-polymorphism dataset with substantial sample sizes of representative populations was assembled by Heppenheimer et al. (2018a) in a step towards resolving this debate. Heppenheimer et al. (2018a) showed that eastern wolves are genetically distinct due to the presence of alleles private to eastern wolves, and they also carry a unique genetic composition of regional alleles associated with the coyote and the gray wolf. In a more recent test of these competing hypotheses related to the origin and identity of the eastern wolf, Vilaça et al. (2023) sequenced 25 high-coverage whole genomes of individuals representative of extant Canadian wolf-like canid types of known origin and levels of contemporary hybridization. These analyses point to eastern wolves being a distinct taxonomic entity that has evolved separately from gray wolves for approximately the past 67,000 years with an admixture event with coyotes about 37,600 years ago. Importantly, about 63% of the genome of the eastern wolf was found to be unique to eastern wolves and not found in present-day gray wolves or coyotes (Vilaça et al. 2023). Although the taxonomy of the eastern wolf remains unsettled, we will hereafter refer to this canid by its common name, eastern wolf, without implying acceptance of one taxonomic view or the other.

Regardless of their origins, based on the published literature summarized here, it seems likely that eastern wolves and red wolves were once part of the same continuous distribution of small-bodied wolves in the New World that occupied eastern deciduous forests (Kyle et al. 2006, Sacks et al. 2021). Following changes in geographic distribution, hybridization occurred among eastern wolves, coyotes, and gray wolves, as well as domestic dogs, and contemporary genetic differences between eastern wolves and red wolves may reflect recent genetic bottlenecks experienced by each, genetic drift, and varying amounts of introgression from other canid species (Wilson et al. 2000; Kyle et al. 2008; vonHoldt et al. 2011, 2016; Rutledge et al. 2015; Sacks et al. 2021).

Although eastern wolves were thought to have once occurred across southern Ontario, southern Québec, and south into the eastern U.S., most remaining eastern wolves are found only in Ontario and a few areas of southern Québec, north of the St. Lawrence River (Fig. 32.6). They are not known to currently occupy any other Canadian province or U.S. state. Although a mtDNA haplotype and an ATPase haplotype (C3/Ccr13/GL2; Catp13) associated with eastern wolves have been found in wolves in Manitoba, Canada (Stronen et al. 2010, Rutledge et al. 2010a), most wolves in Manitoba have mtDNA associated with gray wolves (Stronen et al. 2010). Genes of eastern wolves (termed New World mtDNA to differentiate from Old World mtDNA associated with gray wolves) are found across the Québec-Saskatchewan region and the western Great Lakes states and are interpreted under the 3-species hypothesis as evidence that wolves in the region are hybrids of eastern and gray wolves (Wheeldon 2009, Wheeldon and White 2009, Fain et al. 2010, Wheeldon et al. 2010).

In May 2015, COSEWIC designated the eastern wolf as *Canis sp. cf. lycaon* (i.e., *Canis* species believed to be *lycaon*) with a threatened status, but it is listed as Special Concern status under Canada's Species at Risk Act (SARA) until a decision is made by the Governor in Council to change the official status (Environment and Climate Change Canada 2021). Referring to the eastern wolf as the Algonquin wolf in 2016, the provincial government of Ontario reclassified the animal as threatened provincially (Committee on the Status of Species at Risk in Ontario [COSSARO] 2016). Although the status assessments by COSEWIC and COSSARO refer to the same taxonomic entity, COSSARO renamed the eastern wolf because of a long history of hybridization among eastern wolves, gray wolves, and coyotes, which they believed has led to a hybrid taxon that is evolutionarily distinct from other canids. On 25 January 2023, COSSARO amended the Species at Risk in Ontario List to reflect a name change for this entity back to eastern wolf.

Red Wolf

Since 1973, the red wolf has been federally listed in the U.S. as an endangered species under the ESA throughout its historical range. However, the reintroduced population in northeastern North Carolina, USA, is deemed a nonessential experimental population allowing for flexible management of wolves on privately owned lands (Parker and Phillips 1991). The taxonomy of the red wolf also remains controversial based on recent genetic investigations, which are summarized by Waples et al. (2018). Several competing descriptions of the origin of the red wolf have been proposed, including: 1) an ancient (pre-European contact) hybrid between the gray wolf and the coyote (McCarley 1962, Brzeski et al. 2016), 2) a recent (post-European contact) hybrid between the gray wolf and the coyote (Wayne and Jenks 1991; Vilà et al. 1999; vonHoldt et al. 2011, 2016), 3) a distinct species that evolved from a common ancestor with the coyote (Nowak 2002, Chambers et al. 2012, Brzeski et al. 2016, NAS 2019, Chafin et al. 2020), 4) the same species as the eastern wolf (Wilson et al. 2000, Kyle et al. 2008, Rutledge et al. 2015), and 5) a subspecies of gray wolf (Audubon and Bachman 1851, Lawrence and Bossert 1967). Nevertheless, the

most recent and definitive scientific evaluation of the taxonomy of the red wolf (NAS 2019) determined that: 1) historical red wolves constituted a taxonomically valid species; 2) extant red wolves are distinct from extant gray wolves and coyotes; 3) extant red wolves trace some of their ancestry to the historical red wolves; and 4) present species status is supported based on the available genetic, morphological, behavioral, and ecological evidence.

Taxonomy of the red wolf has been complicated because the extirpation of the species from its historical range left few specimens with information on their origin, and facilitated recent genetic introgression by coyotes into the extant genome of the red wolf (Paradiso and Nowak 1973, Hinton et al. 2013, Brzeski et al. 2016). Moreover, the captive population used for propagation and reintroduction into the wild was derived from a small number of individuals captured from a remnant population in southeastern Texas that experienced introgression from coyotes (McCarley 1962, Paradiso 1968, Paradiso and Nowak 1973, Nowak 1979). Despite this introgression, Nowak (1979, 2002) reported no differences between the morphology of extant red wolves and *Canis rufus* that persisted in the eastern U.S. about 10,000 years ago. Additionally, Brzeski et al. (2016) sequenced pre-Columbian (350–1,900 years ago) wolf specimens ($n = 3$) from within the historical range of the red wolf and suggested their findings indicated relatively recent divergence between red wolves and coyotes rather than hybridization. Sacks et al. (2021) postulated that the endemic North American wolf may have been the red wolf which diverged from coyotes about 60,000 years ago.

Notably, the ancestry of the red wolf persists in canid populations in southwestern Louisiana, USA (Murphy et al. 2018, vonHoldt et al. 2022), and on Galveston Island, Texas (Heppenheimer et al. 2018b, Barnes et al. 2022), indicating that admixed populations continue to occur along the Gulf Coast, where red wolves were last known to exist prior to their presumed extirpation from the wild. These admixed populations likely represent a unique hybrid population with a substantial number of private alleles that likely encompasses lost genetic ancestry (i.e., ghost alleles) of red-wolf lineages that was lost from the extant red wolf population when the captive-breeding program was initiated (vonHoldt et al. 2022). Additionally, morphological (Mech and Nowak 2010) and genetic (vonHoldt et al. 2021) evidence of admixture was found in north-central Texas, and Heppenheimer et al. (2020) further described persistence of red-wolf ancestry across the southeastern U.S. using a genome-wide survey rather than less informative microsatellite-based methods.

DISTRIBUTION

Hampton (1997) estimated pre-Columbian abundance of gray, eastern, and red wolves in North America at about 400,000 (range = 145,000–850,000), based on estimated population densities of wolves in modern ecological studies. Genetic analyses suggest the pre-Columbian population of wolves may have been 380,000 (range = 290,000–560,000) within Mexico and the conterminous U.S. (Leonard et al. 2005). Although lower than Hampton's (1997) estimate, this genetically based population estimate may be high compared to typical population densities estimated for wolves (Fuller et al. 2003, Cariappa et al. 2011). Leonard et al. (2005)

used 3 years as the generation time for wolves in their estimate, which is less than the generation time of 4.3–4.7 years reported by Mech et al. (2016). The shorter generation time used by Leonard et al. (2005) would likely yield an inflated estimate compared to the actual population size of wolves. Regardless of the actual abundance of wolves in pre-Columbian time, it is apparent that populations were substantially reduced by humans by the mid-1900s, especially throughout most of the conterminous U.S. and southern Canada (Young and Goldman 1944, Pimlott 1961, McCarley 1962, Mech 1970). Wolves compete with humans and consequently there is a long history of persecution of wolves by people (Young and Goldman 1944). Cluff and Murray (1995) reviewed the history of wolf-removal methods in North America. Some of the same conflicts have persisted, but new approaches have replaced some older removal methods, especially those that were considered less humane.

Presently, wolf populations exist in the Canadian provinces and territories of Alberta, British Columbia, Labrador, Manitoba, the Northwest Territories, Nunavut, Ontario, Québec, Saskatchewan, and the Yukon (Fig. 32.6). Population size within each of the 10 Canadian provinces and territories where they occur ranges between 200 and 9,000, with the greatest number of wolves residing in the Northwest Territories and Nunavut combined (Table 32.2). Based on the results of a national survey similar to that used by Hayes and Gunson (1995), the wolf population in Canada was estimated to be 52,000–57,000 in 2018 (B. R. Patterson, unpublished data; H. D. Cluff, Government of the Northwest Territories, unpublished data; Table 32.2). However, assessing population sizes and trends continues to be difficult at the national scale because there is no consistent methodology within and among jurisdictions (Hayes and Gunson 1995).

Wolves (gray and eastern combined) originally occupied all regions of Canada except Prince Edward Island in the east, and Haida Gwaii (formerly Queen Charlotte Islands) in British Columbia (Hayes and Gunson 1995, McCloskey 2011). A general decline in the distribution and abundance of wolves in Canada occurred with increasing human populations and expansion of agricultural land use (Paquet and Carbyn 2003). Wolves were exterminated in the Canadian Atlantic region between 1870 and 1921, and in southern parts of Québec and Ontario from 1850 to 1900 (Paquet and Carbyn 2003, McCloskey 2011). Farther west in the prairies, wolf populations declined with the extirpation of bison during the 1860s and 1870s (Paquet and Carbyn 2003).

Wolf populations recovered somewhat during the 1930s, but then declined to low levels again during the 1950s when wolf-control programs became widespread in Alberta, British Columbia, the Northwest Territories, and the Yukon (Pimlott 1961, Theberge 1973, Paquet and Carbyn 2003). Wolf abundance subsequently increased from Québec through Alberta following cessation of control programs in most areas during the mid-1970s, and concurrent with increases in deer and moose populations (Hayes and Gunson 1995). Wolves in northern Canada continue to be abundant, but their populations are thought to have declined since Hayes and Gunson (1995) published their estimates from 1992, due to recent population declines of barren-ground caribou (*Rangifer tarandus groenlandicus*; Vors and Boyce 2009).

Wolves in eastern Greenland were exterminated during the 1920s by commercial hunting and in northern Greenland, sightings of wolves or their tracks were rare (Marquard-Petersen 2009). Wolves gradually made their way back to eastern Greenland in 1979, and a small population has since become established there (Marquard-Petersen 2009). Recent genetic evidence suggests a distinct polar linkage of wolves between Greenland and Ellesmere Island (Sinding et al. 2018). Muskoxen (*Ovibos moschatus*) are the only primary, year-round prey species for wolves in northern and eastern Greenland, but muskoxen have a low population density and a patchy distribution (Marquard-Petersen 2009). Wolves continue to exist at low population density in Greenland and tend to have an insular and disjunct distribution (Marquard-Petersen 2009, 2011).

In the conterminous U.S., intensive campaigns to eradicate wolves to increase livestock production had reduced wolf populations to less than a few thousand by the early 1900s (Young and Goldman 1944). By 1930, there were no viable populations of gray wolves in the western conterminous U.S. (Mech 1970), but a few isolated populations of Mexican wolves remained in Mexico (Mech 1970), as well as a declining population of red wolves along the Mississippi River Basin and American Gulf Coast (McCarley 1962, Nowak 1967, Paradiso and Nowak 1972). Although wolves remained abundant in Alaska and Canada, by the 1940s, eradication efforts in the conterminous U.S. reduced gray wolf populations to exist only in the Great Lakes region of Michigan, Minnesota, and Wisconsin (Beyer et al. 2009, Erb and DonCarlos 2009, Wydeven et al. 2009). In southeastern U.S., a few red wolves remained in Arkansas, Louisiana, Missouri, Oklahoma, and eastern Texas (Young and Goldman 1944; McCarley 1962; Paradiso and Nowak 1972; Nowak 1967, 1979). Following the extirpation of red wolves from the Gulf Coast, red wolves from a captive-breeding program were reintroduced to northeastern North Carolina in 1987 to begin recovery efforts for the species (USFWS 1989, Hinton et al. 2013; Fig. 32.6). Also, gray wolves from western Canada were reintroduced to YNP and Idaho during 1995–1996 to increase populations and expand distribution in the NRM (Fritts et al. 2020). As of 2022, populations of gray wolves exist in the U.S. in Alaska, Arizona, Colorado, Idaho, Michigan, Minnesota, Montana, New Mexico, Oregon, Washington, Wisconsin, Wyoming, and northern California (Fig. 32.6, Table 32.1).

Population sizes of gray wolves in the U.S. (Table 32.1) are considerably smaller than they are in Canada (Table 32.2), with most wolves in the U.S. located in Alaska (about 7,000–11,000 wolves; Alaska Department of Fish and Game 2019), the Great Lakes region (about 4,400 wolves; Erb and Humpal 2020, Wiedenhoeft et al. 2020, Michigan Department of Natural Resources 2022a), and the NRM (about 2,700 wolves; Idaho Department of Fish and Game 2021; Oregon Department of Fish and Wildlife 2021; Washington Department of Fish and Wildlife et al. 2021; Wyoming Game and Fish Department et al. 2021; Parks et al. 2022). Gray wolves began naturally recolonizing the Pacific Northwest through dispersal and it is estimated that about 73 wolves outside of the NRM currently inhabit the region (Oregon

Department of Fish and Wildlife 2019, California Department of Fish and Wildlife 2020, Washington Department of Fish and Wildlife 2019). The respective state fish and wildlife agencies in Idaho and Montana recently transitioned from minimum counts of wolves to statistically based population estimates designed to more accurately reflect true abundance and population trends.

By the late 1920s, the resident population of Mexican wolves was extirpated from the U.S., but individuals from Mexico occasionally dispersed into the U.S. and were killed through the mid-1970s; within a decade, there were no Mexican wolves in the wild and they were presumed extinct (Brown 1983). Between 1970 and 1980, 5 wild Mexican wolves were captured in Arizona and Mexico, which with the few individuals already in captivity, resulted in 7 Mexican wolves as founders in the captive-breeding program (Hedrick et al. 1997). In 1998, 11 captive-raised Mexican wolves were the first of many to be released into east-central Arizona, followed by releases in Mexico in 2011. As of February 2023, there was a minimum of 241 Mexican wolves in reintroduced populations in Arizona and New Mexico (J. R. Heffelfinger, Arizona Game and Fish Department, unpublished data), which is classified as a nonessential experimental population (USFWS 2019). In Mexico, approximately 40–45 wolves live in the wild (C. Lopez-Gonzales, Universidad Autonoma de Queretaro, personal communication). Captive facilities in Mexico and the U.S. have a combined 366 wolves in 57 institutions (23 in Mexico, 34 in the U.S.) as of July 2022.

Presently, the reintroduced population of red wolves is restricted to the Albemarle Peninsula of northeastern North Carolina (Hinton et al. 2013). Prior to European settlement, red wolves or their ancestors were common in the eastern U.S. and inhabited an area from the Atlantic Coast west to central Texas, and from the Ohio River Valley, northern Pennsylvania, and southern New York south to the Gulf of Mexico (Nowak 2002, Hinton et al. 2013). Native to the eastern U.S., the historic distribution of red wolves did not overlap with gray wolves or coyotes, as gray wolves were not known to have historically occurred in the eastern U.S. and, until the twentieth century, coyotes were absent from the region for nearly 15,000 years (Nowak 1979, 2002). However, coyotes currently occupy the entire historic range of the red wolf (Nowak 2002). As discussed in more detail earlier in this chapter, a small population of reintroduced red wolves occurs in northeastern North Carolina, where human-caused mortality and hybridization continue to hinder recovery efforts (USFWS 1989; Hinton et al. 2013, 2017a, 2017b; Bohling and Waits 2015).

LIFE HISTORY

Reproduction

Wolves typically spend most of their lives living in packs that generally include an adult breeding pair, pups of the year, and offspring from previous years, but also sometimes unrelated adult wolves (Mech and Boitani 2003, Stenglein et al. 2011, Stahler et al. 2013). Pack sizes can range from 2 to 42 individuals during winter, although 4 to 10 is more common (Fuller et al. 2003). Traditionally, the adult breeding pair was referred to as alphas,

but more recently are simply called the breeding pair or dominant pair (Mech 1999). Small pack sizes typically include only a single breeding pair, but some larger packs may include 2 or 3 breeding females (Murie 1944, Harrington and Mech 1982a, Mech et al. 1998, Paquet and Carbyn 2003, Stahler et al. 2013, Ausband 2018). Breeding generally occurs from late January through March, with later dates farther north (Mech 1970, 2002; Paquet and Carbyn 2003). Both male and female gray wolves may first breed at 22 months of age (Rausch 1967, Stahler et al. 2013); breeding at <22 months of age occurs rarely (Rausch 1967, Medjo and Mech 1976, Fuller et al. 2003), and for some female wolves, primiparity (first breeding) may be as late as 7 years of age (Mech et al. 2016). Mean age of primiparity for female gray wolves was 2.7 years in YNP (Stahler et al. 2013), and 3.0 years in Minnesota (Mech et al. 2016). Median age of first reproduction for gray wolves in Scandinavia was 3 years for females and 2 years for males, but ranged from 1 year to 8–10 years for both sexes (Wikenros et al. 2021). As with gray wolves, red wolves (Sparkman et al. 2010) and eastern wolves typically do not breed until at least their second year.

All female wolves (eastern, gray, and red) are monoestrous, with the cycle typically lasting about 1 week, but ≤ 15 days has been recorded in captivity (Packard 2003). Unlike domestic dogs that can breed year-round, spermatogenesis levels that support breeding of male wolves occur primarily from December through March, and decline thereafter (Asa 1997, Kreeger 2003). Pups are born after a gestation period of about 62–63 days (Mech 1970, Paquet and Carbyn 2003). Mean dates of parturition include early to mid-April in the southwestern U.S. (J. P. Greer, Arizona Game and Fish Department, personal communication), NRM of the U.S. (Stahler et al. 2013; D. K. Boyd, University of Montana, unpublished data), and the Great Lakes states and provinces (Fuller 1989, Mills et al. 2008), then shifting later to May in most of Alaska and mainland Canada (Mech 2002, McNay et al. 2006), late May in the Northwest Territories (Mech 2002), and early June in the Canadian High Arctic (Mech 1995a). Median date of denning ($n = 388$ wolves) was 4 May across Alaska and Canada between 51° and 68° latitude, which seems to be occurring earlier with climate change (Mahoney et al. 2020).

Wolves have 3 primary activity periods throughout the year, including denning period in spring (Mar–Jun), rendezvous period in late spring to early fall (May–Oct), and nomadic period in fall and winter (Oct–Mar). The start of each period varies somewhat based on latitude, where initiation is later as latitude increases (Mech 1970, Paquet and Carbyn 2003, Anderson et al. 2016, Mahoney et al. 2020). During the denning and rendezvous periods, wolves occupy specific home sites where pups remain, and adults and yearlings often forage by themselves or in small groups (Barber-Meyer and Mech 2015) and return to the home site with food for the pups and breeding female. The breeding female generally remains near the den during the denning period, but may join others to hunt during the rendezvous period. By late September or early October, the pups are generally large enough to travel, and the pack becomes nomadic in their territory, traveling as a group, and no longer consistently occupies the home site.

Dens are typically burrows dug into the ground by wolves, sometimes by enlarging burrows from other mammals, but wolves also use abandoned lodges and dams constructed by North American beavers (*Castor canadensis*), natural caves and crevices, hollow logs or downed tree trunks, snow excavations, beds at the base of trees, or shallow surface beds (Murie 1944, Peterson 1977, Ballard and Dau 1983, Carbyn 1987, Ballard et al. 1997, Paquet and Carbyn 2003, Unger et al. 2009; Fig. 32.8). Wolves in the NRM of the U.S. typically dig a den on a slope during April (Matteson 1992, Trapp 2004, Stahler et al. 2013). The breeding female begins excavating the den 4–5 weeks before whelping, but exploratory digging may also occur during the previous fall (Thiel et al. 1997, Paquet and Carbyn 2003). Burrows typically have entrance holes 33–51 cm (13–20 in) in height, 38–64 cm (15–25 in) wide and extend 1.7–5.5 m (5.5–18.0 ft) underground (Ballard and Dau 1983, Fuller 1989, Thiel et al. 1997, Trapp et al. 2008), and sometimes as much as 14 m (46 ft) underground (Mech 1970).

Dens are typically located near the center of pack territories, where pups are less susceptible to being killed by adjacent packs (Ballard and Dau 1983, Ciucci and Mech 1992, Packard 2003, Theuerkauf et al. 2003, Unger et al. 2009, Joly et al. 2018). In northern Wisconsin and eastern Minnesota, where road densities are relatively high, dens are on average 1.6 km (1.0 mi) from roads (Unger et al. 2009). Avoidance of roads also occurred for eastern wolves in APP in Ontario (Benson et al. 2015a). In Arctic regions of Canada, wolf dens are generally located on eskers, where digging is easier on well-drained sand and gravel (McLoughlin et al. 2004, Klaczek et al. 2015). In a meta-analysis of 26 study areas of den and rendezvous sites in Eurasia and North America, home sites were in areas of forest and scrubland, and wolves avoided agricultural areas and human structures (Sazatornil et al. 2016). However, wolves are adaptable, and with adequate protection, may use agricultural areas and areas with higher levels of human

activities during the denning season (Thiel et al. 1998, Merrill 2000, Heilhecker et al. 2007). The breeding female is almost continuously with the pups for the first 25–26 days (Ballard et al. 1991), staying in the den for the first 8 days (Joly et al. 2018). Pups start emerging from the den at about 3 weeks of age (Mech 1970, Ballard et al. 1987, Packard 2003, Stahler et al. 2013). Pups normally remain at dens for the first 8 weeks, until they are weaned and then may be moved to rendezvous sites (Packard 2003).

Red wolves in northeastern North Carolina use areas of large agricultural fields with low densities of both human population and roads (Dellinger et al. 2013, Hinton et al. 2016, Karlin et al. 2016). Red wolves typically den near forested areas, then use agricultural fields for rendezvous sites because dense understories of forests in the southeastern U.S. can inhibit movements and visual detection of potential threats (Hinton and Chamberlain 2010, Hinton et al. 2016). Prior to European colonization, the historical range of red wolves included areas of widespread use of fire and agriculture by Native Americans throughout the southeastern U.S. (Abrams and Nowacki 2008; Anderson et al. 2010, 2015). Therefore, it is not surprising that red wolves respond positively to agricultural land cover; however, red wolves will establish rendezvous sites in native vegetation when such cover is abundant (Mauney 2005). Red wolves that do not excavate a den may whelp in a daybed and then rotate pups among several daybeds until pups are mobile (J. W. Hinton, Wolf Conservation Center, unpublished data). If they do use a den, red wolves abandon the den after a few weeks and then use daybeds.

Traditionally, litter size was determined by counts of corpora albicantia in ovaries, counts of placental scars, or counts of fetuses in dead female wolves (Rausch 1967). More recent studies have relied more on counts of pups at den sites (Mech et al. 1998, Mills et al. 2008, Stahler et al. 2013, Hinton et al. 2017a). The corpora albicantia represents ovulation from the previous pregnancy, but not all will implant and result in a fetus or a placental scar after parturition (Rausch 1967). Thus, there is a slight decline from counts of corpora albicantia to placental scars and fetuses, and to pups observed near dens. Pups start emerging from dens at 3 weeks of age (Packard 2003), and therefore some mortality from birth to den emergence may not be included in counts of pups at the den.

Litter sizes of gray wolves average 4.4–6.9 pups/female across North America (Fuller et al. 2003), with some local variation across their distribution (Ream et al. 1991, Pletscher et al. 1997, Mech et al. 1998, McNay et al. 2006, Stahler et al. 2013). Average litter sizes are lowest in Greenland at 2.0 pups/litter (Marquard-Petersen 2008). A study in Alaska included the use of ultrasound to estimate a mean of 5.1 fetuses/pregnant female ($n = 49$), and a mean of 5.6 placental scars/post-parturient female ($n = 29$), based on harvested wolves (McNay et al. 2006). Litter size in YNP was affected by age and body mass of females, number of adults in the pack, population density, and disease (Stahler et al. 2013). In YNP, the litter size was consistent for females 2–4 years old, but declined for older females; litter size increased with increasing pack size up to 8 wolves, but declined thereafter; and overall litter size declined with increasing population size of wolves (Stahler et al. 2013).



Fig. 32.8. Wolves (*Canis* spp.) typically utilize underground dens during spring months, including this den located at the base of a tree, Ontario, Canada. Image courtesy of B. Patterson, Ontario Ministry of Natural Resources and Forestry, Canada.

Although female wolves as old as 12 years have produced pups (Holyan et al. 2005), no wolves >9 years old in YNP were confirmed to have whelped (Stahler et al. 2013). Fuller et al. (2003) reported that a six-fold increase in ungulate biomass explained a 31% increase in litter size across 23 studies, and that litter size increased when wolf populations were killed at relatively high rates. Substantial increases in ungulate biomass can result in slightly larger litters, whereby a more productive food base apparently resulted in female wolves carrying larger litter sizes to birth (Fuller et al. 2003). However, Adams et al. (2008) found that litter size does not always increase with an apparent increase in food availability, but rather pup survival may increase, and more females breed, resulting in more pups overall.

Mean litter sizes of Mexican wolves in the den, with pups at 1–6 weeks old, was 4.7 pups/litter, and ranged from 1 to 7 pups (USFWS 2017a). In Ontario, litter size of eastern wolves at den sites with pups 4–8 weeks old averaged 4.6 pups ($n = 10$ litters; Mills et al. 2008). Litters of red wolves in North Carolina averaged 4.2 pups ($n = 126$ litters) during 2001–2013 (Bohling and Waits 2015). The sex ratio of litters of pups seem to be male-biased in some wolf populations (Mech 1975, Sidorovich et al. 2007, Ausband 2022a).

After pups are 6–10 weeks old and are weaned, the pack typically moves pups to a rendezvous site (Packard et al. 1992), but some packs remain at the den during the rendezvous period. Red wolves may move pups to rendezvous sites as early as 4–6 weeks of age (Hinton and Chamberlain 2010). Areas used as dens or rendezvous sites are sometimes used repeatedly over many years (Joslin 1967, Fuller 1989, Unger et al. 2009). When foraging, the pack will typically leave relatively immobile pups at rendezvous sites with an adult who can alert them to danger, a behavior known as pup-guarding (Ruprecht et al. 2012, Ausband et al. 2016).

Pups have been kept at ≤ 10 different rendezvous sites from mid-May through the end of September (Carbyn 1975, Argue et al. 2008) or early October in middle latitudes, but some rendezvous sites are used as late as November (Joslin 1967; Peterson 1977; Harrington and Mech 1982a, 1982b; Fuller 1989; Heilhecker et al. 2007). In the NRM region of the U.S., packs of gray wolves occupied an average of 3.8 sites (both den and rendezvous sites) and moved their pups on average 2.8 times during the pup-rearing period (Ausband et al. 2016). Age of pups was a factor that determined whether Arctic wolves relocated their home site in response to disturbance by humans (Frame et al. 2007). Joslin (1967) first described rendezvous sites for eastern wolves in APP, which were generally grass-sedge areas at forest edge near bogs. Further research has revealed that eastern wolves selected both wetlands and conifer forests for rendezvous sites (Benson et al. 2015a). Rendezvous sites in Minnesota and Wisconsin were associated with aspen (*Populus* spp.), which is preferred by deer and beaver, and near wetlands (Unger et al. 2009). Presence of wet meadows seemed to be a common habitat feature for rendezvous sites (Carbyn 1975, Ausband et al. 2010, Benson et al. 2015b). The availability of prey and proximity to water are apparently critical to pup survival at den and rendezvous sites regardless of the geographic region.

By fall, pups approach adult size and become relatively mobile, so the pack discontinues use of rendezvous sites and becomes more nomadic within their territory (Mech and Boitani 2003). From fall to the next spring denning period, the pack generally travels as a unit throughout their territory, splitting up for short periods, especially during the breeding season (Mech and Boitani 2003, Barber-Meyer and Mech 2015, Benson and Patterson 2015).

Mortality

Throughout much of the distribution of wolves in North America, human-caused mortality is the most important mortality factor affecting wolf populations (Boyd and Pletscher 1999, Fuller et al. 2003, Sparkman et al. 2011, Benson et al. 2014, Hinton et al. 2017a, Hill et al. 2022). Mortality affecting neonatal wolves is less known (Fuller 2003), although knowledge on pup mortality has increased in recent years (Brainerd et al. 2008, Mills et al. 2008, Benson et al. 2013, Stahler et al. 2013, Hinton et al. 2017a). Wolves living in large, protected areas are more affected by natural sources of mortality, especially intraspecific strife, including in Denali National Park in Alaska (Mech et al. 1998), Superior National Forest in Minnesota (Mech and Barber-Meyer 2017), YNP (Cubaynes et al. 2014, Smith et al. 2015), APP (Benson et al. 2014), and Isle Royale National Park (IRNP) in Michigan (Peterson et al. 1998). Infanticide at dens was reported in northeastern Alberta (Latham and Boutin 2011), APP (Benson et al. 2013), and YNP (Smith et al. 2015), during which wolves may also kill other adults near the den.

Human-caused mortalities include legal harvest, depredation-control actions, illegal kill, vehicle and train collisions, and other accidents (Fuller et al. 2003, Paquet and Carbyn 2003, Hill et al. 2022). Wolf-control programs and legal harvest adjacent to protected areas can impact wolf populations in these protected areas (Brainerd et al. 2008, Benson et al. 2014, Borg et al. 2016, Schmidt et al. 2017, Cassidy et al. 2023). Natural mortality factors include accidents, diseases, injuries from predation attempts, intra- and interspecific strife, and starvation (Nelson and Mech 1985, Boyd and Pletscher 1999, Fuller et al. 2003, Paquet and Carbyn 2003, Wydeven et al. 2003). Diseases known to have killed wolves include blastomycosis (Thiel et al. 1987, Krizan 2000), canine distemper (Carbyn 1982, Almberg et al. 2009, Justice-Allen and Clement 2019), canine parvovirus (Johnson et al. 1994, Mech et al. 1997), rabies (Theberge et al. 1994, Ballard et al. 1997), sarcoptic mange (Wydeven et al. 2003, Jimenez et al. 2010), and tuberculosis (Carbyn 1982). Predators that have killed wolves include black bears (*Ursus americanus*; Joslin 1967, Mills et al. 2008), brown bears (*Ursus arctos*; Ballard et al. 2003, Jimenez et al. 2008), and mountain lions (*Puma concolor*; Jimenez et al. 2008).

Nineteen publications reviewed by Fuller et al. (2003) included annual mortality rates ranging from 15% to 68%, with rates >30–35% generally associated with a declining population of wolves. Fuller et al. (2003) determined on average that a level of 22% human-caused mortality would stabilize wolf populations. Adams et al. (2008) updated this analysis to include 25 studies and 41 estimates of mortality rates, and determined that the pattern was a curvilinear relationship, and that human-caused mortality

could be $\leq 29\%$ annually before wolf populations decline. Creel and Rotella (2010) suggested the maximum level of human-caused harvest may be as low as 22% because of the additive effect of harvest, but their findings were challenged by Gude et al. (2012) on the grounds of missing data and failure to consider recruitment. Among recovered populations of wolves, average annual mortality rates were similar with relatively low levels, including 24% in Wisconsin (Stenglein et al. 2018), 25% in Michigan (O'Neil et al. 2017), and 25% in NRM in the U.S. (Smith et al. 2010), but mortality varied spatiotemporally across these regions (Smith et al. 2010, O'Neil et al. 2017, Stenglein et al. 2018).

Annual mortality rate was 20% in Montana and adjoining Alberta and British Columbia (Pletscher et al. 1997), and 25% in Alberta, British Columbia, Idaho, Montana, and Wyoming from 1982 to 2004 (Smith et al. 2010), prior to federal delisting in the U.S. and implementation of legal harvest. Mortality rates of wolves in harvested populations and populations controlled for livestock depredation in Montana during 2012–2021 ranged from 26% to 43% of the wolf population (Inman et al. 2020, Parks et al. 2022). Mortality rates were lowest for gray wolves in protected areas, such as YNP (20%; Cubaynes et al. 2014), and for eastern wolves in APP (15%; Benson et al. 2014), but even in core habitat of less-protected areas in Wisconsin, annual mortality was as low as 18–22% (Stenglein et al. 2018). Telemetry-based data and counts of pups at dens collected during 2009–2014 from the wild population of Mexican wolves in the U.S. indicated mortality rates of 28% for pups (0–1 yr), 32% for subadults (1–2 yr), and 19% for adults (≥ 2 yr; USFWS 2017b). For eastern wolves, overall mortality rates were relatively high (61%) outside of protected areas, whereas mortality rates of coyotes (33%) and coyote-wolf hybrids (44%) were much lower (Benson et al. 2014). Mortality rates may be high for red wolves in North Carolina, where average annual mortality for 2–4-year-old wolves was 64%, a level that requires high survival of pups and occasional population augmentation for population persistence (Hinton et al. 2017a).

Mortality rates of adult gray wolves generally were $< 30\%$ in both protected and harvested populations, unless killed at relatively high rates, but mortality rates of pups varied substantially. In Wisconsin, indirect measures of pup survival from birth to end of winter resulted in an estimated annual mortality of about 70% (Wydeven et al. 2009). In APP, eastern wolf pups 3–8 weeks old were captured near dens and monitored to the end of the year using implanted radio-transmitters (Fig. 32.9); their estimated annual mortality rate was 25% in eastern portions of APP and 75% in western portions of APP (Benson et al. 2013).

In YNP, pups observed at dens and into fall had average mortality rates of 35% (Stahler et al. 2013). In the NRM, annual mortality of pups estimated from fall to spring was high in northwestern Montana (60%), but low in Greater Yellowstone (24%) and central Idaho (11%; Smith et al. 2010). Average mortality of pups during summer averaged 34% across 9 studies (Fuller et al. 2003). Ungulate biomass was positively correlated with higher survival rates for gray wolf pups (Fuller et al. 2003), and high abundance of beavers was associated with high survival rates for eastern wolf pups (Benson et al. 2013). Diseases such as



Fig. 32.9. Eastern wolf (*Canis lycaon*) pups had transmitters surgically implanted to assess their survival rates, Algonquin Provincial Park, Ontario, Canada. Image courtesy of K. Mills, Wyoming Game and Fish Department, USA.

canine parvovirus, canine distemper virus, and sarcoptic mange can have major impacts on mortality rates of pups (Mech and Goyal 1993; Wydeven et al. 1995; Almberg et al. 2009, 2010, 2015; see section on Diseases and Parasites).

ECOLOGY

Habitat

Wolves are habitat generalists and existed across diverse landscapes in the northern hemisphere in areas that had adequate prey (Mech 1970). In North America, wolves (gray, eastern, and red) historically occupied nearly all areas from 75° N to 15° N latitude, with the gray wolf occupying the greatest amount of area (Nowak 1979, 2002, 2003). Despite the contraction of their range due to persecution by humans, wolves still occupy most major ecosystems from the High Arctic to dense forests, open steppe, and deserts (Fig. 32.6). Habitat assessments have been useful for determining potential locations, direction of recolonization, and persistence of wolf packs on the landscape (Mladenoff et al. 1995, 1997, 2009; Boyd-Heger 1997; Mladenoff and Sickley 1998; Carroll 2003; Carroll et al. 2003a, 2006, 2014; Ratti et al. 2004; Potvin et al. 2005; Larsen and Ripple 2006; Oakleaf et al. 2006; Oregon Department of Fish and Wildlife 2015; Hinton et al. 2016; Karlin et al. 2016; Smith et al. 2016; Martinez-Meyer et al. 2017; O'Neil et al. 2019; van den Bosch et al. 2022).

Habitat selection by wolves is a hierarchical process in which wolf populations respond to limiting factors, such as prey availability and human presence (Fuller et al. 2003, McLoughlin et al. 2004, McPhee et al. 2012, Benson et al. 2015b). At the regional scale, the distribution and persistence of wolf territories may be characterized by several primary predictors, such as forest cover (Mladenoff et al. 1995, 1999; Oakleaf et al. 2006), prey availability (Oakleaf et al. 2006; Lesmerises et al. 2012; Kittle et al. 2017; O'Neil et al. 2019, 2020), density of streams (O'Neil et al. 2019), area of public lands (Mladenoff et al. 1995, 1999, 2009;

O'Neil 2019; van den Bosch et al. 2022), area of agricultural land (Mladenoff et al. 2009, Gantchoff et al. 2022, van den Bosch et al. 2022), and densities of roads (Thiel 1985; Mladenoff et al. 1995, 1999; Carroll et al. 2003b; Zimmermann et al. 2014). At smaller spatial scales (e.g., within territories), however, habitat selection by wolves commonly reflects their responses to local conditions in prey availability, vegetation complexity, and topography that improve encounter rates with prey, ease of movements, and pup rearing (Whittington et al. 2005, Kauffman et al. 2007, Ausband et al. 2010, Latham et al. 2011, Benson et al. 2015b, Sazatornil et al. 2016, Kittle et al. 2017).

The gray wolf has the broadest geographic distribution among North American wolves, and therefore exhibits the greatest amount of variability in habitat use. For example, wolves in the tundra exhibit distinct migratory patterns associated with the movements of caribou, their primary prey, but wolves pause their movements to den along glaciofluvial landscape features known as eskers (Walton et al. 2001, McLoughlin et al. 2004). Elsewhere, wolves are predominately nonmigratory and usually restrict their foraging patterns within defended territories (Mech 1973, Fuller 1989, Geffen et al. 1996, Benson and Patterson 2013, Kittle et al. 2015, Hinton et al. 2016).

Territoriality entails wolves routinely visiting areas and using spatial features and topography that improve their ability to detect, encounter, and capture prey, as well as selecting den and rendezvous sites for pup rearing. Because human-caused mortality is the primary limiting factor affecting persistence of gray wolves in most regions, long-term persistence of territories may require low densities of both roads and human populations (Thiel 1985; Mech 1989; Mladenoff et al. 1995, 1999; Oakleaf et al. 2006; Sazatornil et al. 2016; Martinez-Meyer et al. 2017). During early stages of recolonization, wolf populations will most likely persist if population densities of prey are sufficient and road densities remain $<0.6 \text{ km}/1.0 \text{ km}^2$ ($0.97 \text{ mi}/1.0 \text{ mi}^2$; Thiel 1985, Mech 1989, Fuller et al. 1992, Mladenoff et al. 1995, Wydeven et al. 2001, Oakleaf et al. 2006).

As wolf populations reach ecological carrying capacity in an area, wolf packs will tolerate higher densities of roads, but occupy primarily wildlands with limited agricultural land use (Merrill 2000, Mladenoff et al. 2009). In recovering populations, wolves seem to initially occupy the most suitable habitat preemptively in a density-dependent fashion and occupy less suitable habitat as population density increases (O'Neil et al. 2020). Road densities have little influence on wolf persistence in the northernmost landscapes of their range, which contain low densities of both human populations and roads, which therefore facilitates increased travel rates and predator efficiency for wolves (Kittle et al. 2017; Dickie et al. 2017; Newton et al. 2017; Kautz et al. 2021; L. G. Adams, Alaska Department of Fish and Game, personal communication).

Wolves in the High Arctic may have little, if any, contact with people and may closely approach or follow people when encounters occur. This apparent curiosity with people is atypical of wolves in lower latitudes and may lead to misinterpretations of bold behavior and perceptions of conflict risk. Marquard-Petersen (2022) cautioned that this behavior, coupled with potential

increased human access to areas within the range of Arctic wolves, could adversely affect the conservation of these small populations of wolves.

Restricted to APP and its surrounding areas in Ontario, eastern wolves inhabit the transitional zone between northern boreal forests and the Great Lakes-St. Lawrence lowlands (Rutledge et al. 2010a, Benson et al. 2012, COSEWIC 2015). Most territories of eastern wolves persist on protected lands within APP, indicating road density and human activities are the primary factors that limit occurrence of wolves across the region (Rutledge et al. 2011; Benson et al. 2012, 2014, 2015b). Eastern wolves establish territories in areas that maximize predation success and at greater distances from anthropogenic land uses, presumably to minimize disturbance and mortality risks (Benson et al. 2012, 2014, 2015b). Within home ranges, patterns of habitat selection by eastern wolves correspond to factors such as prey availability and access to water, which improve reproductive success. Although eastern wolves prey primarily on moose and white-tailed deer (Pimlott et al. 1969, Theberge and Theberge 2004, Benson et al. 2017), deer abundance varies enough that maintaining home sites near wetlands provides wolves with access to beavers as an alternative food resource and decreases the probability of starvation of pups during summer months (Benson et al. 2015a).

Once found throughout most of the temperate forests of the eastern U.S., the current distribution of the red wolf is restricted to the Albemarle Peninsula of eastern North Carolina, the only current location of reintroduction (Nowak 2002, Stoskopf et al. 2005, Hinton et al. 2013). This region is a mosaic of large tracts of agricultural land, managed plantations of loblolly pine (*Pinus taeda*), coastal bottomland forests, and pocosin (peatlands with a low and dense evergreen shrub layer), wherein wolves establish territories along the edges of agricultural fields and forested areas (Dellinger et al. 2013, Hinton et al. 2016, Karlin et al. 2016). The persistence of red wolves is limited by anthropogenic mortality (Sparkman et al. 2010, Hinton et al. 2017a), but wolves are incapable of avoiding landscapes extensively altered by humans (Dellinger et al. 2013).

Red wolves exhibit strong preferences for privately owned, unprotected lands that are intensively managed for crops (e.g., corn, winter wheat) and commonly use road networks for traveling because of the highly fragmented habitat on the peninsula (Dellinger et al. 2013, Hinton et al. 2016). Den and rendezvous sites are commonly established within or proximate to agricultural fields and managed plantations of loblolly pine with well-drained soils (Beck et al. 2009, Hinton and Chamberlain 2010). Although this may seem counter to the general consensus among studies that wolves cannot persist in areas with high densities of roads and intensive anthropogenic uses (Thiel 1985; Mladenoff et al. 1995, 2009; Wydeven et al. 2001; Oakleaf et al. 2006; but see Chavez and Gese 2006), territories of red wolves were generally located farther from roads and proximate to conifer and wetland (e.g., pocosin) cover types than adjacent unused areas, a selection pattern observed in some populations of both eastern (Norris et al. 2002; Benson et al. 2014, 2015b) and gray (Mladenoff et al. 1995, Ausband et al. 2010) wolves.

Potential habitat for additional recolonization by or recovery of wolves continues to exist across portions of the U.S., including the Appalachians and northeastern U.S. (Harrison and Chaplin 1998, Mladenoff and Sickley 1998, Wydeven et al. 1998, Carroll 2003, van den Bosch et al. 2022), southern Rockies (Carroll et al. 2006), Pacific Coast (Larson and Ripple 2006, Oregon Department of Fish and Wildlife 2015), and possibly the Great Plains (Smith et al. 2016, van den Bosch et al. 2022). Smith et al. (2016) and van den Bosch et al. (2022) suggested potential for recolonization of wolves into the Great Plains of the U.S., but they relied extensively on levels of human population density for assessing potential habitat. Despite extensive dispersal into North Dakota and South Dakota (Licht and Fritts 1994), short-term persistence was observed only in the forested Turtle Mountains of north-central North Dakota (Licht and Huffman 1996). In the western Great Lakes region, suitable habitat for wolves seems to be nearly fully occupied (Mladenoff et al. 2009, Gantchoff et al. 2022), except a portion of Lower Peninsula of Michigan that has yet to be colonized by wolf packs (Stricker et al. 2019). Although the northeastern U.S. and Appalachian Chain may have potential for population expansion of wolves, it is currently unclear whether the area was historically occupied by eastern wolves, gray wolves, red wolves, or some combination of these (Nowak 2003, 2009; Chambers et al. 2012), and the ability of wolves from source populations to disperse into this region seems to be limited (Wydeven et al. 1998, van den Bosch et al. 2022).

Population Dynamics

Investigations of population dynamics of wolves involve quantitative descriptions of spatial and temporal changes in population sizes, and the factors and processes associated with these changes. The dynamics of wolf populations are driven primarily by prey availability, population density of wolves, and level of killing by humans (Keith 1983, Fuller et al. 2003, Paquet and Carbyn 2003). The potential for wolves to inhabit an area is influenced by prey densities, which are known to limit the size and distribution of wolf populations (Keith 1983, Fuller et al. 2003). Population densities of wolves, supported by sufficient prey populations, facilitate metapopulations wherein subpopulations are connected and maintained by dispersing wolves from adjacent populations (Gese and Mech 1991, Mech et al. 1995, Oakleaf et al. 2006, vonHoldt et al. 2010, Hinton et al. 2016, Jimenez et al. 2017, Martinez-Meyer et al. 2017).

Because packs are the reproductive units in a wolf population and territoriality can negatively affect the per capita birth or survival rates of wolves as population sizes increase, several authors have suggested wolf populations may be intrinsically regulated through intraspecific competition and spatial heterogeneity (Murie 1944, Pimlott 1967, Mech 1970, Van Ballenberghe et al. 1975, Cariappa et al. 2011, Cubaynes et al. 2014, Cassidy et al. 2015, Smith et al. 2020). Others, however, have argued that wolf populations are regulated by abundance of ungulate prey and that territoriality helps stabilize population dynamics by closely linking the feedback loop to population densities of local prey (Packard and Mech 1980, Keith 1983, Fuller 1989, Fuller et al. 2003, McRoberts and Mech

2014, Mech and Barber-Meyer 2015). Finally, anthropogenic factors result in direct or indirect mortality of wolves. These mortalities influence the distribution and abundance of wolves and are often influenced by government policy and may decrease population abundance regardless of ungulate abundance (Linnell et al. 2001, Laliberte and Ripple 2004, Ripple et al. 2014, Schmidt et al. 2017, Hill et al. 2022).

Throughout North America, population densities of gray wolves are typically <50 wolves/1,000 km² (range = 3–54 [129 wolves/1,000 mi²]), and densities are correlated with amount of ungulate biomass/wolf (Keith 1983, Fuller and Murray 1998, Fuller et al. 2003, McRoberts and Mech 2014, Mech and Barber-Meyer 2015). Population densities increase with increasing amount of ungulate biomass because food increases reproduction and survival rates for wolves, but population densities of wolves can also change with increased vulnerability of prey (e.g., severe winters) when prey densities remain unchanged (Adams et al. 2008). Nevertheless, as abundance of gray wolves increases in an area, increasing population density may begin to negatively affect the per capita growth rate of the wolf population.

When reproduction and survival rates decline with increasing population densities (Van Ballenberghe et al. 1975, Cariappa et al. 2011, Cubaynes et al. 2014, Cassidy et al. 2015, Stenglein et al. 2018), dispersal rates may increase, as younger individuals will leave natal areas in search of new territories when population densities are high (Gese and Mech 1991, Mech et al. 1998, Webb et al. 2011). Other studies, however, have found that high population density decreased dispersal rates, presumably because philopatry is favored over dispersing into risky, saturated habitat (Jimenez et al. 2017, Sells et al. 2022a). A review by Morales-Gonzalez et al. (2022) showed a non-linear relationship between dispersal rate and population density of wolves, with dispersal rates higher at both low and high population densities. Dispersal has facilitated recolonization by gray wolves in several regions, such as the Great Lakes, NRM, and Pacific Northwest regions of the U.S. (Wydeven et al. 1998, Boyd and Pletscher 1999, Treves et al. 2009, Jimenez et al. 2017). Interestingly, dispersal may allow gray wolves to increase population size through geographic expansion without changing population densities in core population areas via metapopulation dynamics (Hanski and Gilpin 1991, Hanski 1998). Therefore, areas of high population density (e.g., source populations) likely play a crucial role in the maintenance of populations that are harvested at relatively high rates by humans or in low-quality habitat, as well as in the establishment of new populations.

With adequate levels of prey biomass, abundance, and population densities, the distribution of gray wolves may be influenced primarily by human behaviors that result in the direct or indirect killing of wolves (Linnell et al. 2001, Fuller et al. 2003, Creel and Rotella 2010, Gude et al. 2012). There is growing interest in understanding how gray wolf populations respond to various levels of human-caused mortality (Murray et al. 2010, Gude et al. 2012, Stenglein et al., 2018, Liberg et al. 2020, Hill et al. 2022). Murray et al. (2010) investigated whether anthropogenic mortality was additive for 3 populations of gray wolves in the NRM; they found that 80% of wolves with known

fates were killed either directly or indirectly by humans. Further, Murray et al. (2010) reported additive effects of human-caused mortality on wolf populations in northwestern Montana, but not in populations in Idaho and YNP. They attributed this to the risk of anthropogenic mortality being lower for wolves in Idaho and YNP than for wolves in Montana. Their models indicated that increasing population density of wolves promoted greater risks of anthropogenic mortality, which suggests demographic responses of wolves were compensatory at low population densities, but became additive as wolf populations increased.

Wolf populations can fluctuate widely within a given year, so the time of year selected for surveying wolf populations is important for management purposes. For example, population abundance is at the lowest annual level during late winter, and abundance substantially increases during spring. To illustrate, assume that the population consists of 180 packs, 10% of the population are lone wolves and 90% are pack members, mean pack size is 5 wolves, mean litter size at birth is 5 pups (Fuller et al. 2003), and 85% of packs produce pups (Mech et al. 1998). These values would result in a population of 1,765 wolves during early spring if the population during the previous late winter was 1,000 wolves. Thus, there is a considerable difference between the lowest and highest population levels within the annual cycle. By fall, the population normally would consist of 30–50% pups, but in declining populations that experience relatively high levels of harvest, the population may consist of >60% pups (Fuller et al. 2003, Adams et al. 2008).

The population size of eastern wolves in Ontario is estimated to be <1,000 wolves (COSSARO 2016). The population density of eastern wolves in APP has remained at approximately 30 wolves/1,000 km² (78 wolves/1,000 mi²) with about 230 wolves within park boundaries (Rutledge et al. 2010b, COSEWIC 2015). Although eastern wolves tend to occur in areas with relatively high population densities of ungulates, human-caused mortality has generally spatially limited the population to APP and surrounding areas (Rutledge et al. 2010a; Benson et al. 2012, 2014). Prior to 2001, 56–66% of the total mortality of eastern wolves in APP was attributed to human causes, such as hunting and trapping of wolves that moved outside of APP boundaries (Rutledge et al. 2010b; Benson et al. 2012, 2014; COSEWIC 2015). However, a ban introduced in 2001 to prevent the harvest of wolves in a 6,340-km² (2,448 mi²) area surrounding APP decreased harvest-related mortality from 67% to 16% (Rutledge et al. 2010b, COSEWIC 2015). This reduction in harvest-related mortality was associated with a comparable increase in natural mortality rates, but overall abundance stabilized at least through 2010 (Benson et al. 2014).

More recently, decreased abundance of prey and reduced compliance with the harvest ban have contributed to increased mortality rates and a subsequent decrease in both pack sizes and population abundance, particularly in eastern APP (B. R. Patterson, unpublished data). Although gray wolves commonly exhibit spatial overlap with coyotes (Paquet 1991; Berger and Gese 2007; Atwood and Gese 2008, 2010), eastern wolves and coyotes were spatially segregated on the landscape and exhibited little overlap in their home ranges (Benson and Patterson 2013). Coyotes are

rare within, but common outside of, APP (Benson et al. 2012), and therefore, interspecific territoriality between eastern wolves and coyotes may be preventing wolves from expanding outside of APP (Benson and Patterson 2013).

By 1980, the red wolf was declared extinct in the wild, but was reintroduced into eastern North Carolina during 1987 (USFWS 1989, Phillips et al. 2003). Beginning with the release of 4 breeding pairs, the red wolf population reintroduced to eastern North Carolina increased to between 100 and 150 wolves during 2000–2014 (Gese et al. 2015, Hinton et al. 2017a, Hinton and Chamberlain 2022). During that time, the annual population growth rate (λ) ranged 0.78–2.07 (Hinton et al. 2017a), as wolves occupied most of the Albemarle Peninsula, where relative population densities of deer were greatest (Dellinger et al. 2013, Hinton et al. 2016, Karlin et al. 2016). Because the human-caused mortality rate was low, red wolves were limited primarily by amount of space on the peninsula, wherein only about 60% of the 6,000 km² (2,317 mi²) was considered habitable both for wolves (USFWS 2007, Hinton et al. 2016) and for the expanding population of coyotes (Kelly et al. 1999, USFWS 2007, Hinton et al. 2022).

As with eastern wolves, red wolves spatially segregated from coyotes on the landscape and exhibited little overlap in home ranges (Hinton et al. 2017c). However, unsuitable land cover and human-caused mortality, rather than population density of coyotes, limited population growth of the red wolf and facilitated colonization of coyotes on the Albemarle Peninsula (Hinton et al. 2017a, 2022). For example, between 2004 and 2014, illegal shooting of red wolves during the fall and winter deer-hunting seasons increased 2.8 times compared to previous years (Hinton et al. 2017a), and the wolf population experienced a substantial decline, from 151 wolves during 2004 to 20 wolves during 2022. Furthermore, the annual rates of population growth of red wolves declined and number of mortalities due to illegal shooting were strongly correlated with hybridization between red wolves and coyotes (Bohling and Waits 2015; Bohling et al. 2016; Hinton et al. 2017a, 2017b). Consequently, the wild population of red wolves in North Carolina remains imperiled with only about 20 wolves remaining (USFWS 2023). Long-term persistence of red wolves will require similar strategies used to protect the eastern wolf population in and around APP (Way 2014; Hinton et al. 2015, 2017b).

Space Use and Movements

Wolves exhibit a well-developed social organization that provides the basis for territorial spacing mechanisms and maximizes reproductive fitness (Mech and Boitani 2003). Territorial behavior in wolves ranges from nomadism during winter, when wolves live with migratory ungulates at northern latitudes (Parker 1973, Walton et al. 2001), to well-defended territories where ungulate prey are abundant year-round at lower latitudes (Messier 1985a, Fuller 1989). When resident populations of ungulate prey are at a level of abundance that is sufficient for territories to be established by wolves, these territories are defended home ranges that are spatially segregated from those of other conspecifics and are

spaced contiguously across the landscape in a cobblestone-like pattern (Mech 1973, Van Ballenberghe et al. 1975, Fuller 1989, Ballard et al. 1997, Fuller et al. 2003, Benson and Patterson 2013). The other extreme is nomadism of wolves living with migratory barren-ground caribou during winter. Some wolf populations are somewhere in between, with packs exhibiting large overlapping home ranges that are difficult to delineate or defend (Adams et al. 2008). Another variation is the tendency for some packs of wolves to spend considerable time (i.e., weeks to months) away from their defended territories during winter while pursuing migratory deer that have seasonally vacated those territories and surrounding areas (Messier 1985b, Forbes and Theberge 1996).

Each home range is controlled and maintained by a breeding pair of wolves with their offspring. Offspring typically disperse from natal territories by 2–3 years of age (Gese and Mech 1991, Boyd and Pletscher 1999, Karlin and Chadwick 2012, Jimenez et al. 2017). Pack members that maintain home ranges are classified as residents, whereas solitary wolves that are dispersing or emigrating to new areas are classified as floaters (Carroll et al. 2003a, Latham and Boutin 2011, Stronen et al. 2012) or transients (Thurber and Peterson 1993, Adams et al. 2008, Hinton et al. 2016). Transient wolves are typically young dispersers or older animals that have been displaced, but that play a functional role in the population dynamics of wolves through emigration and replacement of breeding residents that experienced mortality (Fuller et al. 2003, Brainerd et al. 2008, Borg et al. 2015, Cassidy et al. 2015, Hinton et al. 2016).

As with habitat selection, space use and movements can be described as hierarchical processes that reflect responses of wolves to limiting factors. For example, within home ranges, space use and movements by resident wolves are influenced by foraging needs and territory maintenance (Carbyn 1981, Mech and Boitani 2003). However, movements within home ranges can differ among biological seasons (e.g., winter vs. pup rearing). During fall through spring, when dispersal is common, younger wolves begin to disassociate with pack members and make extraterritorial movements (Messier 1985b, Mech 2020), and eventually become transients. Alternatively, transient movements are likely influenced by the availability of mates, food resources, and exclusivity of areas within the existing mosaic of home ranges on the landscape (Mech and Boitani 2003, Hinton et al. 2016, Jimenez et al. 2017).

Home-range sizes for packs of gray wolves have been well studied throughout North America, with sizes varying 33–2,600 km² (13–1,003 mi²). Average home-range size in Montana was 600 km² (231 mi²; Montana Fish, Wildlife, and Parks 2018; Parks et al. 2022), in northwestern Alaska was 1,868 km² (721 mi²; Ballard et al. 1997), and in Wisconsin was 136 km² (53 mi²; Wydeven et al. 2009). Average home-range sizes for wolves can be attributed to variation in prey biomass, and in general, wolves have smaller home-range sizes in areas with greater biomass of ungulates (Messier 1985a, Wydeven et al. 1995, Fuller et al. 2003, Rich et al. 2012). Indeed, the size and shape of home ranges of gray wolves and their movements therein reflect their response to the distribution of food resources, availability of denning sites, and population density of humans (Mech and Boitani 2003).

Daily movements of gray wolves ranged 1–70 km/day (0.6–43.5 mi/day (Burkholder 1959, Mech 1966, Peterson 1977, Paquet and Carbyn 2003, Mech and Cluff 2009, Dickie et al. 2017), with travel patterns that were influenced by landscape features (e.g., natural and industrial linear corridors, ruggedness, vegetation communities) and the distribution of ungulate prey (James and Stuart-Smith 2000, Kauffman et al. 2007, Latham et al. 2011, Rich et al. 2012, Kittle et al. 2017). Although gray wolves prefer to use areas with low densities of roads (Thiel 1985, Fuller et al. 1992, Mladenoff et al. 1995, Oakleaf et al. 2006, Martinez-Meyer et al. 2017), they generally take advantage of trails, roads, and seismic lines to enhance the range and efficiency of their movements (James and Stuart-Smith 2000, Latham et al. 2011, Zimmermann et al. 2014, Dickie et al. 2017, Newton et al. 2017, Kautz et al. 2021). However, the positive effect of linear features on wolf movements is dependent on the type of linear feature (Newton et al. 2017). For example, Dickie et al. (2017) reported that wolves moved 3 times faster on roads than they did on unaltered habitat, but wolf movements were 53% slower on newer low-impact seismic lines in the winter compared to unaltered habitat. In northern Ontario, selection for anthropogenic linear features increased with increasing density of these features on the landscape, whereas selection for natural linear features declined, indicating compensatory selection for the former (Newton et al. 2017). Kautz et al. (2021) determined that carnivores such as wolves traveled 1.8–3.8 times faster on roads than off roads in Michigan.

Gray wolves disperse throughout the year, but peak dispersal tends to occur during fall through spring (Gese and Mech 1991, Boyd and Pletscher 1999, Mech and Boitani 2003, Jimenez et al. 2017). Prior to dispersing from their natal home ranges, gray wolves may exhibit extraterritorial movements that involve exploratory movements outside their home ranges (Messier 1985b, Mech and Boitani 2003). However, a wolf may occasionally disperse a long distance without notable exploratory movements (Boyd and Pletscher 1999, Treves et al. 2009, Jimenez et al. 2017). These movements eventually involve the pairing of mates and establishment of breeding territories that are critical for populations to persist throughout their historic range and to recover populations in regions where wolves are killed by humans (Mech and Boitani 2003, Adams et al. 2008, Jimenez et al. 2017).

For gray wolves in the NRM (Jimenez et al. 2017), 10% of the known population dispersed annually, which was composed of 59% adults ($n = 156$), 37% yearlings ($n = 99$), and 4% pups ($n = 10$). Mean duration of dispersal in the NRM was 5.5 months and mean straight-line distances of dispersals were 88 km (55 mi) and 98 km (61 mi) for females and males, respectively (Jimenez et al. 2017). Jimenez et al. (2017) further found that the opportunities for dispersing wolves to find social openings in packs decreased with the number of packs on the landscape and that dispersal rate was negatively correlated with density of packs in an area (but see Hayes and Harestad 2000, Mech and Boitani 2003). Mean dispersal distance in Minnesota was similar, with 65 km (40 mi) for females and 88 km (55 mi) for males (Gese and Mech 1991), but less in Wisconsin, with an overall mean of 55 km (34 mi) for all dispersers (Treves et al. 2009). The maximum straight-

line distance known for dispersal of a wolf is 1,092 km (679 mi), which occurred in Scandinavia (Wabakken et al. 2007). Dispersal in some wolf populations is male-biased (Jimenez et al. 2017, Morales-Gonzalez et al. 2022), with males showing a propensity to disperse to find breeding opportunities, whereas females more often delay dispersal for a breeding opportunity in their natal pack (Jędrzejewski et al. 2005, Ausband 2022b).

Eastern wolves are territorial and exhibit socio-spatial organization closely resembling that of gray wolves (Benson and Patterson 2013). Mean home-range size for eastern wolves is 190 km² (73 mi²; COSEWIC 2015). Theberge and Theberge (2004) reported that home ranges varied in size from 54 to 395 km² (21–152 mi²). Annual dispersal probabilities for eastern wolves monitored during 2002–2010 were 0.22, 0.51, and 0.14 for pup, yearling, and adults, respectively (B. R. Patterson, unpublished data [cited in COSEWIC 2015]). Dispersal distances vary, but eastern wolves have dispersed ≤800 km (497 mi; B. R. Patterson, unpublished data [cited in COSEWIC 2015]). Human-caused mortality is correlated with road density and is considered an impediment to dispersal outside of APP (Benson et al. 2013, 2014). Benson et al. (2015b) reported that eastern wolves avoided secondary roads (i.e., generally paved arterial, local, street, or collector roads) more during the day than they did at night, and that wolves that exhibited the strongest selection against using roads as travel corridors had greater survival rates than those that used roads as travel corridors; they suggested eastern wolves exhibited adapted behaviors to roads by exploiting the beneficial attributes of roads while mitigating mortality risk.

Relative to other wolf species in North America, red wolves have small home-range sizes, which averaged 68 km² (26 mi²) and ranged 25–190 km² (10–73 mi²; Hinton et al. 2016). Resident red wolves have stable, year-round home ranges consistent in size among seasons. Space use by transient red wolves averaged 319 km² (123 mi²) and ranged 122–680 km² (47–263 mi²; Hinton et al. 2016). Although movements of transients were somewhat nomadic, their movements periodically localized for several weeks before they moved to another area (Hinton et al. 2016). Karlin and Chadwick (2012) reported that dispersal of red wolves occurred throughout the year, but dispersal behavior peaked during December and January; they also noted that preference for natal habitat was evident in dispersing red wolves, as wolves preferred dispersing into areas with habitat conditions similar to their natal areas.

The Role of Wolves in Trophic Cascades

Much has been written about the ecological changes in plant and animal communities, or trophic cascades, following the return of wolves to formerly occupied habitat (Fortin et al. 2005, Ripple and Beschta 2012, Callan et al. 2013, Newsome and Ripple 2015, Peterson et al. 2020). There are 2 primary pathways for predators to potentially cause such cascading effects. First, wolves could decrease population abundance of herbivores enough to decrease the level of herbivory such that there is an increase in vegetation structure and species diversity. This direct effect on the herbivore-vegetation relationship is called a density-mediated trophic cascade (DMTC) because it is the decrease in density of herbivore

populations that causes effects at lower trophic levels (Hebblewhite et al. 2005; Kauffman et al. 2010; Peterson et al. 2014; Flagel et al. 2016; Allen et al. 2017a, 2017b). The second pathway involves wolves changing the behavior and habitat use of their prey enough to decrease herbivory in some areas, such as wet meadows and riparian areas (Ripple and Beschta 2003, 2004a, 2004b, 2006; Laundré et al. 2010). This is an indirect effect termed a behaviorally mediated trophic cascade (BMTC). The DMTC and BMTC are most discussed in relation to population recovery of wolves and their impacts on prey populations and plant communities. Both scenarios are possible under some circumstances, but elucidating their existence and strength is often confounded by a multitude of other ecological interactions (Peterson et al. 2014). Working on IRNP, McLaren and Peterson (1994) were among the first to suggest wolves may drive trophic cascades.

The mechanisms that may precipitate trophic cascades following the recolonization of wolves have been a hotly debated topic among scientists for the past 25 years (Kauffman et al. 2010, 2013; Mech 2012; Peterson et al. 2014; Allen et al. 2017a, 2017b; Bruskotter et al. 2017). While some see the return of the wolf as a panacea to restore balance to overgrazed ecosystems, others dismiss the importance of wolves to overall ecological health and stability. These analyses are further complicated by the presence of black bears, grizzly bears (*Ursus arctos horribilis*), mountain lions, and humans, each of which kill or otherwise alter the distribution of ungulates (Vucetich et al. 2005, MacNulty et al. 2020, Metz et al. 2020, Brice et al. 2022). Drought and climatic changes can also impact forage production and ungulate populations as well. Most studies of wolf-related trophic cascades have been conducted in national parks (i.e., no harvest of wolves or prey) in Canada and the U.S., including Banff National Park in Alberta, IRNP, and YNP (McLaren and Peterson 1994; Hebblewhite et al. 2005; Hebblewhite and Smith 2010; Laundré et al. 2010; Peterson et al. 2014; Allen et al. 2017a, 2017b).

One of the most-studied ecosystems in the world, particularly regarding trophic cascades, is YNP. The Northern Range herd of elk (*Cervus canadensis*) in YNP ranged from a low of 3,172 individuals counted during 1967–1968 at the conclusion of efforts to decrease populations, to a high of 19,045 individuals during 1993–1994 (Hamlin 2009). Following a 60-year absence, 14 wolves from western Canada were reintroduced into YNP in 1995, with an additional 17 wolves from Canada released in YNP in 1996. Ten gray wolves from Montana were released in YNP in 1997 (Fritts et al. 2020; see section on Recovery through Translocation Efforts). The population of wolves steadily increased, peaked at 171 in 2007, and decreased to 80 by December 2018 (Smith et al. 2019). The year before translocation of wolves in YNP (1994), the Northern Range herd of elk began to decline and reached a low of 3,900 elk counted in 2013, but increased to 7,600 by 2018 (U.S. National Park Service 2020). It is important to note that count data may not reflect true population size because it does not account for systematic undercounting (Singer and Garton 1994). Additionally, the most severe winter on record in Montana (Dusek et al. 2006) and Wyoming occurred during 1996–1997, which resulted in massive die-offs of bison, deer, and elk due to starvation (Dusek et

al. 2006, Hamlin 2009). The dynamics among elk, wolves, plants, climatic changes, other large carnivores, hunting by humans, and interrelated factors continue to be the subject of much research in YNP (Vucetich et al. 2005; White and Garrott 2005; Varley and Boyce 2006; Ripple et al. 2011; Peterson et al. 2014, 2020; Allen et al. 2017a, 2017b).

During early efforts for population recovery of wolves, researchers measured upland and riparian woody vegetation in YNP and concluded that the reintroduction of wolves had initiated a landscape-scale recovery of vegetation (Ripple and Beschta 2003, 2004a, 2004b). The substantial decrease in elk abundance that occurred in YNP eventually decreased browsing and grazing pressure on the vegetative community, consistent with a DMTC. However, even in the early stages of wolf population recovery, before elk populations had substantially decreased, the focus quickly shifted to the hypothesis that trophic cascades were being driven by behavioral changes in elk caused by wolves, which influenced where elk grazed, consistent with a BMTC. Several studies concluded that shrub cover was recovering at faster rates in areas where elk were at a higher risk of predation by wolves compared to areas with lower risk (Ripple and Larsen 2000; Ripple et al. 2001; Ripple and Beschta 2003, 2004a, 2004b, 2006, 2007). These researchers concluded that elk avoided the riskier riparian areas, and that wolf behavior was redistributing elk on the landscape and precipitating a BMTC. However, others argued that the aforementioned studies had poor experimental design, failed to quantify predation risk across their study areas, and had biased sampling (Kauffman et al. 2013; Ford and Goheen 2015; Allen et al. 2017a, 2017b; Brice et al. 2022).

Using an empirical landscape-level map of predation risk constructed with the first 10 years of data on wolf-killed elk, along with elk browsing exclosures, Kauffman et al. (2010) also measured shrub cover in riparian areas of YNP and found no widespread decrease in browsing on aspen by elk, nor an increase in plant height; they found no evidence to support a BMTC. They also noted that plant height and browsing on plants are both strongly influenced by many environmental factors unrelated to wolves (Kauffman et al. 2013). Middleton et al. (2013) found no relationship between the risk of elk being preyed upon by wolves and body fat and pregnancy of elk, which also failed to support a BMTC as a dominant force in the Greater Yellowstone Ecosystem. Although elk do respond behaviorally to wolves and predation risk, these responses are more nuanced than previously understood (Cusack et al. 2020). Kohl et al. (2018, 2019) showed that elk changed their foraging times around wolf activity, and therefore rejected a BMTC as an important influence on the vegetative changes in YNP. Kohl et al. (2019) showed that elk responded to predation risk from both mountain lions and wolves, but the response was stronger in relation to stalking-ambush predators, such as the mountain lion. This is particularly relevant because mountain lions reestablished a viable, year-round population in northern YNP during the 1980s, which was a period of high abundance of elk and absence of wolves, resulting in a relatively rapid growth rate for mountain lion populations. Following restoration of wolf populations during the mid-1990s, annual

population growth of mountain lions continued to increase $\leq 10\%$ /year through 2001, when ≤ 42 mountain lions inhabited northern YNP (Ruth et al. 2019).

Numerous studies conducted in the Northern Range of YNP demonstrated that fire and hydrological changes strongly influenced growth and recruitment of willow (*Salix* spp.; Johnston et al. 2007, Bilyeu et al. 2008, Tercek et al. 2010). Additionally, snow depth and structure strongly influenced foraging behavior of elk, including habitat selection (Mao et al. 2005), use of aspen sites (Brodie et al. 2012), and intensity of browsing and grazing (Creel and Christianson 2009). Other studies in YNP have cast doubt on the cascading effects of population recovery of wolves on willows (Bilyeu et al. 2007, 2008; Johnston et al. 2007, 2011; Creel and Christianson 2009, Tercek et al. 2010).

In addition, other ecological changes that can impact prey demographics and vegetation recovery have occurred in YNP concurrent with population recovery of wolves (Peterson et al. 2014). In recent decades, population abundance of grizzly bears substantially increased in the Greater Yellowstone Ecosystem (Schwartz et al. 2006), with a three-fold increase in predation rates of elk calves (Barber-Meyer et al. 2008). Population abundance of moose substantially declined after 36% of YNP was affected by wildfire in 1988 (Tyers 2006). Additionally, drought during the mid-to-late 1990s decreased recruitment of elk calves (Middleton et al. 2013). Harvest of antlerless elk accelerated the decline of elk populations (Vucetich et al. 2005, Peterson et al. 2014), and high snow depths impacted population abundance of elk (Creel and Christianson 2009).

Understanding the dynamics and causal links between predators, prey, and vegetation will become more important as population recovery of wolves continues to progress across their former range. Researchers and managers have recently highlighted potential weaknesses in the literature associated with wolf-related trophic cascades, namely, poorly designed studies, lack of rigorous testing of alternative hypotheses, confusion about the appropriate response variables to measure, and reliance on correlative (rather than causative) methods (Kauffman et al. 2013; Ford and Goheen 2015; Allen et al. 2017a, 2017b). In general, these limitations have been more common among studies purporting to demonstrate strong indirect effects of wolves compared to studies that found no effects. Wildlife research is often observational rather than experimental, and this may limit inferences. Although most wildlife biologists and ecologists agree that top-down forces can occur and that large carnivores can have important ecological roles (Allen et al. 2017a, 2017b; Peterson et al. 2020; Stahler et al. 2020), the scenario of wolves being the primary driver of increased plant growth and recovery in YNP may be an oversimplification of a multitude of complex ecological interactions (Brice et al. 2022).

Clearly, substantial decreases in ungulate populations through direct predation by a restored predator can cascade into ecological changes to the vegetative community and subsequently other fauna in the ecosystem. Mech (2012) questioned whether these effects would be realized or consequential on working landscapes outside of large, protected areas such as natural parks, but there is also evidence of trophic cascades in managed forests precipitating

from wolf predation on ungulates (Bouchard et al. 2013; Callan et al. 2013; Flagel et al. 2016, 2017; Chandler et al. 2020). These studies demonstrated that within wolf territories, there is increased growth of browse-sensitive plants (Bouchard et al. 2013), greater diversity of shrubs and forbs (Callan et al. 2013, Flagel et al. 2016), and decreased browsing and increased growth on seedlings of deciduous trees (Flagel et al. 2016).

High abundance of wolves was associated with decreased abundance of coyotes, and a greater abundance of red foxes (*Vulpes vulpes*), which in turn decreased abundance of deer mice (*Peromyscus maniculatus*; Levi and Wilmers 2012, Flagel et al. 2017), and resulted in decreased removal of tree seeds, apparently due to predation by foxes on mice (Chandler et al. 2020). Collectively, these studies demonstrate potential effects of trophic cascades in managed forests. However, where ungulates are managed at ecologically appropriate population densities, the restoration of wolves would be expected to produce only modest, positive ecological changes relative to those documented in areas with chronically overabundant populations of ungulates.

Diseases and Parasites

Wolves are particularly susceptible to pathogens because of their pack-based social structure, which promotes close contact among social group members (Woodroffe et al. 2004, Brzeski et al. 2015). As a result, diseases and parasites can be acquired through grooming of infected conspecifics, scent communication with infected feces and urine, and sharing of infected prey (Brand et al. 1995, Woodroffe et al. 2004). A wide range of pathogens have been reported for wolves (Kreeger 2003), and epizootics are increasingly recognized as an important factor influencing the management of wolf populations because they: 1) may negatively impact population growth (Chapman 1978, Brand et al. 1995, Ballard and Krausman 1997, Mech et al. 2008), 2) could hinder recovery efforts for endangered wolves (Brzeski et al. 2015), and 3) canid-borne zoonoses can be transmitted between wolves and domestic animals (Woodroffe et al. 2004). Although pathogens seldom have long-term population-level effects (Fuller et al. 2003, Almborg et al. 2009, Brzeski et al. 2015), they can have negative short-term impacts on wolf populations and therefore require continuous monitoring and management (Chapman 1978; Carbyn 1982; Mech et al. 1986; Bailey et al. 1995; Wydeven et al. 1995; Ballard and Krausman 1997; Almborg et al. 2009; Brzeski et al. 2015; Brandell et al. 2020, 2021).

Canine parvovirus (CPV) is a contagious disease that causes acute gastrointestinal illness in young wolves (Mech et al. 1986, Kreeger 2003). Clinical CPV is characterized by severe hemorrhagic diarrhea and vomiting, which leads to dehydration and debility and may lead to death (Kreeger 2003). Following the emergence of CPV from domestic dogs during the late 1970s (Zarnke and Ballard 1987, Kreeger 2003), serological evidence from wild wolves suggested CPV infection is a survivable disease, as populations may develop immunity and withstand effects of the disease (Mech and Goyal 1995, Almborg et al. 2009). This may explain why blood antibodies indicating non-lethal exposure to CPV have been detected in nearly every wolf population in

North America (Mech et al. 1986; Zarnke and Ballard 1987; Mech and Goyal 1993, 1995; Johnson et al. 1994; Bailey et al. 1995; Hedrick et al. 2003; Kreeger 2003; Zarnke et al. 2004; Smith and Almborg 2007; Almborg et al. 2009; Nelson et al. 2012; Brzeski et al. 2015; Carstensen et al. 2017; Justice-Allen and Clement 2019; Brandell et al. 2021), but occurrences of morbidity and mortality in adult wolves due to CPV are rare (Kreeger 2003). Nonetheless, studies suggest once CPV becomes prevalent in a population, it decreases survival of pups, subsequent dispersal, and the overall rate of population growth (Johnson et al. 1994, Wydeven et al. 1995, Mech et al. 2008). Most populations eventually develop immunity and withstand the severe effects of the disease (Mech and Goyal 1993). For example, in Minnesota, CPV decreased annual survival of pups by 40–60%, limited the annual population rate of increase to about 4% during 1973–2004, and likely decreased dispersal and recolonization in the region (Mech et al. 2008). Although wild Mexican wolves and red wolves have been exposed to CPV and experienced some resulting pup mortality, CPV is not believed to be a threat to reintroduction efforts (Justice-Allen and Clement 2019).

Canine distemper virus (CDV) is an acute fever-causing disease caused by a paramyxovirus that infects canid (and other wildlife) populations, including wolves. It is not known if CDV is enzootic in wolf populations or sporadically introduced by domestic dogs (Kreeger 2003). Like CPV, most evidence of CDV in wild wolves comes from serological evidence that demonstrates exposure to the virus (Kreeger 2003). Because CDV is spread by aerosol or direct contact of nasal and eye fluids, feces, and urine, and is highly contagious, the virus is thought to be transmitted quickly through wolf populations (Almborg et al. 2009, 2010). Although CDV is infrequently reported as a mortality factor, the disease is probably widely distributed amongst most wolf populations in North America, including Alaska (Peterson et al. 1984), Arizona and New Mexico (USFWS 2018a, Justice-Allen and Clement 2019), Manitoba (Carbyn 1982), Minnesota (Carstensen et al. 2017), North Carolina (Brzeski et al. 2015), NRM (Almborg et al. 2010, Nelson et al. 2012), and Wisconsin (Wydeven and Wiedenhoeft 2003).

The seroprevalence of CDV in North American wolves ranges between 7% and 80% (Stephenson et al. 1982; Zarnke and Ballard 1987; Johnson et al. 1994; Wydeven and Wiedenhoeft 2003; Almborg et al. 2009, 2010; Stronen et al. 2011; Nelson et al. 2012; Watts and Benson 2016; Carstensen et al. 2017). High levels of recruitment in populations where CDV persists suggest the virus may cause short-term population declines, but that CDV does not seem to threaten the long-term persistence of wolf populations (Brand et al. 1995, Kreeger 2003, Almborg et al. 2009). For example, wolves in YNP experienced 3 major CDV outbreaks (1999, 2005, and 2008), in which pup survival averaged 28%; this suggested CDV may cause periodic, but unpredictable CDV-related declines in pup survival approximately every 4 years (Almborg et al. 2009, 2010; Brandell et al. 2020). Additionally, recent evidence suggests selection may favor wolves choosing mates that are heterozygous for the allele responsible for black pelage, which has been correlated with higher survival during

distemper outbreaks (Cubaynes et al. 2022; Fig. 32.10). Although CDV-induced mortality has been documented in wild Mexican wolves, the disease is not considered a threat to their recovery (Justice-Allen and Clement 2019).

Sarcoptic mange is an infectious disease of the skin caused by sarcoptic mites (*Sarcoptes scabiei*) burrowing into the skin, feeding, and laying eggs, and is the most conspicuous ectoparasite of wolves and other canids (Brand et al. 1995, Kreeger 2003). Mange is transmitted primarily through direct contact among conspecifics or through contact with infested bedding and feeding sites. The waste secreted by mites during their burrowing activity triggers an allergic reaction that causes severe itchiness, resulting in hair loss due to scratching infected areas of the skin and, in the most severe cases, the hair loss accompanied with crusted lesions and thickened, slate-gray skin over much of the body of the host. Mortality may occur because of exposure to inclement weather and resulting hypothermia, emaciation, and secondary infections (Kreeger 2003).

The prevalence of mange ranges between 3% and 24% of infected populations, with peak prevalence during winter, and with negative effects on pup survival and growth rates of wolf populations in some areas (Todd et al. 1981; Almberg et al. 2009, 2015; Jimenez et al. 2010; Brandell et al. 2020). However, evidence suggests individuals can overcome mange and therefore prevent chronic outbreaks (Kreeger 2003; Almberg et al. 2009, 2015; Wydeven et al. 2009; Jimenez et al. 2010). In YNP, infected wolves living in large packs survived at higher rates than infected wolves living in smaller packs (Almberg et al. 2015, Brandell et al. 2020). Larger packs with healthy pack mates may be able to provide food and defend territories of infected individuals

(Almberg et al. 2015, Cross et al. 2016). During 1987–2014, at least 18 red wolves in North Carolina died from mange, but this did not have long-term demographic effects (Brzeski et al. 2015). During that same period, 46 cases of mange in wild red wolves were successfully treated with Ivermectin™ when those wolves were captured, and then released back into the wild after symptoms of the infection subsided (Brzeski et al. 2015). Mange-related mortality is generally rare among eastern wolves (Benson et al. 2014), but approximately 12% of the wolves in APP died of mange-related causes during winter 2007 (B. R. Patterson, unpublished data).

Rabies is an acute, incurable viral infection of the central nervous system that has been widely documented in free-ranging wolves across the globe (Sikes 1981, Federoff 2001). The rabies virus persists as an infection of the salivary gland and is transmitted primarily via animal bite. Once the virus is deposited in bite wounds and replicated, it gains entry to the central nervous system by peripheral nerves and spreads to the salivary glands (Sikes 1981). The incubation period in wolves is 8–21 days (Rausch 1972, Cherkasskiy 1988). Clinical manifestations of canine rabies can be classified as dumb and furious forms. The dumb form is characterized by excessive salivation, loss of voice, progressive paralysis, and death (Chalmers and Scott 1969). The furious form is characterized by agitated and aggressive behavior, increased salivation, progressive paralysis, and death (Rausch 1972). Signs of rabies in wolves are largely anecdotal, as no controlled studies on wolves have been conducted (Kreeger 2003).

Although rabies was commonly documented in Ethiopian wolves (*Canis simensis*) in Africa (Sillero-Zubiri et al. 1996, Randall et al. 2006, Johnson et al. 2010), and gray wolves in



Fig. 32.10. Recent evidence suggests wolves (*Canis* spp.) chose mates that are heterozygous for the allele associated with black pelage, which has been correlated with higher survival during distemper outbreaks, including in Yellowstone National Park, USA. Image courtesy of B. Landis, Landis Wildlife Films, USA.

Asia (Boldbaatar et al. 2010, Gholami et al. 2017) and Europe (Cherkasskiy 1988, Holmala and Kauhala 2006, Linnell and Alleau 2016), epizootics in populations of wolves in North America have been rare and limited primarily to the Arctic and boreal regions (Theberge et al. 1994, Ballard and Krausman 1997, Federoff 2001, Kreeger 2003). Except for several studies in Alaska (Chapman 1978, Weiler et al. 1995, Ballard and Krausman 1997), accounts of mortality in wolves caused by rabies are limited to individual wolves (Rausch 1972, Theberge et al. 1994). Ballard and Krausman (1997) reported a population decline from 4.4 wolves/1,000 km² to 1.5 wolves/1000 km² (11.4/1,000 mi² to 3.9/1,000 mi²) in association with rabies outbreak in Alaska. They reported that rabies was the second-most important cause of mortality during the study, with harvest by humans being the most important, and suggested rabies epizootics have the potential to limit population growth. Similarly, Theberge et al. (1994) reported that rabies was the second-leading cause of wolf mortality in APP during 1990–1991, followed by human-related causes.

Studies also noted the potential for the virus to spread, as infected wolves were observed leaving packs and dispersing ≤80 km (48 mi; Chapman 1978, Cherkasskiy 1988, Theberge et al. 1994). However, the lack of occurrence of rabies epizootics in wolf populations in the conterminous U.S., and the general rarity of epizootics, suggests the virus may be self-limiting in areas of outbreaks after infected packs disband (Kreeger 2003). The fear of rabies raises substantial social alarms because of its historical role in human deaths and anti-wolf attitudes (Fritts et al. 2003). Although rabid wolves have been known to attack people, these events are rare, especially in North America (Linnell et al. 2021). Vaccination programs for domestic dogs and wildlife have decreased the risk of exposure and should an encounter occur, post-exposure treatments for humans can further mitigate the risk posed by rabies (Linnell et al. 2021).

Tapeworms (*Echinococcus canadensis*, *Echinococcus multilocularis*, and *Echinococcus granulosus*), for which wolves can serve as definitive hosts, can be potentially transmitted to humans from wolf scats (Kreeger 2003, Cerda et al. 2018), although this is quite rare. Some popular-press articles have exaggerated concerns by those opposed to wolf-recovery programs (Dovel 2010), despite the species (*Echinococcus canadensis* [= *Echinococcus granulosus*, northern biotype]) most often found in wolves having low pathogenicity to humans (Foreyt et al. 2009, Cerda et al. 2018, Schurer et al. 2018). The northern type *Echinococcus canadensis* commonly occurs in wolves in Alaska, across Arctic and boreal regions of Canada (Schurer et al. 2013, 2014, 2016, 2018), and in Idaho and Montana, often infecting 30–60% of wolves (Rausch 2003, Foreyt et al. 2009). Although wolves are unaffected by *Echinococcus* infections, ungulates that serve as intermediate hosts can be debilitated by tapeworm cysts in the lungs, which may predispose them to predation (Mech 1966, Joly and Messier 2004).

Other diseases and parasites have been documented in wolf populations, including anaplasmosis, blastomycosis, brucellosis, canine adenovirus, canine heartworm, canine hepatitis, coccidiosis,

eastern equine encephalitis, ehrlichiosis, herpesvirus, hookworm, Lyme disease, *Neospora caninum*, *Toxoplasma gondii*, and West Nile virus, but their impacts on populations are likely negligible (Brand et al. 1995, Kreeger 2003, Dubey et al. 2011, Jara et al. 2016, Carstensen et al. 2017, Brandell et al. 2021). However, a recent study reported that *Toxoplasma gondii* infection influenced risk-taking behaviors of gray wolves in YNP (Meyer et al. 2022). Specifically, infection rates were greatest in wolf packs that spatially overlapped with mountain lions, the definitive host of *Toxoplasma gondii*, and that seropositive wolves were more likely to disperse or become pack leaders than were seronegative wolves. Meyer et al. (2022) suggested the impact of the protozoan parasite on the brains of wolves made them bolder and less likely to retreat during inter- and intraspecific strife. These findings demonstrate how disease and parasitic pathways may influence wolf behavior, survival, and interspecific interactions.

Food Habits

In terms of costs and benefits, searching for enough food to provide sufficient energy for survival and reproduction is a major task for wolves. Because the mean body mass of adult North American gray wolves is 40 kg (88 lb; Mech 1970), pursuing small prey requires food-intake rates that are energetically cost prohibitive for most wolves, thus limiting their ability to meet absolute energy requirements (Carbone et al. 1999, 2007). Therefore, wolves are obligate carnivores with a feeding economy that is generally dependent on ungulates and augmented with smaller mammals, such as beavers, lagomorphs (*Lepus* spp., *Sylvilagus* spp.; Paquet and Carbyn 2003, Peterson and Ciucci 2003, Mech 2007b, Newsome et al. 2016), and salmon (Salmonidae; Szepanski et al. 1999, Darimont et al. 2008, Adams et al. 2010).

Throughout North America, gray wolves typically occur in regions where population densities of ungulates exist at adequate levels to serve as a stable prey base (Mech et al. 2015), with western populations of wolves existing in systems with ≤9 ungulate species (i.e., bighorn sheep [*Ovis canadensis*], bison, Dall sheep [*Ovis dalli*], mountain goat [*Oreamnos americanus*], caribou, elk, moose, mule deer [*Odocoileus hemionus*], and white-tailed deer; Peterson and Ciucci 2003). In eastern Canada and the Great Lakes region of the U.S., gray wolves subsist primarily on white-tailed deer, and secondarily on beavers and moose (Frenzel 1974, Van Ballenberghe et al. 1975, Messier and Crete 1985, Fuller 1989, Hayes and Gunson 1995, DelGiudice et al. 2009, Newsome et al. 2016, Gable et al. 2018a). On IRNP, moose are the primary prey, with beavers serving as a supplemental prey species during ice-free seasons (Mech 1966, Peterson 1977). In southeastern British Columbia and northwestern Montana, white-tailed deer were the primary prey of wolves, elk were secondary, and moose were less frequently used as prey (Boyd et al. 1994, Kunkel 1997). In parts of western Canada and the NRM of the U.S., wolves prey predominantly on elk and, to a lesser extent, deer. In YNP, approximately 85% of wolf diets included elk, and the remaining diet consisted mostly of bison and deer (Stahler et al. 2006, Metz et al. 2012). However, in northeastern Alberta, deer, moose, and beavers were important seasonal prey items found in wolf scats despite the presence of woodland caribou (*Rangifer*

tarandus caribou; Latham et al. 2013). In northern Alberta, bison were the major food source of wolves, although moose and beavers were periodically preyed upon (Carbyn et al. 1993). This contrasts with YNP, where bison are available, but for which wolves have preyed upon much less than elk. With changing population dynamics, predation preferences of wolves and prey vulnerabilities can shift among prey species.

In the Pacific Coastal regions of British Columbia and southeastern Alaska, diets of gray wolves are composed predominantly of black-tailed deer (*Odocoileus hemionus colombianus*, *Odocoileus hemionus sitkensis*) and supplemented with marine resources such as salmon and seals (*Phocidae* spp.; Darimont et al. 2004, 2008; Stanek et al. 2017). Within this region, there is a dietary shift by wolves during summer and fall to exploit marine subsidies of Pacific salmon (*Oncorhynchus* spp.), which made up 28–58% of their diets (Darimont et al. 2004, 2008; Stanek et al. 2017). However, inland in Alaska and the western provinces of Canada, moose were the predominant prey for wolves in these systems, which lack elk or deer, whereas caribou were the most common prey where abundant (Stephenson and James 1982, Ballard et al. 1997). North of continuous forests of mainland Canada, wolves rely on migratory caribou, whereas on the Arctic islands, muskoxen are the primary ungulate prey (Miller 1995, Cluff and Mech 2023), supplemented by Arctic hares (*Lepus arcticus*; Tener 1954, Mech 2004), and the occasional Peary caribou (*Rangifer tarandus pearyi*). Though gray wolves are primarily carnivorous, berries (e.g., *Rubus* spp., *Vaccinium* spp.) can comprise a substantial portion of their diet during summer (Van Ballenberghe et al. 1975, Fuller 1989, Gable et al. 2018b, Homkes et al. 2020), and occasionally, ants (Formicidae) are consumed (Larter 2016).

Early studies in APP documented that eastern wolves preyed primarily on white-tailed deer and beavers, but rarely moose (Pimlott et al. 1969, Forbes and Theberge 1996). However, recent studies demonstrated that moose have become more prevalent in the diet of eastern wolves, concordant with moose becoming the most abundant ungulate in APP. For example, Theberge and Theberge (2004) reported that the predominant prey items found in scats of eastern wolves were white-tailed deer (41%), moose (32%), and beavers (22%). More recently, Benson et al. (2017) found that eastern wolves were capable of killing moose at rates similar to those documented for gray wolves, but generally only did so when deer were scarce. Beavers were an important food resource for eastern wolves during summer; starvation risk for pups was lowest for packs that occupied territories with greater population densities of beavers (Benson et al. 2013, 2015a).

The diet of Mexican wolves in their historical range was thought to be predominantly Coues' white-tailed deer (*Odocoileus virginianus couesi*), supplemented with Gould's wild turkeys (*Meleagris gallopavo mexicana*), lagomorphs, and rodents (*Neotoma* spp., *Sigmodon* spp.). This smaller-sized subspecies of gray wolf likely preyed upon a wider diversity of smaller food items just as coyotes do in southern latitudes (Hidalgo-Mihart et al. 2001). In the current recovery area in the U.S., which is at the northern periphery of their historical range, diets of Mexican

wolves are predominantly elk (77–90%; Reed et al. 2006, Carrera et al. 2008, Merkle et al. 2009), a species that was absent in much of the historical range of Mexican wolves.

Based on analysis of scats, white-tailed deer were the dominant prey item for red wolves, with rabbits (*Sylvilagus* spp.) and small mammals serving as secondary and tertiary prey, respectively (Dellinger et al. 2011, Hinton et al. 2017c). Dellinger et al. (2011) reported that white-tailed deer accounted for 37–66% of the diet of red wolves, and that 2 packs in close proximity to a garbage dump and carcass pit regularly consumed foods associated with humans. Hinton et al. (2017c) reported that white-tailed deer comprised 60% of prey items found in scat. They also observed a positive relationship between the body mass of red wolves and the proportion of their diet that consisted of deer, suggesting larger wolves consumed more deer than did smaller wolves.

BEHAVIOR

Direct observations of wolf behavior in the wild were initiated by Adolph Murie with his study of wolves in Mount McKinley National Park, Alaska (Murie 1944). Most of his observations were of wolves at den sites. Later research on IRNP (Mech 1966, Peterson 1977) and APP (Pimlott et al. 1969) provided aerial glimpses of wolf-hunting behavior. At the time of publication of Mech (1970), much of what was known of wolf behavior was gleaned from observing animals in captivity. Studies by Mech (1994, 1995b, 1999, 2004, 2007a, 2007b) of wolves on Ellesmere Island in Nunavut Territory, Canada, and the reintroduction of wolves into YNP during 1995–1996, substantially increased the opportunity to observe behavior of wolves in the wild, including hunting behavior (Smith et al. 2003, MacNulty et al. 2007, 2009a, 2009b, 2012, 2014; Mech et al. 2015, McIntyre et al. 2017, McIntyre 2019; Fig. 32.11). As a result of this research and increases in technological capabilities (e.g., GPS collars, genetics, motion-sensing cameras), a more complete picture of wolf behavior in the wild has been emerging.

Wolves are primarily monogamous breeders (Mech and Boitani 2003; Packard 2003, 2012; Milleret et al. 2017) that live in packs within defended territories (see also section on Reproduction, section on Space Use and Movements). However, there are exceptions and the probability of multiple individuals that breed within in packs can be predicted by group size and population density (Ausband 2018). Monogamous pairs can breed together for ≤ 12 years and duration of pair bonds can have a significant positive effect on pup survival (Ausband 2019a). Most pair bonds last only 2–3 years, however, and cease with the death of one member of the pair (Milleret et al. 2017, Ausband 2019a). Most wolves leave their natal territories as they approach adulthood or as young adults, to disperse and remain solitary until establishing their own territories with a mate, or joining another pack. Some wolves, particularly females (Ausband 2022b), remain in their natal pack throughout their life, and these bidders may become breeders when a new wolf joins the pack after death of one of the members of an existing breeding pair, with the new pack member bonding with a young adult in the pack instead of the existing member of the breeding pair (Mech and Boitani 2003).

The pack is maintained via a dominance hierarchy controlled by the breeding pair (Harrington and Mech 1979). Historically, the 2 members of the breeding pair were referred to as the alphas, but it has been questioned whether this is appropriate because in most packs, most of the other pack members are offspring of the breeding pair (Mech 1999, Packard 2003). In larger packs with several breeders, the term alphas may still be appropriate (Packard 2003, McIntyre 2019).

Adults and yearlings often hunt by themselves or in small groups during the denning period in spring and rendezvous period in summer and early fall (Murie 1944; Harrington and Mech 1982a, 1982b; Benson and Patterson 2015; McIntyre 2019). During the nomadic period in the fall and winter, the pack travels and hunts mostly as a cohesive group within its territory (Mech and Boitani 2003, Barber-Meyer and Mech 2015, Benson and Patterson 2015). During winter, the pack may split up for short periods, and some yearlings and young adults will leave the pack territory for varying periods of time on exploratory trips, and some will completely disperse from the natal pack (Mech and Boitani 2003). Packs that fail to produce pups tend to be more nomadic throughout the summer, and yearlings occasionally make use of rendezvous sites (Mech 1995b).

Wolves communicate amongst themselves through a broad variety of auditory, gustatory, olfactory, tactile, and visual means (Harrington and Asa 2003). Wolf vocalizations range from squeals and yelps of pups; moans, whines, and barks of subadults; to woofs, squeaks, and howls of adults (Harrington and Asa 2003). Most of these vocalizations are used in social interactions among pack members at close distance, but howls, and occasionally woofs and barks, are used for long-distance communication, both among pack members and between packs. In forested environments, wolves can hear the howl of another wolf ≤ 11 km (7 mi) away, and in open tundra ≤ 16 km (10 mi; Harrington and Mech 1979). Thus, wolves in forests can advertise their presence across 380 km² (147 mi²), an area as large or larger than average territory size in forested habitat, and this plays an important role in territory maintenance (Harrington and Mech 1979). Howling is also used for intrapack communications for coordinating pack activities and gathering pack members before or after a hunt (Harrington and Mech 1978, McIntyre et al. 2017).

Wolves communicate using a broad range of olfactory signals including via anal sac, apocrine sweat glands on feet, feces, preputial gland on penile sheath, saliva, skin glands, supracaudal gland on the tail, urine, and vagina (Harrington and Asa 2003).



Fig. 32.11. Wolves (*Canis* spp.) work cooperatively to acquire food in the form of the most efficiently available biomass. Image courtesy of D. Smith, National Park Service, USA.

Urine and feces are especially associated with scent-marking behavior to assert dominance, facilitate pair-bonding, achieve reproductive synchrony, aid with spatial orientation, maintain territory, and mark empty food caches (Peters and Mech 1975, Rothman and Mech 1979, Paquet 1991, Zub et al. 2003). Urine scent-marking patterns increase as wolves approach breeding season, and are associated with an increase in serum testosterone in both males and females, but typically only the dominant male and female mark with urine (Asa et al. 1990). Scat deposition has less seasonal variation, and scents are accentuated with deposits of anal-gland secretions, which occur more regularly in dominant males (Asa et al. 1985).

Peters and Mech (1975) in Minnesota had proposed a model of scent marking more frequently along peripheries than in the core of the territory, but studies in Manitoba and Poland found more varied marking patterns and based more on valuable parts of the territory (Paquet and Fuller 1990, Zub et al. 2003). Ground scratching, which provides opportunity for marking with apocrine sweat glands on the feet, is often associated with feces and urine, and rates of ground scratching may be higher for gray wolves in Europe than in North America (Peters and Mech 1975, Paquet 1991, Zub et al. 2003). Urine marking, typically raised-leg urinations, is performed primarily by the adult breeding pair, but subordinate males also have been observed raised-leg urinating on the scent mark of the dominant male (McIntyre 2019). Lone wolves typically do not perform raised-leg urinations, though in cases where former breeding males remained in territories where all other pack members had died or disbanded, the lone adult male continued to scent mark and maintain the former pack's territory (Schultz and Wilson 2002).

Wolves use a wide variety of visual displays to socially communicate to other pack members, as well as in interactions with other packs and potential mates (Mech 1970, Zimen 1981, Harrington and Asa 2003, Packard 2012). The extensive variety of physical postures used by wolves in social communication were discussed by Mech (1970), Zimen (1981), and Harrington and Asa (2003). Facial expressions range from ears back and mouth closed or partially closed for fearful submissive displays, to open mouth and ears forward for dominant aggressive displays. Tails are held in upward angles by dominant wolves, but held low by subordinate animals, and held between the hind legs by very submissive wolves. Dominant animals tend to stand tall, whereas subordinate wolves more often crouch or lay down in social interactions. Wolves that display dominant behaviors initiate most pack activities, and breeding females lead packs as often as breeding males (Peterson et al. 2002). A careful blending of dominant and submissive behaviors are used by individual wolves when trying to integrate into a new pack (Stahler et al. 2002).

The reintroduction of wolves in YNP has contributed greatly to our understanding of hunting behavior of wolves, especially on elk and bison (MacNulty et al. 2007, Mech et al. 2015). Wolves are coursing predators that are highly adapted to hunting medium- and large-sized ungulates. In YNP, wolves used their mouths to grab prey <200 kg (440 lb) by the neck, grab prey 200–270 kg (440–595 lb) by the hind end and neck, and grab prey >270 kg (595 lb) by the

hind end (Mech et al. 2015). MacNulty et al. (2007) developed an ethogram of predator behavior used to describe hunting behavior of wolves, which included search, approach, watch, attack-group, attack-individual, and capture. The distance that wolves chase prey is typically 100–1,000 m (330–3,300 ft), with a recorded maximum chase and tracking distance of a white-tailed deer of 20.8 km (12.9 mi), but it was not determined if those wolves were successful (Mech et al. 2015).

Success in killing an individual prey animal ranges 10–49%, but varies by species, season, location, and circumstances (Mech et al. 2015). The optimal size of a group for killing elk was 4 wolves, and additional wolves did not increase kill rates (MacNulty et al. 2012); for hunting bison, 9–13 or more wolves seemed optimal (MacNulty et al. 2014). Wolves reach peak hunting ability at 2–3 years old, and thereafter begin to decline (MacNulty et al. 2009a, 2009b). Although coursing is the more common hunting pattern for wolves, they do at times use ambush attacks, especially when hunting beavers (Gable et al. 2016, 2018a).

Wolves tend to be cryptic and avoid humans in most areas of their range. However, notable exceptions do occur, especially where they are not routinely harvested (e.g., YNP, High Arctic). Wolves that become habituated to humans can lead to conflict whether intentional (Linnell et al. 2021) or through misinterpretation (Marquard-Petersen 2022). Nevertheless, the exceedingly rare instances of attacks of wolves on humans are notable for such a large, cursorial predator (Linnell et al. 2021).

GENETICS

Advances in resolution of molecular techniques have added tremendously to our understanding of wolves, but have also created taxonomic challenges. We discuss genetics throughout this chapter with special application to classification, management, and population surveys using noninvasive genetic techniques. Below, we present background information and provide more details and references related to wolf genetics.

Wolves have 39 pairs of chromosomes (Wurster-Hill and Centerwall 1982). Wolves can successfully interbreed and produce fertile hybrids with domestic dogs (Anderson et al. 2002, Randi and Lucchini 2002) and coyotes (Adams et al. 2007, Hailer and Leonard 2008, Wilson et al. 2009, Rutledge et al. 2010a, vonHoldt et al. 2011). However, there is uncertainty regarding whether gray wolves have directly hybridized with coyotes, or rather gene flow between coyotes and gray wolves has been mediated through hybridization with eastern wolves or red wolves (Hailer and Leonard 2008, Rutledge et al. 2010a, Wheeldon et al. 2010). As discussed in the section on Taxonomy and Legal Status, recent breeding experiments, including artificial insemination, associated with coyotes and gray wolves (Mech et al. 2017) were partly successful, but difficulties experienced by some individuals suggested coyotes and gray wolves are unlikely to successfully hybridize under natural conditions.

Although the genetics of wolves is most often thought of in terms of its role in understanding taxonomy and evolutionary history of wolves, it is an important reminder that most details of the physical being, and much of the behavior of a wolf are

governed by its genetics. In summarizing molecular genetic studies of wolves, Wayne and Vilà (2003) presented an impressive list of subjects that have been addressed via studies involving molecular genetics. This list of studies and applications making use of genetics of wolves has only increased in the ensuing years. Briefly, topics relying on molecular genetics included, but are not limited to, studies of population differentiation (Wayne et al. 1992, Roy et al. 1994, Forbes and Boyd 1997, Carmichael et al. 2001, Rutledge et al. 2010a, Wheeldon et al. 2010), population connectivity (Munoz-Fuentes et al. 2009, Hebblewhite et al. 2010, Rick et al. 2017, Rutledge et al. 2017), distribution and population abundance (Adams et al. 2007, Caniglia et al. 2012, Stansbury et al. 2016), interspecific hybridization (Adams et al. 2007, Benson et al. 2012), taxonomic status (Wayne and Jenks 1991, Wilson et al. 2000, Wheeldon and White 2009), evolutionary history (Wayne et al. 1997; Wheeldon and White 2009; vonHoldt et al. 2011, 2016; Sacks et al. 2021; Bergstrom et al. 2022), pack structure (Lehman et al. 1992, Rutledge et al. 2010b, Ausband et al. 2017a), genetic variability (Leonard et al. 2005, Hedrick et al. 2017, Ausband and Waits 2020), genetic bottlenecks (Ellegren 1999, Vilà et al. 2003), inbreeding depression (Hedrick et al. 2014), loss of genetic diversity (Leonard et al. 2005, Hedrick et al. 2014), and identification of individuals responsible for livestock damage (Caniglia et al. 2013).

Detailed discussion of these topics is beyond the scope of this chapter, but some information has been included in other sections. The field of molecular genetics is still relatively new, but it has already provided numerous insights into the ecology and conservation of North American wolves. Ongoing technological advances will only increase the application and utility of genetic studies of wolves.

MANAGEMENT AND CONSERVATION

Sexing Techniques

Determining the sex of wolves is useful for monitoring their population dynamics (e.g., pregnancy rates), assessing conservation genetics, and interpreting behavior (Sparkman et al. 2017). Identifying sex based on pelt characteristics may be an important parameter for harvest management. Sex identification of wolves is generally done through examination of external genitalia, which is visible at close range from time of birth, and in fetuses 45 days post coitus or 18 days before parturition (Hillis and Mallory 1996). Although wolves are sexually dimorphic, observation of genitalia is usually necessary to determine sex. However, some adult females may be visually sexed by teat development, especially during lactation. Breeding females generally have nipples about 1.0-cm (0.4 in) long and are about 2.6-cm (1.0 in) long during periods of peak lactation (Mech et al. 1993). Nonbreeding females generally have teats between 0.6 and 1.0 cm (0.2–0.4 in) in length, whereas teats of yearling females are usually <0.6 cm (0.2 in) in length (Mech et al. 1993). Penile scar or opening, vaginal opening, or prominent nipples can be used as characteristics to identify sex by examining the pelt.

Identifying sexes of wolves from a distance is not definitive, so a combination of traits must be used to decrease uncertainty

(Carbyn 1987). Urination posture may be used to identify sex and status of wolves in the field throughout the year (Kleiman 1966, Mech 1970, Carbyn 1987). Additionally, adult males are about 20% larger in body size than adult females, and males have a larger and sturdier body shape with a more massive head than adult females; adult females are usually the fastest runners (D. W. Smith, personal communication). In pups and yearlings, these morphological characteristics are more difficult to assess because the adult traits are not yet well developed.

During capture operations via helicopter, sex of running wolves can be assessed through comparisons of physical size, observation of a vulva when the tail is raised, and differences in behavior while running. Klaczek et al. (2016) selected for breeding females while conducting net-gunning capture efforts during the early denning season on the tundra by also looking for wolves that had distended nipples within unfurred inguinal areas. Attending behavior of the breeding female at the den and escape behavior of the male were also reliable indicators of sex for aerial-based capture efforts near dens on the tundra in the Northwest Territories and Nunavut (Klaczek et al. 2016). Nonbreeding wolves at a den site could confound sex identification if they are similar in size to the breeding pair. Furthermore, aerial-based capture efforts for wolves near dens are not normally feasible at latitudes below the northern limit of trees (i.e., treeline). Most aerial-based capture efforts for wolves below treeline occur during winter when lakes and rivers are frozen because wolves travel these corridors, and the open space facilitates capture efforts via darting or net-gunning wolves from a helicopter.

For molecular-based sexing, sex-specific DNA markers are often used for a variety of wildlife, such as testing for the presence of a testis-determining factor gene (SRY) in mammals (Strah and Kunej 2019). Specific primers for sex determination have been developed for wolves using fecal, hair, saliva, tooth, and urine samples (Sastre et al. 2009). Genetic methods of sex determination often make use of samples collected noninvasively and therefore do not require handling the animal. Genetic methods are also considered accurate, inexpensive, time efficient, and may often be able to utilize degraded DNA (Seddon 2005, Hrovatin and Kunej 2018).

Aging Techniques

Accurate determination of age classes for wolves is important for assessing population dynamics and ecology (Gipson et al. 2000, Mech 2006, Webb et al. 2011). Distinguishing pups from older wolves is fundamental to quantifying annual recruitment. Fortunately, pups <6–8 months of age are easily distinguished from adults through differences in physical size (Van Ballenberghe and Mech 1975), after which other criteria (e.g., behavior, tooth replacement, tooth wear) may be necessary (Carbyn 1987). Six-month-old pups look physically similar to adults, and by 10–12 months of age are very difficult to distinguish from adults (Mech 1970).

Deciduous teeth of pups are replaced by permanent teeth at about 5.5–6 months of age, allowing for pups to easily be distinguished from older animals during summer and early fall (Mech 1970, Van Ballenberghe and Mech 1975). Van Ballenberghe

and Mech (1975) also used permanent canines <21 mm (0.83 in) in length to identify pups. Internally, pups can also be distinguished by the protruding uncalcified epiphysis at the distal end of the radius-ulna, which is found only in pups ≤10–11 months and not present in yearlings or adults (Rausch 1967, Boertje and Stephenson 1992).

Methods used to estimate the age of older wolves have included tooth wear (Fig. 32.12), cranial suture fusion, closure of canine pulp cavity, and cementum annuli analysis (Landon et al. 1998). Parker and Maxwell (1986) used the maximum width of the dentine-cementum wall in canine teeth of harvested wolves to identify pups killed in their first versus second winter of life. However, cranial sutures, pulp-cavity measurements, and tooth wear are less accurate for older age classes and typically have greater error rates (Ballard et al. 1995, Landon et al. 1998, Lyons et al. 2012, White et al. 2023 [Chapter 14]). Nevertheless, tooth-wear patterns in 2-year increments continue to be the most accurate way to age wolves in the field during post-capture handling (Gipson et al. 2000).

In addition, tooth-wear patterns (e.g., Gipson et al. 2000) and other monitoring programs that require age determination more specific than pup, juvenile, and adult may rely on cementum annuli analysis, an invasive approach that requires tooth extraction. For dead wolves, the canine is the preferred tooth, whereas for live wolves, the first premolar is preferred as it is a smaller, single-root tooth and better suited for extraction (Matson's Laboratory 2019). Extracting any tooth from a live wolf is difficult and may be traumatic even when analgesics or anesthetics are used and is therefore not recommended. Tooth wear (Gipson et al. 2000) is the predominant method for estimating age of live wolves.

Cementum annuli analysis of teeth from dead wolves is the most widely used method for estimating age of older animals

and is the only currently available method to estimate age to the nearest year (Patriquin and Carbyn 1976, Goodwin and Ballard 1985, Landon et al. 1998, Gipson et al. 2000), except for marking pups that can later be identified as known-aged individuals (Mech 1988). Aging wolves via cementum annuli analysis is considered to have moderate (80–90%) accuracy based on their annuli pattern being somewhat distinct and consistent (Matson's Laboratory 2019). Matson (1981) reported that the first opaque cementum layer (first annulus) in the canine of wolves is formed late in the second year of life. Goodwin and Ballard (1985) confirmed this by noting the first annulus deposition occurred between 20 and 22 months of age (based on $n = 4$ wolves). Training is necessary to age teeth via cementum annuli analysis to achieve an overall error of ≤1 year of age, based on comparison to known-age wolves (Goodwin and Ballard 1985, Gipson et al. 2000). Error can be 1–3 years for wolves ≥9 years old (Landon et al. 1998, Gipson et al. 2000). Recently, Thompson et al. (2017) demonstrated that DNA-methylation correlates with age in dogs and wolves as it does in humans. Further refinements in this approach may yield a reliable and accurate method for aging wolves and other mammals based on their molecular clocks (Thompson et al. 2017, Wilkinson et al. 2021).

Growth of the baculum (*os penis*) in male wolves can be informative about age and time of puberty. However, Walleser et al. (2016) could accurately classify pups, but not yearlings or adults, based on baculum length and weight and therefore could not recommend the technique for further use. Other methods that have been used to age other animals may have potential for aging wolves, but need to be evaluated (see White et al. 2023 [Chapter 14]). Some of these methods include gum-line recession (e.g., mountain lions; Landré et al. 2001), front foot-pad width (e.g., Brooks et al. 1998), fatty acids (e.g., beluga whales [*Delphinapterus leucas*]; Marcoux et al. 2015), and telomeres (e.g., Pauli et al. 2011, Remot et al. 2022).

Population Monitoring and Survey Techniques

Biologists currently possess unprecedented opportunities for surveying and monitoring wildlife populations due to recent advances in technology, survey tools, and computational power. Despite this, we are still faced with persistent, nagging questions: the why, what, and how of population monitoring and surveying. The first step in deciding what survey technique to use is to clearly articulate the question(s) of interest because different questions require different survey approaches (Fig. 32.13). Once a question is posed and a decision made about what parameter (e.g., adult survival, population density) to estimate, many survey methods exist to apply to wolf populations and an abundance of analytical tools are available to derive metrics of interest (Table 32.3). Data resulting from some wolf-survey methods have been used as indices and, quite often, the link between the index and true population state (e.g., abundance, survival) was unknown. Recent advances in technology and a host of contemporary survey methods (e.g., genetic sampling, motion-sensing cameras) allow for relatively simple estimation of detection probabilities and better estimation of the true population state.



Fig. 32.12. Excessive tooth wear in wolves (*Canis* spp.) in northern Canada. Image courtesy of D. Cluff, Government of the Northwest Territories, Canada.

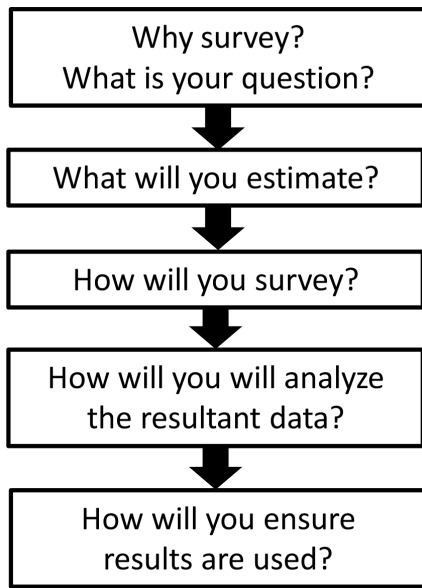


Fig. 32.13. Process flow for designing a population-monitoring program for wildlife species.

Aerial-based Surveys

Surveys from fixed-wing aircraft and helicopters have been used extensively for wolves (Mech 1966, Van Ballenberghe et al. 1975, Theberge and Theberge 1998). Aerial surveys can provide visual observations of wolves, which allows for group counts and possibly composition (adults, pups), as well as ancillary data (e.g., predation behavior). Many extensive long-term studies have estimated or assessed home-range sizes, population density, dispersal behavior, and reproduction from aerial surveys. Generally, aerial surveys require radio-marked individuals or suitable snow conditions for locating and following wolf tracks. Costs of aerial surveys can be considerable, and consistent, fresh snow cover may be a limiting factor.

For many decades, aerial observations, either with or without radio-collared wolves, have been used in APP (Theberge and Theberge 1998), Denali National Park (Mech et al. 1998), IRNP (Mech 1966, Peterson 1977), Kenai (Peterson et al. 1984), Minnesota (Mech 1973, Van Ballenberghe et al. 1975), Wisconsin (Wydeven et al. 1995, 2009), and in nearly all other areas where wolf populations are monitored. Population abundance of wolves is estimated generally during winter when aerial observation rates of wolves are high or tracks are visible in snow (Fuller et al. 2003, Kunkel et al. 2005).

Table 32.3. Survey methods used to monitor wolf (*Canis spp.*) populations in North America. Most useful spatial scale is based on local (<1,000 km² [<386 mi²]) and broad (>1,000 km²).

Method	Advantages	Disadvantages	Most useful spatial scale
Acoustic surveys	Do not necessarily need experienced personnel or large amounts of equipment; can use spectral analysis of howls to enumerate individuals	Labor intensive; requires favorable environmental conditions; potential to double-count individuals and groups	Local; very labor intensive at broader scales
Aerial surveys	Can obtain group counts and possibly composition (adults, pups); can provide ancillary data such as predation behavior	Typically requires radio-marked individuals or ideal snow and vegetative cover conditions; flights can be dangerous for personnel	Local; very expensive at broader scales
Motion-sensing cameras	Do not need experienced personnel; annual survey costs are low once cameras are purchased	Analytical tools still largely under development; data management can be cumbersome	Both local and broad scales; cost of initial equipment may limit broad-scale use
Genetic sampling	Can use abundant fecal, hair, urine and tissue samples; do not necessarily need experienced personnel; can obtain many metrics of interest (e.g., density, diet, relatedness, movements)	Laboratory costs can be expensive; genotyping error rates in scat, hair, and urine samples can be high	Local; costs typically prohibitive at broad scales
Harvest data and public surveys	Inexpensive; potential to obtain other biological samples from harvested individuals (e.g., teeth for aging)	Difficult to replicate annual effort; slow response to potential population decline	Broad
VHF-only collars	Can obtain many metrics of interest (e.g., movements, group size, reproduction); can assess animal condition and health during capture	Requires experienced personnel; expensive; difficult to maintain in dynamic wolf populations (e.g., harvested population); aerial monitoring can be dangerous	Local; associated costs (e.g., subsequent aerial monitoring) typically prohibitive at broad scales
GPS collars	Can obtain many metrics of interest (e.g., habitat use, dispersal, predation); can obtain measures of animal condition during capture; safer than traditional radio-telemetry because aerial monitoring may be unnecessary	Requires experienced personnel; expensive; difficult to maintain in dynamic wolf populations (e.g., harvested population)	Local; associated costs (e.g., collar cost, subsequent aerial monitoring) typically prohibitive at broad scales
Scat transects	Do not necessarily need experienced personnel or large amounts of equipment	Labor intensive; potential to double-count individuals and groups (unless analyzing DNA)	Broad
Scent-stations	Can attract animals and elicit detections; do not necessarily need experienced personnel or expensive equipment	Potential to double-count individuals; can be labor intensive to obtain adequate sample sizes for low-density species	Broad
Snow-tracking	High detection probability; do not necessarily need experienced personnel	Requires optimal snow conditions; potential to double-count individuals and groups	Broad

Acoustic-Howling Surveys

Wolves respond to recorded or human-mimicked howling, therefore, acoustic or howling surveys have been used to monitor wolves and to estimate their distribution and abundance (Pimlott et al. 1969, Russell and Shaw 1971, Harrington and Mech 1979, Fuller and Sampson 1988, Gazzola et al. 2002, Nowak et al. 2007, Gable et al. 2018c, O’Gara et al. 2020). Careful use of triangulation with information from howling surveys may provide a useful means for locating wolves and their home sites (Gable 2018b, O’Gara et al. 2020). Spectral analysis of recordings can help enumerate individuals during chorus howls (Russell and Shaw 1971, Harrington and Mech 1982c, Palacios et al. 2015). Technological advances allow for automated devices to be used for acoustic surveys, thus decreasing labor costs (Ausband et al. 2011, Suter et al. 2017).

Motion-sensing Cameras

Motion-sensing cameras can provide inferences for wolf behavior, disease detection, distribution, habitat use, occupancy, and population density (Trolle et al. 2007, Rowcliffe et al. 2008, Ford et al. 2009, Oleaga et al. 2011, Galaverni et al. 2012, Garland et al. 2020). Steenweg et al. (2015) found that olfactory lures did not increase detections of wolves at cameras, and recently the Idaho Department of Fish and Game (Thompson et al. 2022) placed cameras without such lures in predicted rendezvous-site habitat to estimate statewide abundance of wolves. Data from camera surveys have been combined with an occupancy modeling framework to monitor distribution and trends in population abundance of wolves (Ausband 2019b). Additionally, recent advances in modeling populations of unmarked animals (e.g., random encounter model; Rowcliffe et al. 2008, Moeller et al. 2018), and comparisons between cameras and an independent measure of population density of wolves suggest population density can be accurately estimated from a high-density array of cameras (1 camera/50 km² [1/19 mi²]; Ausband et al. 2022).

Russo et al. (2022) collected >7 million images (13,317 of which were images of Mexican wolves) in Arizona from 124 cameras and used a spatial mark-resight analysis to estimate abundance during winter and summer with and without the use of location data from GPS-collared wolves. They found all estimates were lower than the current method of locating radio-collared pack members and obtaining a minimum count. Abundance during winter was so unacceptably underestimated that they recommended focusing on only the summer period. The coming years will almost certainly bring new analytical approaches to use camera data for population monitoring of wolves.

Genetic Sampling

DNA of appropriate quality from hair, scat, tissue, and urine may be used to identify individuals (Waits and Paetkau 2005). Genotypes from individuals may then be used to estimate genetic relatedness and diversity, population density, and several other metrics (Marucco et al. 2009; Stenglein et al. 2010, 2011; Caniglia et al. 2014; Roffler et al. 2019). Recent advances using single nucleotide polymorphisms and genomics have shed light on mechanisms of

evolution and population differentiation in wolves (Heppenheimer et al. 2018a, Pilot et al. 2018, Robinson et al. 2019, vonHoldt et al. 2020). Genomics is a rapidly advancing field and will likely yield unparalleled insights for wolf ecology in the coming years.

Genetic sampling, mark-recapture models (Marucco et al. 2009, Marescot et al. 2011), and single-session maximum-likelihood models (Stenglein et al. 2010) have been used to estimate vital rates of wolf populations. Collecting noninvasive genetic samples is generally easier than capturing, radio-collaring, and monitoring an individual wolf. Thus, analytical approaches to population estimation via genetics will likely continue to become more popular. DNA may also be extracted from tissue samples of harvested wolves. The resulting genotypes can be used in sibship analyses to estimate the minimum number of litters present and effective population size prior to harvest (Clendenin et al. 2020).

Harvest Data and Public Surveys

Harvest data from hunters and trappers are routinely used by wildlife managers as cost-effective, recurring data and are particularly useful for species such as wolves that are difficult to detect and exist at low population densities (Hiller et al. 2021, 2023 [Chapter 10]; White et al. 2023 [Chapter 9]). With mandatory harvest reporting, managers can obtain information on harvest method, location, and timing, as well as sex, age, pelt coloration, and collection of tissue, organs, and hair samples for genetic, reproductive, and dietary analyses. In addition to coarse metrics such as hunter success, data from hunters and trappers have been used to infer distribution and population trends (Crête and Messier 1987, Robichaud and Boyce 2010, Rich et al. 2013). Harvest data may also be integrated into a statistical population reconstruction approach with additional data (Gove et al. 2002). The reliability of estimates using hunter or public survey data can be affected by difficulties in estimating hunter effort and precisely replicating conditions between years.

Radio-marking

Capturing and radio-collaring wolves has provided a wealth of knowledge about their ecology and population dynamics (Kolenosky and Johnston 1967, Mech 1970, Fuller et al. 2003). Radio-marked individuals may be monitored, and data collected to provide estimates of abundance, dispersal, mortality, pack size, reproduction, and space use (Mech 1974b; Messier 1985a, 1985b; Fuller and Snow 1988; Burch et al. 2005; Smith et al. 2010; Jimenez et al. 2017). Additional marks may be applied to captured wolves to facilitate identification (e.g., lip and ear tattoos, ear tags, passive integrated transponder [PIT] tags, visual marks on the radio-collar).

Radio-collars that use GPS systems offer several advantages over radio-collars with only Very High Frequency (VHF) capabilities because GPS collars collect data that can be remotely downloaded via radio signals and are not reliant on, for example, aerial-based telemetry flights limited by daylight or adverse weather. Further, GPS collars typically have onboard storage of GPS data and can be programmed to collect numerous locations of a radio-marked individual at specific time intervals over a specified period.

Finally, GPS collars typically also have independent VHF systems, which also allow for use of traditional telemetry methods to monitor radio-marked individuals, such as signals that may indicate mortality. Such advances in technology allow for estimation of metrics (e.g., dispersal, habitat use, predation) of interest that would be very difficult, if not impossible, to obtain with VHF-only systems (Merrill and Mech 2003, McLoughlin et al. 2004, Cusack et al. 2020). Because flights are often not necessary to obtain location information from GPS-collared individuals, GPS-collared wolves are often not observed and thus pack counts are not obtained. Compared to VHF-only collars, GPS collars can have higher rates of electronic failure, shorter battery life, and are generally much more expensive. However, the costs of subsequent telemetry flights should be factored into the realized cost of VHF-only collars. The decision of whether to use GPS or VHF-only collars depends on data needs, ability to capture wolves, economics, and availability of aircraft.

Snow-tracking Surveys

Locating wolf tracks in snow through ground- and air-based surveys has been used across a variety of landscapes (Patterson et al. 2004, Beyer et al. 2009, Wydeven et al. 2009, Liberg et al. 2012, Erb 2019). Wolves exist at relatively low population densities, yet a canvas of snow cover records tracks of wolves and can provide many opportunities to detect wolves that are otherwise unavailable during snow-free times of year. Generally, snow-tracking yields a high detection probability and, at least from the ground, requires only limited training for personnel. Ground-based snow-track surveys are conducted along snow-covered forest roads and trails in Michigan and Wisconsin to obtain minimum counts of wolves at regional and statewide scales (Beyer et al. 2009, Wydeven et al. 2009), and as an index of population abundance of wolves and other furbearers in Minnesota (Erb 2019). There are several techniques for estimating population density of wolves from track surveys (Becker et al. 1998, Patterson et al. 2004, Mattson et al. 2009, Gardner and Pamperin 2014, Latham et al. 2014). In Wisconsin, population estimates have changed from minimum counts to estimates from scaled-occupancy modeling, but snow-track surveys continue to be the means for determining occupancy by wolves (Stauffer et al. 2021).

Model-based Approaches

Overarching models can make use of any of the aforementioned data streams (e.g., DNA, telemetry). For example, occupancy models have been used to integrate multiple sources of data (e.g., DNA surveys, harvest surveys, radio-marked individuals) and estimate abundance, distribution, and population trend of wolves (Rich et al. 2013, Ausband et al. 2014, Latham et al. 2014, Stauffer et al. 2021, Sells et al. 2022b). Occupancy models incorporate detection probability and use detection-nondetection data, often an economically feasible data stream to obtain for wolves. Such models generate the probability that a given area is or will be occupied. However, progressive layers of assumptions (e.g., mean territory size, mean pack size) are required to generate estimates of abundance. Additionally, integrated population models and

individual-based population models have been populated with empirical data and then used to estimate wolf abundance and other vital rates of interest (Chapron et al. 2016, Horne et al. 2019). Such modeling approaches can be computationally intensive and may be challenging to distill for the general public, although these issues do not preclude their usefulness.

Harvest Management

Canada

Harvest management of gray wolves in Canada is conducted with the goal of long-term population sustainability (Tables 32.4 and 32.5). The gray wolf is classified as both a furbearer and a game animal in most Canadian jurisdictions. Harvest of gray wolves in Canada occurs in all 7 provinces and 3 territories in which wolves occur and is managed through provincial and territorial wildlife acts with regulations that provide a framework for sustainable harvest management and monitoring (Carbyn 1983, Hayes and Gunson 1995). Wolves are currently allowed to be trapped, and more recently hunted, in Saskatchewan, albeit only by residents of Saskatchewan, but generally with liberal season lengths (Saskatchewan Ministry of Environment 2019).

Regarding the management of eastern wolves in Québec, no wolf species is listed under the *Lois sur les espèces menacées ou vulnérables* (Act respecting threatened or vulnerable species in Québec; Government of Québec 2023). Harvest of wolves is permitted in wildlife reserves in Québec, but not in federal or provincial parks. To protect the provincially listed eastern wolves in Ontario, all wolves are protected from regulated hunting and trapping in APP, in the townships surrounding APP, and in all provincial Crown (government) Game Preserves. Indigenous communities retain constitutional rights to harvest wolves for sustenance and ceremonial purposes, including in protected areas.

Harvest of wolves in Canada occurs primarily through trapping, except in the Northwest Territories and Nunavut where more wolves are harvested by hunting, specifically by hunters using a rifle. Wolf harvest in the Northwest Territories and Nunavut can fluctuate widely in consecutive years because wolves follow migratory barren-ground caribou, and the winter ranges of caribou can shift annually and may also overlap with adjacent caribou herds (Cluff et al. 2010). Most Canadian jurisdictions use registered traplines on Crown land, whereby every trapper is assigned a specific trapline and given exclusive rights for that area. This system encourages close cooperation between trappers and wildlife managers, but there is no bag limit for wolves on individual traplines in most provinces and territories (Table 32.5). Trapping on privately owned land requires the permission of the landowner and harvest quotas for privately owned land are generally assigned based on size and productivity of that area, and past levels of harvest.

In 2018, an estimated 4,383–4,423 wolves were harvested in Canada (B. R. Patterson, unpublished data), considerably less than the peak level of harvest of 21,000 during the 1927–1928 season (Carbyn 1987). Harvest levels of wolves in Canada declined during the late 1940s and remained at <2,000/year through 1968–

Table 32.4. Harvest regulations for hunting gray (*Canis lupus*) and eastern (*Canis lycaon*) wolves in Canada by jurisdiction during 2018. Bag limit = maximum number of wolves that may be legally harvested by an individual hunter.

Jurisdiction	Management unit(s)	Bag limit	Month														
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
Alberta ^a		No limit															
British Columbia	507–509, 601–630, 719–722, 731–736, 742–758	3															
	334–344, 702–718, 723–730, 737–741	No limit															
	101 – 115, 205, 206, 211–216, 312–320, 326–333, 801–815, 821–826, 401–404, 409, 414–416, 419, 421–426, 432, 434–436	3															
	510–511	3															
	405–408, 417–418, 420, 428–431, 433, 437–440	No limit															
501–506, 512–515	No limit																
Labrador		1															
Manitoba		1															
Northwest Territories		No limit ^{b,c}															
	Area 1																
Area 2																	
Nunavut		No limit															
Ontario		2															
Québec		No limit															
Saskatchewan		1															
Yukon		7 ^c															

^aA resident may, without a license, hunt (but not trap) wolves under specific circumstances during big-game hunting season.

^bBag limit of 2 wolves in a subset of management units.

^cBag limit of 1 or 2 wolves for nonresident hunters.

Table 32.5. Harvest regulations for trapping gray (*Canis lupus*) and eastern (*Canis lycaon*) wolves in Canada by jurisdiction during 2018. No jurisdiction imposed a bag limit (defined as the maximum number of wolves that may be legally harvested by an individual trapper) associated with trapping wolves.

Jurisdiction	Region	Month														
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec			
Alberta																
British Columbia	1															
	2															
	3–8															
Labrador																
Manitoba																
Northwest Territories																
Nunavut																
Ontario																
Québec																
Saskatchewan																
Yukon																

69 (Carbyn 1983, 1987). Beginning in 1969–1970, harvest levels increased each year until about 5,000–7,000 wolves/year were harvested from the mid-1970s through the mid-1980s (Fig. 32.14).

Wolf pelts remain popular for use in fur garments, but the guard hairs are brittle and not as durable as those of some other furbearing species (Carbyn 1987). Wolf fur is used primarily for parka trim, fur coats, and rugs. Hair fibers of wolves do not mat or hold frost, as do those of most other furbearers; hence, parka trim made from wolf and other canid pelts is second only to those made from wolverine (*Gulo gulo*) fur (Carbyn 1987). Pelts of white and

black color phases of wolves tend to be more valuable than those of brown and gray phases; black wolves are sought after in the Northwest Territories and those pelts bring higher prices there (H. D. Cluff, unpublished data).

United States

In Carbyn (1987), wolves were harvested only in Alaska and Canada. With recovery of gray wolves in the conterminous U.S., regulated harvest in recent years was also conducted in Idaho, Michigan, Minnesota, Montana, Washington (only on the Colville

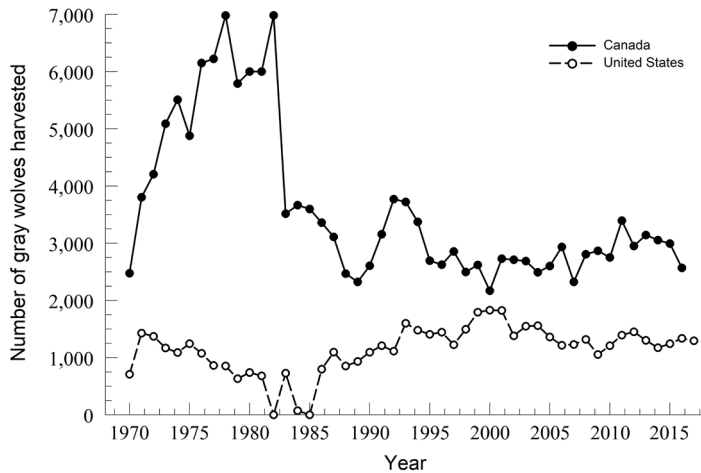


Fig. 32.14. Estimated annual minimum harvest of wolves (*Canis* spp.) in Canada and the U.S. during 1970–2015, based on data from Association of Fish and Wildlife Agencies (2018), Statistics Canada (2019), and Fur Institute of Canada (2022b).

Reservation), Wisconsin, and Wyoming (Association of Fish and Wildlife Agencies 2018; Fig. 32.14, Table 32.6). Regulated harvest began in Idaho and Montana after federal delisting occurred in 2009, discontinued with relisting in 2010, and resumed with delisting in 2011 (Hayden 2017; Montana Fish, Wildlife, and Parks 2018; Parks et al. 2022). Harvest of wolves occurred in Wyoming in 2012 and 2013 with federal delisting, ended with relisting in 2014, and resumed with delisting in 2017 (Wyoming Game and Fish Department et al. 2021). Harvest was allowed in the Great Lakes states during 2012–2014, when wolves were federally delisted (MacFarland and Wiedenhoef 2013, 2014, 2015; Stark and Erb 2013, 2014), but wolves were subsequently relisted in 2014, and then delisted in 2021 (USFWS 2020). During recent delisting of gray wolves between 4 January 2021 and 10 February 2022, only Wisconsin within the Great Lakes states had a harvest season in February 2021, resulting in 218 wolves harvested in 3 days (Johnson and Schneider 2021). In eastern Washington, the Colville Reservation has had limited harvest since 2013 on reservation lands in areas federally delisted as part of the Northern Rocky Mountain Distinct Population Segment.

Alaska has the highest number of wolves harvested at the state level in the U.S., with an annual total of 1,050–1,300 wolves (Parr 2018, Spivey 2019), or about 12% of the estimated annual wolf population, assuming a statewide population of about 9,500 wolves (Alaska Department of Fish and Game 2019; Table 32.6). Idaho currently has regulations that support a relatively liberal harvest of wolves, representing 28–48% of the estimated wolf population (estimated during winter), designed to meet the objective of the state fish and wildlife agency to decrease population abundance (Idaho Department of Fish and Game 2023). The current harvest rate in Idaho is consistent with rates expected to lead to population declines (e.g., >29–35% [Fuller et al. 2003], >29% [Adams et al. 2008]; but see Creel and Rotella 2010, Gude et al. 2012).

Montana used a patch-occupancy model for estimating populations (Inman et al. 2020, Parks et al. 2022), and harvest rates

varied from 9% to 36% of the statewide population. Populations in Montana seemed to have stabilized or slightly declined during the past decade (Inman et al. 2020). In Idaho, both pack size and density have declined across several study areas (Ausband et al. 2017b, Bassing et al. 2020). Limited harvest was conducted on Colville Reservation in delisted areas of eastern Washington, but this represented $\leq 3\%$ of the statewide population of wolves (Washington Department of Fish and Wildlife 2019).

In the Great Lakes region, Minnesota and Wisconsin had moderate levels of harvest during 2012–2014, whereas Michigan had a very limited harvest (23 wolves) in 2013. A harvest of 32% of the statewide population did lead to a minor population decline in Wisconsin in 2014, but the decreased level of harvest of 23% the following year resulted in the population increasing slightly (Table 32.6). Stenglein et al. (2015) demonstrated that a stable level of harvesting 30% of the wolf population across 6 zones in Wisconsin over a 100-year modeling simulation led to extinction 14% of time, and otherwise resulted in substantial declines in the population. Other scenarios that included lower levels of harvest in 3 zones in core habitat for wolves, but liberal harvest in zones at the periphery of wolf range, resulted in minor declines in the population or in stabilizing populations (Stenglein et al. 2015).

As apparent from the Stenglein et al. (2015) modeling effort and harvest observed across the U.S., regulated trapping and hunting can be used to decrease or stabilize wolf populations without causing substantial declines. When contemporary regulated harvest is first implemented in a wolf population, that population should be closely monitored to avoid potentially negative impacts (Horne et al. 2019), including decreased opportunities for viewing wolves in protected areas adjacent to harvest zones (Borg et al. 2016, Schmidt et al. 2017); excessive loss of breeding individuals (Brainerd et al. 2008, Borg et al. 2015, Ausband et al. 2017a); increased risk of hybridization of eastern wolves or red wolves with domestic dogs or coyotes (Rutledge et al. 2011, Moura et al. 2014); increased stress and reproductive steroids (Bryan et al. 2014); disrupted social structure (Rutledge et al. 2010b); and decreased recruitment (Ausband et al. 2015). High levels of harvest (>34% of the fall population) in areas of high access for humans may not be sustainable (Person and Russell 2008).

Regulated hunting and trapping of gray wolves occurs across the world, including most areas of Alaska and Canada (Musiani and Paquet 2004, Webb et al. 2011, Hill et al. 2022), yet harvest of wolves can be controversial, especially for populations in the U.S. that have recently been considered recovered under the ESA (Treves 2009, Vucetich and Nelson 2017, Vucetich et al. 2017). There is evidence that legal killing of wolves through regulated harvest and livestock depredation control may decrease illegal killing in some areas (Bradley et al. 2015, Olson et al. 2015, Liberg et al. 2020). In a meta-analysis of 21 studies, Hill et al. (2022) did not detect a decreased level of illegal killing of wolves, but did determine that number of wolves in management removals declined in harvested populations of wolves.

Although regulated harvest of wolves seems to decrease the level of conflicts (Robichaud and Boyce 2010, Webb et al. 2011, DeCesare et al. 2018), there is debate as to when harvest should

Table 32.6. Metrics associated with estimated state-level harvest and population abundance for gray wolves (*Canis lupus*) in USA, during 2009–2017. Metrics include: Harvest (combined) = cumulative number harvested by hunting and trapping; Harvest (hunting) = estimated annual number harvested by hunting; Harvest (trapping) = estimated annual number harvested by trapping; Harvest (%) = estimated total number harvested divided by estimated population abundance metric during winter × 100; Population (midpoint) = midpoint of range of estimated population size; Population (min) = annual minimum number of wolves counted; Population (estimate) = estimated annual population size. NA = not available.

State	Metric	Year								
		2009	2010	2011	2012	2013	2014	2015	2016	2017
Alaska^a										
	Harvest (combined)	1,070	1,209	1,261	1,264	1,116	1,019	1,045	1,145	1,210
	Harvest (%)	11	13	13	13	12	11	11	12	13
	Population (midpoint)	9,500	9,500	9,500	9,500	9,500	9,500	9,500	9,500	9,500
Idaho^b										
	Harvest (hunting)	181	0	253	195	187	138	145	143	NA
	Harvest (trapping)	0	0	123	121	104	119	125	83	NA
	Harvest (%)	21	0	48	44	43	33	34	28	39
	Population (min)	856	777	760	722	684	785	786	850	850
Michigan^c										
	Harvest (hunting)	0	0	0	0	23	0	0	0	0
	Harvest (%)	0	0	0	0	3	0	0	0	0
	Population (min)	577	557	687	NA	658	636	NA	618	NA
Minnesota^d										
	Harvest (hunting)	0	0	0	214	119	148	0	0	0
	Harvest (trapping)	0	0	0	199	119	124	0	0	0
	Harvest (%)	0	0	0	NA	11	11	0	0	0
	Population (estimate)	2,900	NA	NA	NA	2,211	2,423	2,221	2,278	2,856
Montana^e										
	Harvest (hunting)	72	0	166	128	143	130	134	164	166
	Harvest (trapping)	0	0	0	97	87	76	76	83	88
	Harvest (%)	9	0	17	25	21	23	21	30	30
	Population (estimate)	847	862	971	915	1,088	898	981	814	854
Washington^f										
	Harvest (hunting)	0	0	0	0	1	0	3	3	3
	Harvest (%)	0	0	0	0	2	0	3	3	2
	Population (estimate)	15	19	35	51	52	68	90	115	122
Wisconsin^g										
	Harvest (hunting)	0	0	0	56	77	30	0	0	0
	Harvest (trapping)	0	0	0	61	180	124	0	0	0
	Harvest (%)	0	0	0	14	32	23	0	0	0
	Population (min)	637	704	782	815	806	660	746	866	925
Wyoming^h										
	Harvest (hunting)	0	0	0	41	23	0	0	0	43
	Harvest (%)	0	0	0	15	18	0	0	0	12
	Population (min)	320	343	328	277	306	333	382	377	347

^aParr 2018, Alaska Department of Fish and Game 2019, Spivey 2019.

^bHayden 2017, Idaho Department of Fish and Game 2020.

^cVucetich et al. 2017, Michigan Department of Natural Resources 2022b.

^dStark and Erb 2013, 2014; Erb et al. 2015, 2018.

^eMontana Fish, Wildlife, and Parks 2018.

^fWashington Department of Fish and Wildlife et al. 2019.

^gMacFarland and Wiedenhoeft 2013, 2014, 2015.

^hWyoming Game and Fish Department et al. 2018.

occur (Creel et al. 2014, Epstein 2017, Vucetich et al. 2017). For example, even the very limited harvest of 23 wolves in Michigan was challenged (Vucetich et al. 2017). Across most of their global range, harvest of wolves is usually accepted and expected by the public (Ericsson et al. 2004, Treves and Martin 2011, Treves et al. 2013, Holsman et al. 2014). Continued use and expansion of hunting and trapping opportunities in additional areas within the range of wolves, along with sound biological justification, will also need to incorporate ethics and good wildlife governance (Decker et al. 2016).

Damage Management

Levels of depredation by gray wolves on domestic animals vary with population abundance of wolves and livestock-grazing practices across U.S. states (Table 32.7). In the U.S., depredation of cattle was generally less frequent in the Great Lakes states compared to western states, except in Minnesota, where the population abundance of wolves is higher than the cumulative number of wolves in Idaho, Montana, and Wyoming (Table 32.7). Higher levels of depredation on cattle and sheep in these 3 western states was probably due in part to the presence of livestock grazing on public lands (Hanley et al. 2018), whereas in the Great Lakes region, cattle and other livestock graze only in fenced pastures on privately owned lands (Fritts et al. 1992, Treves et al. 2002, Ruid et al. 2009). The highest level of depredation on sheep generally occurred in Idaho (Table 32.7). Cattle killed were usually calves, and generally single mortalities; however, sheep killed often included both lambs and adults, and often multiple animals during each depredation event. Highest levels of depredation on domestic fowl occurred in the Great Lakes region, especially on turkey farms, where surplus killing often occurred (Fritts et al. 1992, Ruid et al. 2009). Other domestic or captive species killed by wolves included alpacas, bison, deer, donkeys, emus, goats, horses, llama, pigs, and rabbits. Some depredations of domestic fowl may have been pooled into a miscellaneous category by some government agencies, and included chickens, ducks, geese, pheasants, and turkeys.

The level of depredation of domestic dogs was especially high in Great Lakes states (Table 32.7), but was also high in Idaho, where hounds are used for hunting black bears and mountain lions. In the Great Lakes region, most dogs killed by wolves were hounds used for hunting black bears in Michigan and Wisconsin; but in Minnesota, where use of hounds for hunting bears is not allowed, attacks were primarily on dogs near homes (Ruid et al. 2009). Higher levels of attacks on hunting dogs in Wisconsin compared to Michigan may be due to the relatively lengthy period of legally using bait for hunting bears in the former; these bait sites, where hounds are released to track and pursue bears, are used by both wolves and bears (Bump et al. 2013).

Lethal methods to reduce depredation levels on domestic animals have been available in most of the NRM, where wolf populations in the U.S. have been classified as nonessential experimental and endangered under the ESA since reintroductions in 1995. Early in the recovery of wolves in the NRM, the potential utility for incremental removal and translocation of livestock-killing wolves was tried and tested. However, survival of translocated wolves was low, and few lived long enough to contribute to reproduction and population growth. Wolves were translocated after confirmed livestock depredations, but sometimes they were moved preemptively when conflict seemed imminent. By around 2005, translocation became less practical as a means of mitigating livestock damage within both the NRM and the Great Lakes region because rapid population growth resulted in fewer sites available for releasing translocated wolves (Bradley et al. 2005).

In the Great Lakes states, lethal control was authorized in Minnesota during 1978, when wolves were downlisted from endangered to threatened under the ESA (Fritts et al. 1992). Lethal control authority did not occur in Michigan and Wisconsin until down-listing occurred in 2003, and several changes in status of wolf populations resulted in shifting of management authority between state and federal agencies (Refsnider 2009, Olson et al. 2015, USFWS 2020). The highest levels of lethal management of wolves for livestock depredation was in Minnesota, averaging 173 wolves annually with a high of 215 wolves, nearly as high as

Table 32.7. Annual mean (and range) number of confirmed kills of domestic species that were attributed to gray wolves (*Canis lupus*), annual number of gray wolves lethally removed in response to depredations, and trends in number of depredations in the U.S. during 1998–2018. Other species included alpaca, bison, deer (captive), donkeys, emu, fowl (when not reported separately), goats, horses, llama, pigs, and rabbits. NA = not available.

State	Years	Species					Number of wolves removed	Trend in number of depredations
		Cattle	Dogs	Fowl	Sheep	Other		
Arizona and New Mexico ^a	1998–2015	15.3 (0–48)	NA	NA	NA	NA	3.8 (0–19)	Increasing
Idaho ^b	2007–2015	80.3 (44–128)	7.1 (1–15)	0.0	245.2 (107–442)	1.7 (1–6)	77.3 (50–108)	Declining
Michigan ^c	1996–2017	14.9 (0–58)	5.3 (0–17)	8.1 (0–90)	2.5 (0–11)	1.0 (0–12)	8.5 (1–26) ^d	Stable
Minnesota ^e	2006–2018	77.0 (52–91)	6.4 (2–16)	97.8 (0–554)	10.8 (0–22)	12.5 (2–30)	172.7 (95–215)	Stable
Montana ^f	2008–2017	63.1 (37–97)	1.2 (0–4)	0.0	49.5 (5–202)	6.2 (0–19)	84.8 (39–141)	Declining
Oregon ^g	2009–2018	7.5 (1–17)	0.3 (0–2)	2.3 (0–23)	8.9 (0–30)	0.6 (0–2)	5.0 (3–7) ^h	Increasing
Washington ⁱ	2009–2018	4.5 (0–11)	0.0	0.0	3.1 (0–28)	0.0	3.1 (0–7) ^j	Increasing
Wisconsin ^k	1995–2018	29.5 (0–67)	16.2 (0–47)	8.0 (0–68)	4.2 (0–27)	4.0 (0–29)	20.9 (0–57) ^l	Stable
Wyoming ^m	2006–2018	63.8 (20–123)	1.2 (0–7)	0.0	55.6 (6–195)	0.5 (0–1)	51.2 (31–113)	Stable

^aU.S. Fish and Wildlife Service 2018c.

^bHayden 2017, Idaho Department of Fish and Game 2020.

^cC. Norton, Michigan Department of Natural Resources, personal communication.

^d2003–2016.

^eU.S. Department of Agriculture-Wildlife Services 2018.

^fMontana Fish, Wildlife, and Parks 2018.

^gOregon Department of Fish and Wildlife 2019.

^h2016–2018.

ⁱWashington Department of Fish and Wildlife 2019.

^j2012–2018.

^kD. B. Ruid, U.S. Department of Agriculture-Wildlife Services, personal communication.

^l2003–2018.

^mWyoming Game and Fish Department 2021.

the harvest levels during 2013 and 2014. Higher levels of lethal control occurred in Minnesota, compared to Idaho and Montana, perhaps because the western states consistently had regulated harvest since 2011, whereas Minnesota had regulated harvest only during 2012–2014. Regulated harvest can reduce the number of wolves removed at depredation sites (Hill et al. 2022). During the 3 years that wolves were harvested in Minnesota and Wisconsin, the number of livestock depredations declined, and the number of wolves killed for depredations declined, as was predicted through modeling (Haight et al. 2002, Stenglein et al. 2015).

Although some researchers have questioned the effectiveness of lethal methods for minimizing livestock depredations by wolves (Treves et al. 2016, Santiago-Avila et al. 2018), simulation modeling supports use of lethal methods, especially reactive approaches at livestock depredation sites (Haight et al. 2002, Stenglein et al. 2015). Rigorous examination of depredation-management programs has demonstrated benefits of lethal management (Harper et al. 2008, Bradley et al. 2015, Poudyal et al. 2016). Direct reactive approaches at depredation sites are generally most effective at addressing depredations, but regulated harvest can also contribute to reduced number of depredations (Haight et al. 2002, Stenglein et al. 2015, DeCesare et al. 2018, Hill et al. 2022).

A variety of nonlethal methods may also reduce the level of wolf-related depredations on livestock and pets. Translocation of problem wolves was used in Minnesota during 1975–1979 (Fritts et al. 1984, 1985), Michigan and Wisconsin during 1991–2002 (Ruid et al. 2009, Mech 2015), and in the NRM during 1995–2005 (Bangs et al. 1995, 1998; Bradley et al. 2005). Other nonlethal methods have included changes in animal-husbandry practices (Stone et al. 2017), and use of electric fencing (Gehring et al. 2010a), fladry (Musiani et al. 2003), guard dogs for livestock (Fritts et al. 2003, Gehring et al. 2010b), radio-activated electronic-guard devices (Breck et al. 2002), shock collars on wolves (Hawley et al. 2013); and other methods (Shivik 2014, Stone et al. 2017). However, radio-activated electronic-guard devices and shock collars require that wolves be captured, handled, and released, which is a costly and time-consuming task, and thus only suitable for the most critical local situations, such as where wolves are endangered.

In the conterminous U.S., all states with a breeding population of wolves currently support financial compensation programs to reimburse citizens for losses caused by wolves, but programs vary somewhat on rates of reimbursement and eligibility of individual species. Wisconsin includes payments for missing beef and dairy calves and dogs used for hunting. The state of Wisconsin spent US\$2.5 million on compensation for depredations in the state from 1985 to 2018, which included about one-third paid for injured or killed hounds (Wisconsin Department of Natural Resources 2020). Average annual payments for depredation compensations were US\$170,334 in Wisconsin during 2009–2018 (Wisconsin Department of Natural Resources 2020), US\$131,669 for Minnesota during 2009–2018 (U.S. Department of Agriculture-Wildlife Services 2018), US\$14,068 for Michigan during 2006–2015 (Michigan Department of Natural Resources 2022b; C. Norton, Michigan Department of Natural Resources, personal

communication), and US\$87,899 for Montana during 2008–2017 (Montana Fish, Wildlife, and Parks 2018). Although compensation payments do not always improve stakeholder attitudes toward wolves (Naughton-Treves et al. 2003), such payments are strongly supported by the public (Holsman et al. 2014).

Risk-mapping systems have been used to predict future depredation areas in Michigan (Edge et al. 2011), Washington (Hanley et al. 2018), and Wisconsin (Treves et al. 2004, 2011; Olson et al. 2019). In the Great Lakes region, livestock depredations tend to occur more often at the periphery of wolf distribution or in more marginal habitat with larger patches of pasture and cropland, and lower proportions of forest cover compared to land cover in the core range of wolves (Treves et al. 2004, 2011; Edge 2011). Conversely, hound depredation by wolves in Wisconsin occurred in core habitat (Olson et al. 2019). In Washington, areas with high risk of depredations included grazing allotments on public lands located within core habitat (Hanley et al. 2018). High-risk areas for livestock depredation in Wisconsin included only 10% of the wolf distribution in the state (Treves et al. 2011). Risk maps can be useful for planning proactive management approaches, management zones, and harvest zones.

Management of Wolves for Wild Ungulate Populations

During the first half of the twentieth century, predator management was considered important for both human safety and protection of livestock and other wildlife species (Oriens et al. 1997). In fact, the goal of most early research on wolves and other predators was to determine how to reduce their abundance and mitigate conflict (Young and Goldman 1944, Pimlott et al. 1969). Data on life history and ecological roles of predators, including predator-prey relationships, were rarely collected. As public attitudes shifted during the 1960s and 1970s, the use of predator-management programs became increasingly questioned (Theberge 1973), and collection of more broad-based data on wolves became commonplace. However, increased understanding of wolf ecology and predation has not resolved all issues and controversies regarding wolves. For example, the issue of whether predation by wolves on ungulate populations is additive to other sources of mortality remains both complicated and contentious (Mech and Peterson 2003). Depending on the extent of human influence on wolves, the prey species present, habitat conditions, and presence and relative population densities of other predators (e.g., black bears, grizzly bears, mountain lions), the effects of predation by wolves on ungulate population dynamics may be considered strongly limiting, regulating, or in some cases, neither (Van Ballenberghe and Ballard 1994, Hayes et al. 2003, Mech and Peterson 2003).

Messier and Crête (1985) concluded that moose populations in southwestern Québec were regulated primarily by predation from black bears and wolves. However, an experimental killing of black bears and wolves from the same study area failed to produce measurable increases in recruitment of moose calves or in overall abundance of the moose population (Crête and Jolicoeur 1987). The authors attributed their inconclusive results to weak treatments, close proximity of the treatment and control areas, sampling error, and insufficient sample sizes (Crête and Jolicoeur

1987). Gasaway et al. (1992) suggested a reduction in predator populations was often necessary in moose-bear-wolf ecosystems to increase population densities of moose to levels above the low-density equilibria maintained by predation, and thereby increase harvest opportunities for humans. Gasaway et al. (1992) encouraged management for relatively high population densities of moose and high prey:predator ratios to minimize limitation by predators. In so doing, they acknowledged that there was a risk of moose populations exceeding carrying capacity and consequently triggering a decline in moose populations that may be extended by predation.

Boertje et al. (2010) reviewed numerous studies to determine sustainable harvest levels of female moose in Alaska. They suggested results of these studies supported application of long-term, substantial levels of predator control for increasing population abundance of moose in simple systems where moose were a primary prey species for bears and wolves. The state of Alaska has consistently conducted population control of wolves since 2003 under what is called Intensive Management (Alaska Department of Fish and Game 2019). Miller et al. (2022) analyzed harvest data to test hypotheses that nearly 4 decades of effort to decrease population abundance of brown bears, black bears, and wolves in Game Management Unit 13 in south-central Alaska was positively correlated with number of moose harvested in some time-lagged fashion. The number of moose harvested was negatively correlated with the number of wolves harvested during the previous year, but the relationship was weak. Miller et al. (2022) rejected their hypothesis that harvest of predators was positively correlated with harvest of moose in south-central Alaska and recommended that efforts to decrease populations of predators be designed to improve harvest of moose and be conducted within a research framework that permits clear and rigorous interpretation of results. Clark and Hebblewhite (2021) echoed this sentiment and recommended that managers attempting to evaluate experimental practices to increase ungulate populations through predator removal employ an open-standards framework akin to the Open Standards for the Practice of Conservation developed by the Conservation Measures Partnership (2013).

Hayes et al. (2003) conducted wolf-removal programs in the Yukon that also included wolf-sterilization experiments (Spence et al. 1999). The premise for sterilization is that following sterilization of either member of the breeding pair, the pack structure is maintained, but without production of pups. Fertility control was also more socially acceptable than lethal control (Hayes et al. 2003). Hayes et al. (2003) and Farnell (2009) concluded that experiments of wolf-fertility control were effective in decreasing the rate of population growth of wolves, and thereby were successful in the recovery of the Aishihik caribou herd in the Yukon, especially when conducted with wolf-removal efforts and decreases in harvest of caribou compared to a stand-alone approach. However, Hayes et al. (2003) also recommended that managers use habitat enhancement for caribou and regulated trapping of wolves to sustain higher population densities of ungulates and avoid the need for reactive broad-scale control methods for wolves.

Boertje et al. (2017) studied demography of the migratory Fortymile herd of caribou in Alaska using telemetry-based data collection during 1990–2014, which included periods of both non-lethal sterilization and translocations of wolves (1998–2004), and lethal control of wolves (2005–2013). During this time, the size of the Fortymile herd increased from about 22,000 to 52,000 caribou. Boertje et al. (2017) first documented that wolves were the primary predator before and during nonlethal control of wolves. Although they demonstrated that nonlethal control using translocation and fertility control can substantially decrease local abundance of wolves, and that the effects of such a control program on individual packs can persist for ≥ 3 years after cessation of control efforts, too few wolves were affected by nonlethal and lethal control over the summer and annual ranges of the caribou herd to elicit a measurable response in the herd (Boertje et al. 2017). Boertje et al. (2017) echoed Hayes et al. (2003) in cautioning that wolf-control programs must be similar in extent to the annual ranges of the caribou herd in question.

McLaren (2016) reviewed options for wolf management to recover a declining population of migratory barren-ground caribou in the Northwest Territories, and in doing so, considered effectiveness, cost, humaneness of control methods, and involvement of local and Indigenous peoples in such programs. As is the case in Alaska, the migratory behavior of barren-ground caribou likely requires a broad geographic scope for wolf-management actions, and thereby should include adjacent herds of caribou (McLaren 2016). In 2020, a pilot program using aircraft was initiated in the North Slave Region of the Northwest Territories to remove wolves associated with the Bathurst herd of caribou and the adjacent Bluenose East herd of caribou. After the pilot program, the Wek'ezhii Renewable Resources Board recommended that aerial-based removal of wolves not continue for the remainder of the 5-year program, and instead recommended directing removal efforts toward providing increased harvest incentives to the public. The Territorial Government and the Tłı̄chǫ Government accepted the recommendation, but with the caveat that aerial-based removal could still be used if removal goals were not met by public efforts.

The use of lethal-control methods on wolves to conserve woodland caribou in Canada also remains a contentious issue. Woodland caribou are federally classified as threatened in Canada, and in many cases, these caribou are declining in abundance because of human-mediated predation in the form of apparent competition (DeCesare et al. 2010, Hervieux et al. 2014, Johnson et al. 2019, Serrouya et al. 2019). Specifically, land clearing has produced a greater extent of early seral vegetation that is more suitable for other cervid species. Greater abundance and a broader distribution of moose and white-tailed deer have increased the distribution and population density of wolves and other predators. Even under pristine conditions, caribou are less fecund than deer or moose and may be more vulnerable to predation than these other cervid species. High levels of predation resulting from apparent habitat-mediated competition with other cervids has led to substantial population declines, and in some areas, extirpation of caribou populations (Hervieux et al. 2013, Johnson et al. 2019).

Hervieux et al. (2014) used aerial-based gunning and poisoning with strychnine to achieve an annual removal of 40–50% of the initial wolf population from a treatment area for 6 consecutive years in west-central Alberta. The population growth rate of woodland caribou in the treatment area increased to approximately stable levels (Hervieux et al. 2014). Caribou populations in 2 adjacent control areas experienced growth rates that were $\leq 14\%$ /year lower than the treatment area. The concurrent positive response of recruitment in the population on the treatment area seems to support the role of wolves as the proximate cause of population declines of woodland caribou in boreal regions (Hervieux et al. 2014). In British Columbia, Serrouya et al. (2019) reported on a large-scale adaptive-management experiment involving population reductions of wolves, other predators, and overabundant alternative prey; translocations of caribou; and creating refugia (i.e., maternity penning) using a design covering $>90,000 \text{ km}^2$ ($35,000 \text{ mi}^2$).

Combinations of treatments, such as population reductions of wolves and temporary penning of parturient female caribou until calves were safe from predation, increased several vital rates and produced higher rates of population growth among caribou than any single treatment. Subsequently, Harding et al. (2020) demonstrated that this inference was based on an unbalanced analytical approach that omitted a null scenario, excluded potentially confounding variables, and employed irreproducible metrics of habitat alteration. Their reanalysis of available data suggested identity of caribou ecotype was a better predictor of population trends than any of the adaptive-management treatments considered by Serrouya et al. (2019). Therefore, it may be incorrect to assume that adaptive-management strategies shown to benefit one prey species, or even ecotype within a species, are transferable to another.

Irrespective of its demonstrated effectiveness and usefulness, critics of the use of lethal methods for wolves as a tool for population recovery of caribou point out that these methods merely treat the proximate causes of population decline while ignoring the ultimate causes: human development and landscape disturbance (Brook et al. 2015, Proulx 2017). Nonetheless, habitat regeneration takes time to become effective, and without predator management there remains a high likelihood that caribou may become extinct before winter ranges are restored. At the same time, even proponents of lethal methods recognize that support for direct population reduction of predators is likely to wane (Orians et al. 1997), unless governments stop delaying difficult decisions that address the actual causes of population decline (i.e., habitat loss and fragmentation; Serrouya et al. 2019, Johnson et al. 2022).

The contentiousness of killing wolves to conserve ungulate populations highlights the decision to implement predator management is deeply intertwined with societal values. As such, policymakers, not biologists, often have the lead role in determining whether lethal methods will be implemented (Boertje et al. 2010). Advocates on both sides of the debate typically suggest they hold the higher conservation ethic, and both sides may provide contrasting scientific evidence to support their position (Boertje et al. 2010). To maintain credibility and contribute meaningful guidance regarding the need and options for implementation of lethal methods in such a divisive socio-political arena, biologists must be well informed and

provide complete information in an unbiased and respectful manner (Boertje et al. 2010).

From a management and scientific standpoint, biological support for predator-management programs requires convincing evidence that: 1) predators kill substantial numbers of the prey species of interest, 2) decreased abundance of predators will decrease rates of predation, 3) given less predation, landscapes may sustain more of the prey species, and 4) sustainable populations of wolves and other predators will continue to exist inside and outside of management areas (modified from Boertje et al. 2010).

Capture and Handling

Young pups at den sites are normally captured by hand or using nets (Mills et al. 2008, Beck et al. 2009, Hinton and Chamberlain 2010, Benson et al. 2013). Live-trapping of adult wolves for research, monitoring, or management is usually done with foothold traps (Mech 1974b), or cable-restraint devices (i.e., live-capture snares; Gese et al. 2019). Kuehn et al. (1986) evaluated 4 different models of foothold traps for capturing wolves in Minnesota, and found that the Oneida Newhouse No. 14 OS (offset-jaw with teeth) double-longspring foothold trap (discontinued) caused the least injuries. The No. 7 EZ Grip rubber-padded-jaw foothold trap (Livestock Protection Company [LPC], Alpine, Texas, USA) also resulted in few injuries to wolves (Frame and Meier 2007).

Adding tranquilizer devices to traps might further minimize risk of injuries when using foothold traps (Sahr and Knowlton 2000), but their use has become increasingly uncommon. During the 1990s, an international challenge to modern furbearer management resulted in the development of substantial and formalized long-term testing of traps through the Agreement on International Humane Trapping Standards (AIHTS) in Canada (Fur Institute of Canada 2015, Environment and Climate Change Canada 2020), and the Best Management Practices for Trapping (BMPs) program in the U.S. (White et al. 2021, Association of Fish and Wildlife Agencies 2022). Although the BMPs are not regulatory in nature in the U.S., the AIHTS is regulatory in Canada, and both provide guidance that also is relevant for use of capture devices for wolves for research purposes. Along with No. 7 EZ Grip (with either a stake or a drag), other traps tested and certified or approved through either AIHTS or BMPs for wolves include MB-750 coil-spring foothold trap with outside-laminated offset jaws (with either a stake or a drag; Minnesota Trapline Products, Pennock, Minnesota, USA), Belisle No. 8 foot-snare (Belisle Enterprises, Blainville, Québec, Canada), Bridger No. 5 foothold trap with offset and laminated jaws (Bridger Trap Company, Pennock, Minnesota, USA), Bridger No. 5 with rubber-padded jaws, LPC No. 4 double-longspring foothold trap with offset jaws, Rudy Redwolf $4\frac{1}{2}$ plastic-jawed foothold trap (Fabrications Rudy, Lac des Écorces, Québec, Canada), Bridger Brawn No. 9 coil-spring foothold trap with rubber-padded jaws, and MB-650 coil-spring foothold trap with cast offset jaws (White et al. 2021; Association of Fish and Wildlife Agencies 2022; Fur Institute of Canada 2022a, 2022b). In Minnesota, the use of the combination of foothold trapping and chemical immobilization to capture 173 wolves during a 24-year period resulted in the death

of only 2 wolves, or 1.1% of the total number captured (Barber-Meyer and Mech 2014).

Use of cable-restraint devices (i.e., snare-like devices used for live capture) has broadened opportunities for trapping wolves in areas where the use of foothold traps may be restricted, or during the periods when foothold traps may result in frozen toes of the foot secured in the foothold trap (Olson and Tischaeyer 2004, Gese et al. 2019). Cable restraints may provide a safe alternative, but wolves may occasionally chew through cables and escape (Etter and Belant 2011, Garvey and Patterson 2014); important considerations include use of minimum-loop-size stops, avoidance of entanglement with nearby structures (e.g., fences, trees), and selection of cable (e.g., diameter, strand design; Association of Fish and Wildlife Agencies 2009). Gese et al. (2019) compared cable restraints to 3 models of foothold traps and found injury scores were similar, but after capture in cable restraints, wolves more quickly resumed normal movement patterns compared to wolves captured in foothold traps. Gese et al. (2019) experienced 1 mortality (due to mechanical failure of minimum-loop-size stop) among 24 wolves captured in cable restraints, and no mortalities among 23 wolves captured in foothold traps.

Wolves captured in foothold traps or cable restraints are generally chemically immobilized via blowgun, syringe dart, or syringe pole, although wolves <5 months old can often be physically handled with a Y-stick, capture pole, or large net (Kreeger 2003). Commonly used drugs to chemically immobilize wolves include Telazol® (combination of tiletamine hydrochloride and zolazepam hydrochloride; Kreeger et al. 1990); ketamine, in combination with xylazine or promazine (Fuller and Kuehn 1983) and reversed with yohimbine (Kreeger et al. 1987); sufentanil citrate with xylazine (Kreeger and Seal 1990); medetomidine with atropine, reversed with atipamezole (Kreeger et al. 1996); and other drug combinations (Kreeger 2003, Kreeger 2023 [Chapter 17]). Anesthetized wolves need to be closely monitored for respirations, normal pulse (45–115 beats/min; Kreeger 2003), and normal body temperature of 39.6° (103°; Kreeger 2003), with hyperthermia being a common complication during capture and handling. During captures using foothold traps in Minnesota in late spring and summer, body temperatures of wolves ranged from 35.5° (96°) to 42.2° (108°), but no temperature-related mortalities were reported, and body temperature did not seem to impact survival to 1 year for 173 wolves (Barber-Meyer and Mech 2014). Body temperatures of 41.4° (106°) can cause brain damage and 43.3° (110°) can cause death in wolves, but aggressive cooling procedures after capture can minimize these risks (Barber-Meyer and Mech 2014). Field protocols require that wolves are mobile and able to travel on their own before researchers leave the study animals. See Kreeger (2023 [Chapter 17]) for more information.

For research purposes, traps and cable restraints should be checked 1–2 times/day. Trap-transmitter devices can be attached to capture devices to remotely notify the trapper when a trap has been triggered, which then increases efficiency for processing if a capture occurred (Larkin et al. 2003). Conflicts can arise when domestic dogs encounter traps and cable restraints. As an alternative to trapping, wolves can be either darted or captured

with a net fired from a handheld net-gun using helicopter-based efforts, which is often used during winter. Capture efforts during summer months are possible in open landscapes such as tundra (Fig. 32.15).

Darting wolves from a helicopter has been widely used since the 1970s (Ballard et al. 1982, 1991; Carbyn et al. 1993; Adams et al. 2008; Schmidt et al. 2017). For darting via helicopter in Alaska, Schmidt et al. (2017) had no wolves experience capture-related mortality during a 22-year study and capture of 225 wolves. Best practices include using light darts and relatively low velocities to minimize trauma (e.g., an adjustable CO₂-powered rifle with 3-ml [0.1 oz] lightweight plastic darts fitted with a 1.5-cm [0.6 in] barbed needle with side ports; Kreeger and Arnemo 2018, Kreeger 2023 [Chapter 17]). The preferred target on the body of a wolf is the hindquarters (Kreeger 2003) or large muscle mass around the neck and shoulders.

Telazol has been used to chemically immobilize free-ranging gray wolves for >20 years and remains the recommended immobilizing combination (Kreeger and Arnemo 2018). Telazol has a wide margin of safety in gray wolves, but it is a potent anesthetic with a long elimination time and no available antagonist. Consequently, Arnemo et al. (2013) evaluated the use of medetomidine-ketamine and atipamezole for reversible immobilization and anesthesia for 28 immobilizations of free-ranging gray wolves via darting from a helicopter. Although effective, they did not recommend this combination for darting free-ranging wolves at the doses tested because severe hyperthermia was observed in several wolves, 2 individuals died, and prolonged recovery occurred for 1 individual. Chemically immobilized wolves should be monitored until safely recovered from the effects of drugs, as they experience capture-related mortality rates of about 2–3% (Arnemo et al. 2006).

Net-gunning from a helicopter is a widely used method in remote field settings to capture and restrain large mammals that do not require chemical immobilization (Kock et al. 1987, Nelson et al. 2006, Webb et al. 2008). Wolves captured by net-gunning should be physically restrained against the ground by a handler using an appropriate tool (e.g., catch-pole, forked stick), promptly muzzled with a tight-fitting dog-sized muzzle, and hobbled for the safety of both the handlers and the animal. To minimize capture and handling stress, a blindfold should be placed over the eyes and hearing protection attached over the animal's ears to reduce visual and auditory stimuli. Animals should be monitored in case of vomiting and positioned so that breathing is not restricted (see Kreeger 2023 [Chapter 17]).

Although chemical immobilization is generally not required for net-gunned wolves that are intended to be processed and released within a relatively short period (typically <15 min), chemical immobilization is required for detailed health examination and safe transportation of animals (e.g., translocations). Wolves to be transported (max = 40 min travel time) should be sedated with Telazol (approximately 11–14 mg/kg) administered intramuscularly with a handheld syringe (Kreeger and Arnemo 2018). Telazol is preferred over xylazine-Telazol for immobilizing net-gunned wolves because body temperatures tend to fluctuate

more substantially for wolves chemically immobilized using xylazine-Telazol after pursuit with a helicopter (D. W. Smith, personal communication). This dose is higher than typically used for routine processing of wolves (5–10 mg/kg), but Telazol has a wide margin of safety, and this dose will produce the longer time for immobilization desirable for processing and translocation. Wolf capture, marking, and collaring are usually subject to review by the Animal Care and Use Committee within an agency, and some agencies have developed standard operating procedures (e.g., Cattet 2019).

Biologists may ear-tag wolves, but that practice, along with tattooing, has increasingly been replaced by PIT tags. Most biologists insert a PIT tag between the shoulder blades or below the left ear in captured wolves (Mills et al. 2008, Benson et al. 2013). Adult-sized wolves are typically fitted with either a GPS or a VHF-only radio-collar. Pups that are 5–6 months old can be fitted with an adult-sized radio-collar that is lined with foam and a few wraps of either duct tape or electrical tape to secure the foam padding. The goal is for the pup to successfully wear the padded collar until it grows large enough to keep the collar on as the foam

padding wears and eventually falls off, so as not to negatively affect the growing pup (Harrison et al. 1991, Benson et al. 2013). The original radio-collars used in Wisconsin consisted of machine-belt neoprene and resulted in 7 of 11 radio-collars being chewed off by other wolves, although the use of the same collar design in other areas did not result in this issue, and the collar-chewing behavior may have been a learned behavior among some wolves (Thiel and Fritts 1983). Collars with acrylic coating seemed to reduce chewing, and this behavior has not been a serious problem since the early 1980s (Thiel and Fritts 1983, Wydeven et al. 2009).

Conservation

Recovery through Natural Dispersal

Gray wolves have naturally recolonized areas across North America through dispersal, including in California, Colorado, Michigan, Montana, Oregon, Washington, Wisconsin, and Wyoming (Mech et al. 1995, Boyd-Heger 1997, Boyd and Pletscher 1999, Beyer et al. 2009, Wydeven et al. 2009, Jimenez et al. 2017, Colorado Parks and Wildlife 2022). The source of some of the recolonizations in California, Oregon, and Washington



Fig. 32.15. The use of dart-guns or net-guns fired from helicopters is effective for capturing wolves (*Canis* spp.), particularly during winter and in open landscapes, such as tundra in northern Canada. Image courtesy of D. Cluff, Government of the Northwest Territories, Canada.

was almost certainly through dispersal from the reintroduced population of wolves in Idaho. Naturally dispersing wolves within the U.S. have also been documented in Arizona, Colorado, Illinois, Indiana, Iowa, Kansas, Missouri, Nebraska, Nevada, New Mexico, New York, North Dakota, South Dakota, Utah, and Vermont (Kays and Feranec 2011, Odell et al. 2018). Many of these wolves experienced mortality through being shot due to misidentification as coyotes, colliding with vehicles, or being intentionally killed by humans, and apparently did not survive long enough to locate mates and reproduce.

Population recovery of wolves in North America through natural dispersal will likely occur at a slower rate compared to use of translocations, but natural recolonization may be less fraught with socio-political challenges in both the short and long term (Boyd 2020). Smith et al. (2016) suggested about 42% of the Great Plains region (primarily North Dakota south to Texas) was suitable for wolves and van den Bosch et al. (2022) estimated similar areas in the Great Plains. Smith et al. (2016) relied primarily on densities of both roads and human populations for their assessment, whereas van den Bosch et al. (2022) relied primarily on low population densities of humans; however, much of the area may not be suitable for wolves due to lack of forest cover and potential for wolf-livestock conflicts (Licht and Fritts 1994, Licht and Huffman 1996, Oakleaf et al. 2006, Mladenoff et al. 2009).

Population recovery of wolves depends perhaps as much or more on social tolerance than on ecological factors. Management and outreach to potentially increase tolerance by humans to wolf presence includes addressing livestock and pet depredations and implementing regulated harvest (Mech 2017). As habitat generalists with wide flexibility in prey selection, wolves can persist in nearly any rural setting where humans will tolerate their presence. It seems that the persistence of wolf packs may be limited by anthropogenic factors (Mech et al. 2019, Gantchoff et al. 2022). We expect that wolves will continue to recolonize portions of the western U.S., but their establishment in the Great Plains and central Midwest may be more limited (Mech 2017, Mech et al. 2019, Gantchoff et al. 2022).

Recovery through Translocation Efforts

Translocations include reintroductions, population augmentations, cross-fostering, movements to mediate conflict situations, and movements of animals to maximize genetic benefit (International Union for Conservation of Nature 2013). This includes both wild-born and captive individuals. Translocations may include either hard releases (wolves are typically released into the wild ≤ 7 days of capture) or soft releases (wolves are typically held ≥ 28 days before released into the wild; Bradley et al. 2005).

The eastern timber wolf (*Canis lupus lycaon*; classification of gray wolves in eastern U.S. at that time) was listed as endangered in 1967 in keeping with the Endangered Species Preservation Act of 1966. With the passage of the Endangered Species Act of 1973, wolves were provided substantial protections in the U.S., allowing USFWS to develop mechanisms for recovering threatened and endangered wildlife populations. This entailed establishing recovery teams and developing recovery plans for gray wolves in

the NRM and Great Lakes regions of the U.S., and Mexican and red wolves (Phillips et al. 2003, 2004). Soon after federal listing as endangered in 1974, reintroduction of 4 wolves from Minnesota to the Upper Peninsula of Michigan was attempted (Weise et al. 1975). The wolves were held in remotely located pens for 10–12 weeks, fed vehicle-killed white-tailed deer, and released into the wild during March 1974 (Weise et al. 1975). All 4 wolves were in good physical condition when they were killed by humans by November 1974. Weise et al. (1975) concluded that translocation could be a useful tool for restoring wolf populations if increased awareness, education, and legal protections reduced the extent of human-caused mortality.

Starting in 1975, Fritts et al. (1984, 1985) used translocation of naturally recovering wolves in Minnesota as a nonlethal method in collaboration with USFWS to mitigate livestock damage, and later applied that translocation experience for wolf reintroductions in the NRM (Bangs et al. 1995, 1998). Fritts et al. (1984) reported on the short-distance translocations of 104 wolves within Minnesota to mitigate livestock depredation. Most of these wolves were translocated and released < 48 hr after initial capture. All radio-collared wolves that were monitored left their release sites and generally moved toward their respective locations of capture. Although Fritts et al. (1984) concluded that these translocations were largely unsuccessful for mitigating livestock depredations, Fritts et al. (1985) subsequently demonstrated that the survival of translocated 5-month-old pups and adult wolves was comparable to that of resident wolves, and suggested the ability of wolves to survive and reproduce in unfamiliar, wolf-occupied landscapes further demonstrated the potential utility of translocations as a tool for recovery of wolf populations.

In most cases in the NRM, wolves were translocated after confirmed depredations of livestock had occurred, but sometimes they were moved preemptively when conflict seemed imminent (see section on Damage Management). By about 2005, translocation became less practical as a means of mitigating livestock damage within both the Rocky Mountain and western Great Lakes populations because rapid population growth and expansion of the respective wolf populations resulted in fewer suitable sites for release (Bradley et al. 2005).

Following the development of recovery plans, 5 reintroduction efforts (3 efforts for gray wolves, 2 efforts for red wolves [Hinton et al. 2013]) were attempted in the conterminous U.S. between 1987 and 1998. The reintroductions of gray wolves were successful in augmenting and establishing populations in the NRM of the U.S. (Phillips et al. 2004), and for the Mexican wolf in southwestern U.S. Red wolves reintroduced to North Carolina in 1987 had limited success, but the effort in the Great Smoky Mountains National Park in 1991 failed (Henry 1998, Hinton et al. 2013).

The reintroduction of gray wolves into the NRM region during 1995–1996 included 31 wild wolves captured in Alberta and British Columbia that were subsequently released in YNP (Bangs and Fritts 1996, Phillips and Smith 1996, Smith et al. 2003). Additionally, 10 wolf pups from the Sawtooth Pack in Montana were released into YNP in 1997 after the adult pack members were killed for livestock depredations (Fritts et al. 2020), which brought

the total number of wolves released in YNP to 41 individuals. Another 35 wild wolves captured in the same regions in Canada were released in Idaho during 1995–1996 (Bangs and Fritts 1996, Fritts et al. 1997). For reintroduction efforts in YNP, USFWS used primarily soft releases of intact breeding pairs and packs (Fritts et al. 2001). During January 1995, 3 groups of wolves which had been recently captured in Alberta and British Columbia were placed in separate 0.4-ha (1.0-ac) pens in northern YNP. These wolves were fed vehicle-killed ungulates until the pens were opened in late March 1995, which was a soft release. In contrast, most releases into central Idaho were of young, subadult wolves which were hard released immediately after capture and processing.

Currently, the reintroduced populations in Idaho and YNP, coupled with the naturally recolonizing population in northwestern Montana, has increased to about 2,700 wolves across substantial portions of the 72,800 km² (28,108 mi²) Greater Yellowstone Ecosystem, central Idaho and surrounding areas of the NRM (Smith et al. 2003, Inman et al. 2020). Since the initial reintroduction efforts, gray wolves in that region have served as the basis of research (Smith et al. 1999, 2003; Boyce 2018) that has contributed to our knowledge of social ecology of the species (Stahler et al. 2013, Cubaynes et al. 2014, Cassidy et al. 2015), wolf-ungulate interactions (Laundré et al. 2001; Kauffman et al. 2007; MacNulty et al. 2007, 2009a, 2009b, 2012; Barber-Meyer et al. 2008; Mech et al. 2015), and trophic cascades (Ripple and Beschta 2003, Wilmers et al. 2003, Kauffman et al. 2010, Middleton et al. 2013).

During November 2020, citizens of Colorado voted on and passed a ballot measure (Proposition 114) to implement a wolf-reintroduction program in that state (Colorado Parks and Wildlife 2022). The ballot measure created a statute that required the reintroduction of wolves into Colorado by no later than 31 December 2023 (Colorado Parks and Wildlife 2022). This was the first wolf-reintroduction program mandated through a ballot initiative that made the state responsible for wolf reintroduction rather than the U.S. federal government (USFWS 2022). To provide for increased flexibility for management, Colorado Parks and Wildlife requested the designation of an experimental population for the wolves under section 10(j) of the ESA (USFWS 2022). Currently, 1 pack of wolves exists in Colorado, which naturally dispersed from Wyoming, and was first documented in the state in 2020.

During September 2018, the U.S. National Park Service announced a 3–5-year effort to reintroduce and establish 20–30 wolves in IRNP to restore predation as a key part of the island ecosystem (U.S. National Park Service 2018). Prior to this effort, the wolf population had decreased to 2 highly inbred wolves (Hedrick et al. 2017), and the moose population on the island had increased substantially and was severely limiting forest regeneration (Romanski et al. 2020). Four wolves were captured and translocated from Grand Portage Band of Lake Superior Chippewa Reservation to IRNP during September–October 2018. During February–March 2019, an additional 11 wolves were moved from Michipicoten Island and the mainland of Ontario to IRNP. In September 2019, 4 wolves from mainland Michigan were released in IRNP.

Translocations conducted in support of this effort were guided by a comprehensive disease-risk analysis to identify, assess, and mitigate disease risks associated with the reintroduction of wolves to IRNP (Verant et al. 2022). Due to mortalities and dispersals, by March 2020, 12–14 wolves inhabited IRNP and both members of the inbred pair had apparently died (Hoy et al. 2020). By March 2022, the population had increased to 28 wolves (Hoy et al. 2022). In the future, U.S. National Park Service will focus on broad population goals and the opportunity these reintroduced wolves represent for population growth, genetic diversity, and restoration of top-down predation pressure in IRNP (Romanski et al. 2020).

For all North American species and subspecies of wolves, most mortality of translocated wolves tends to be caused by humans, and mortality risk is generally higher for hard-released than soft-released wolves (McLellan and Rabon 2006). Also, homing behavior exhibited by translocated wolves may undermine translocation efforts. For example, Bradley et al. (2005) reported that 16 (20%) of 81 individuals or cohesive groups successfully returned to their capture locations, traveling distances of 74–316 km (46–196 mi). More adults (36%) than subadults (11%) returned to capture locations, and all pups that returned to a capture location did so with an adult. Also, 30% of hard-released wolves and 8% of soft-released wolves returned to their capture locations. Hard-released wolves generally traveled farther after release than soft-released wolves. Wolves that were translocated shorter distances were more likely to return to their capture locations (Fritts et al. 1985). Only 4 translocations resulted in release-site fidelity and all involved groups of wolves that were translocated together. Three of these 4 translocations involved nearly all members of a given family group.

The next reintroduction effort for gray wolves involved restoring Mexican wolves to the wilds of Arizona and New Mexico. The Mexican Wolf Recovery Team was initially formed in 1979, and included representatives from the U.S.-based agencies of Arizona Game and Fish Department, New Mexico Department of Game and Fish, and USFWS, and the Mexico-based Secretaría de Medio Ambiente y Recursos Naturales; this team produced the 1982 Mexican Wolf Recovery Plan (USFWS 1982). In 2003, USFWS reclassified the gray wolf in North America, creating 3 Distinct Population Segments (DPS), and convened a third recovery team to develop a new recovery plan for Mexican wolves in the Southwestern DPS. In 2015, USFWS expanded the 10(j) area for recovery and removed the Mexican wolf from the general ESA listing that included all subspecies of gray wolves and listed it separately as a subspecies (USFWS 2014, 2015). After a series of binational workshops during 2015–2017, a diverse group of representatives, leaders, and experts from U.S. state and federal agencies, Mexican agencies, academia, International Union for Conservation of Nature, and some former recovery team members finalized a revised recovery plan during November 2017 (USFWS 2017b).

Releases from captivity and translocation of Mexican wolves began in 1998, and are guided by an annual Initial Release and Translocation Plan (Mexican Wolf Interagency Field Team 2019) to manage the genetics of the wild population of Mexican

wolves, including the release of cross-fostered pups from captivity beginning in 2016 (Harding et al. 2016) or removing animals from the wild (Fig. 32.16). Cross fostering involves placing captive-born pups (<14 days old) into dens of wild wolves that have similarly aged pups so all original and cross-fostered wolves experience minimal influence from humans (Stoskopf et al. 2005, Gese et al. 2015, Harding et al. 2016). The Mexican wolf recovery program included placement of 83 genetically valuable pups from captivity into litters of wild wolves during 2016–2022 (Harding et al. 2016, USFWS 2018a); 13 of these pups have been successfully recruited into the population and 8 have become breeders (J. P. Greer, personal communication; Fig. 32.17). Additionally, a minimum of 5 offspring of cross-fostered pups have produced ≥ 7 litters, which infused genetic diversity into the wild population. These generations of fosters and their offspring are measurably increasing genetic diversity in the wild population as evidenced by recent improvements in 3 of 4 measures of genetic diversity (E. Spevak, Saint Louis Zoo, personal communication). Translocations occasionally occur for management reasons when a wolf disperses and remains outside of the boundary of the Mexican Wolf Experimental Population Area. The Mexican wolf population in the U.S. has continued to grow at an annual rate of 13%, which is cause for optimism.

As with the Mexican wolf, the red wolf has a history of recovery based on a captive-breeding program initiated with 14 of the remaining 17 red wolves captured from the wild (USFWS 1989, Hinton et al. 2013). The goal of the captive-breeding program for red wolves is to reintroduce individuals into the wild while maximizing genetic diversity in the captive and reintroduced populations (Miller et al. 2003, Hedrick and Fredrickson 2008, Bartel and Rabon 2013, Brzeski et al. 2014). To reduce inbreeding, loss of genetic diversity, and genetic drift that often accumulate in

small populations (Rabon and Waddell 2010, Brzeski et al. 2014), the Red Wolf Recovery Program cross-fosters captive-born pups into litters of wild red wolves (Gese et al. 2018). The Red Wolf Recovery Program began cross-fostering pups into litters of wild red wolves during 2002, and 56% of captive-born pups fostered into the wild survived >12 months (Gese et al. 2018). Of the 16 fostered pups known to have survived their first year, they had an average life span of 5.6 years, and 9 animals whelped or sired a total of 26 litters in the wild (Gese et al. 2018).

To reintroduce red wolves to northeastern North Carolina, USFWS released 42 captive-born red wolves on 15 different occasions between 1987 and 1992 (Phillips 1994). With an adaptive-management plan, USFWS successfully established a wild population of red wolves that fluctuated between 110 and 155 wolves traversing 6,000 km² (2,300 mi²) during 2000–2014 (Gese et al. 2015, Hinton et al. 2017a). This represented 50–70% of the target population size for wild red wolves as set within the recovery strategy of USFWS (1989). However, only 19–21 red wolves remained by 2022, as a result of high rates of human-caused mortality, specifically, shooting of wolves (Hinton et al. 2017a, USFWS 2023), and the decision of USFWS to decrease recovery efforts in northeastern North Carolina (USFWS 2018b). As USFWS considers a path forward for the recovery of a reintroduced population in the wild (Kurth 2018), the fate of red wolf populations in northeastern North Carolina remains uncertain.

The use of sterilization to limit hybridization between coyotes and red wolves is unique to recovery efforts for red wolves (Gese and Terletzky 2015, Hinton et al. 2022). Sterile coyotes and hybrids released back into the wild were referred to as placeholders, and the underlying tenet of the placeholder concept was that space was limiting and all suitable space in the Red Wolf Experimental Population Area should be occupied by breeding pairs of red



Fig. 32.16. Genetic diversity of the wild Mexican gray wolf (*Canis lupus baileyi*) population is bolstered by cross-fostering genetically valuable captive pups into wild litters in Arizona and New Mexico, USA. Image courtesy of D. Majure, Arizona Game and Fish Department, USA.



Fig. 32.17. Genetically valuable fostered pups are raised by wild parents and are indistinguishable from their wild siblings. This litter of Mexican gray wolves (*Canis lupus baileyi*) from the Dark Canyon Pack in Gila National Forest, New Mexico, USA, contains 3 natal pups and 2 fostered pups that went on to become breeders of their own pack. Image courtesy of Mexican Wolf Interagency Field Team, USA.

wolves, and where wolf pairs were absent, space should be occupied by placeholders (Kelly 2000). As the abundance of red wolves increased, territories of placeholders would be usurped by red wolves, either directly by wolves through interspecific strife or indirectly when placeholders were removed by USFWS Red Wolf Recovery Program biologists to create vacancies for dispersing red wolves to occupy (Hinton et al. 2017b). In their assessment of the use of placeholders, Gese and Terletzky (2015) reported that placeholders routinely held territories, had higher survival rates than red wolves, genetic introgression was <4% coyote ancestry in the red wolf population, and approximately 37% of placeholders were displaced by red wolves.

The effect of fertility control on influencing population abundance of coyotes is unknown, but the combination of sterilization of coyotes and presence of red wolves seems to have limited population density of coyotes in the Red Wolf Experimental Population Area to approximately 2.5–21.5 coyotes/1,000 km² (6.5–55.7/1,000 mi²) during 2000–2013 (Hinton et al. 2022). These estimates of population density are less than most estimates reported throughout the distribution of coyotes. Nevertheless, the use of sterile coyotes and hybrids expanded the management capabilities of USFWS to advance goals for population recovery of red wolves by limiting hybridization and mitigating the threat of introgression by coyotes.

Listing, Delisting, and State and Tribal Management

Wildlife species listed as endangered or threatened under the ESA in the U.S. are regulated by the federal government, but once populations recover to previously established levels that allow for delisting, management authority returns to states and tribes. Wolves have been listed since the development of lists of endangered species, but depending on species, subspecies, or locations, have gone through highly varied listing and delisting processes. Gray wolves in the U.S. were listed as endangered in 1967 under the Endangered Species Protection Act of 1966, to protect wolves on public land and prioritize research (Mech 1970). The ESA resulted in federal listing of gray wolves in the Great Lakes region as an endangered species and designation as eastern timber wolves (*Canis lupus lycaon*) in 1974 (Refsnider 2009). Simultaneously, the NRM wolf (*Canis lupus irremotus*) was listed as endangered in the western U.S., and in 1976, the Mexican wolf (*Canis lupus baileyi*) and Texas wolf (*Canis lupus monstrabilis*) were listed as endangered in the southwestern U.S. (Refsnider 2009).

The ESA listing of gray wolves during the mid-1970s was based on classifications by Young and Goldman (1944) and Hall (1981), and more recent classifications have combined *Canis lupus irremotus*, *Canis lupus monstrabilis*, and western Great Lakes versions of *Canis lupus lycaon* as *Canis lupus nubilus* (Nowak 1995, 2003; Chambers et al. 2012). The ESA was revised in 1978, and listing of gray wolves changed from separate subspecies, to designating all gray wolves (including Mexican wolves) in the conterminous U.S. as endangered, except that gray wolves in Minnesota were designated as threatened (allowing use of lethal-control methods to address depredation by wolves) to reflect an increasing population estimated at >1,000 wolves at that time (Erb

and DonCarlos 2009, Refsnider 2009). These protections allowed wolves to re-establish in Wisconsin beginning in 1975, Montana in 1986, and Michigan in 1989 (Ream et al. 1989, Beyer et al. 2009, Wydeven et al. 2009). The growth rates of wolf populations in both Montana and Wisconsin were initially low due to an Allee effect, high rates of CPV (Johnson et al. 1994, Wydeven et al. 1995), and effects of illegal killing (Pletscher et al. 1997, Stenglein and Van Deelen 2016, Stenglein et al. 2018).

Beginning with the first naturally recolonizing wolf in 1979, wolves dispersed into Montana from Canada and increased to an estimated population of 70 wolves in the state by 1995 (Mech 1995c; D. K. Boyd, unpublished data). After reintroduction of gray wolves in YNP and central Idaho during 1995–1997, wolf populations rapidly increased in the NRM (Bangs et al. 1998, 2004). The state of Idaho declined to participate in reintroduction efforts, thus allowing the Nez Perce Tribe to lead management of the wolf-recovery effort in Idaho starting in 1995, and co-manage wolf-recovery efforts with USFWS (Bangs and Fritts 1996, Wilson 1999, Ohlson et al. 2008). The wolf population in the NRM met recovery goals of ≥30 breeding pairs or ≥300 wolves equitably distributed across 3 subpopulations for 3 consecutive years in 2002 (Smith and Sime 2007), with estimated populations of 263 in Idaho, 184 in Montana, and 217 in Wyoming (USFWS et al. 2003). The NRM populations continued to increase and expand, with a breeding pair confirmed in Oregon during 2008 (Oregon Department of Fish and Wildlife 2019), in Washington during 2007–2008 (Washington Department of Fish and Wildlife 2019), in California during 2017 (California Department of Fish and Wildlife 2019, 2020), and in Colorado during 2021 (Colorado Parks and Wildlife 2022; E. Odell, Colorado Parks and Wildlife, personal communication; Table 32.1).

In northwestern Montana, the wolf population that recovered through natural dispersal from Canada was classified as endangered under the ESA. However, reintroduced populations in YNP and central Idaho were classified as nonessential experimental populations. This designation allowed government trappers to capture and euthanize depredating wolves, and gave some authority to landowners to use lethal-control methods on wolves (Bangs et al. 2004). The NRM DPS, except Wyoming, was delisted in April 2009, relisted by court decision in August 2010, and again delisted by Congressional action from a rider attached to a budget bill for Department of Interior during spring 2011 (Blakeslee 2017). With the delisting completed in 2011, the state of Idaho assumed the lead role in wolf management and implemented regulated harvest of wolves. Because Congressional action delisted the NRM DPS, there was no litigation associated with delisting, and no reversals imposed by courts for the Congressional decision, as had occurred for the Western Great Lakes DPS (Mech 2015). Delisting of wolves occurred in Wyoming in 2012, but wolves were relisted based on a court decision in 2014, and again delisted when the court challenge was reversed in 2017. In the U.S., shifts in management authority from the federal government to state and tribal governments require federally approved management plans that provide for sustainable populations into the future through ecological, sociological, and political changes (Smith 2019).

In the Great Lakes states, wolf populations increased during the 1990s, especially in Michigan and Wisconsin (Van Deelen 2009, Stenglein et al. 2018). The wolf population in the Great Lakes states first met the recovery goal in 1998, with a population of approximately 1,300 wolves in Minnesota, and >100 wolves for ≥ 5 years in Michigan and Wisconsin (USFWS 1992). At the time, wolf populations were estimated at 2,445 in Minnesota, 178 in Wisconsin, and 139 in Michigan (Beyer et al. 2009, Erb and DonCarlos 2009, Wydeven et al. 2009). USFWS initiated ESA-based reclassification of gray wolves in the Great Lakes region in 2000, and between 2003 and 2014, down-listed wolves from endangered to threatened once, and delisted wolves 3 times, but each instance of reclassification was reversed by legal challenges through the federal-court system (Refsnider 2009, Olson et al. 2015).

USFWS began a fourth delisting effort during March 2019, including in the Great Lakes region, as part of a delisting rule with the remainder of conterminous U.S., with the exceptions that wolves within the range of the Mexican wolf would remain listed as endangered, and no listing changes for the NRM that were already delisted. All gray wolves within the conterminous U.S., except Mexican wolves, were federally delisted on 4 January 2021 (USFWS 2020), but due to court action, gray wolves were again relisted on 10 February 2022 (Wisconsin Department of Natural Resources 2022). Thus in 2022, gray wolves in the conterminous U.S., other than those throughout the NRM DPS, were federally listed as endangered, with the exception that gray wolves in Minnesota were again listed as threatened. The final rule excluded the Mexican wolf in Arizona and New Mexico, where that subspecies currently remains listed as endangered under the ESA. Delisting would have allowed state and tribal wildlife-management agencies to resume full responsibility for management and monitoring of wolves within their jurisdictions, but resumption of that authority is now deferred until sometime in the future.

Red wolves (listed in 1967) and Mexican wolves (listed in 1976) are currently classified as endangered under the ESA. The eastern wolf in Canada is currently listed as threatened by Ontario, and the advisory body (COSEWIC) to the federal government recommended a threatened listing, but it is currently listed as Special Concern under SARA since 2020. There currently is no federal-listing classification for eastern wolves in the U.S.

RESEARCH NEEDS

Herein, we have provided an update on wolf ecology and management in North America; the pervasive theme throughout has been the recovery and dynamics of wolf populations in human-modified landscapes. Consequently, we expect future research to provide a greater understanding of conflict-management approaches and predator-prey relationships. The landscapes and associated plant and animal communities that wolves inhabit will change and represent a challenge for future generations. The role of new parasites and diseases will increase in prominence and how they impact ecosystems will need to be addressed. As human activities increase and become more ubiquitous, it is unlikely that we can manage for stable populations of wolves in all areas when landscapes and political systems are dynamic because of those

activities. This requires constant re-evaluation and self-reflection on the science, management, and public values surrounding wolves. Best-management practices for wolves will continue to evolve (Mech 2017), and managers and biologists will continue to look to advances in technology and new research to improve them.

CONCLUSIONS

The management focus for wolves in North America has shifted away from recovering populations of wolves to increasing human tolerance of wolves in increasingly human-dominated landscapes. The wolf is a top-level carnivore that precipitates controversy and passion amongst the public. Its global distribution and inherent resiliency virtually guarantee that wolves will persevere into the next century. Along the way, societal tolerance of wolves will continue to be a cornerstone of successful coexistence. We have highlighted many of the advances made during the past 30 years in understanding this interesting, and socially and ecologically important carnivore, but undoubtedly more remains to be discovered. In recent times, societal attitudes toward wolves have shifted from primarily fear to tolerance and even affection, particularly in the urban areas. This presents challenges and opportunities to help people connect with nature.

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