

Deer, wolves, and people: costs, benefits and challenges of living together

Jean-Louis Martin^{1*} , Simon Chamaillé-Jammes¹ and Donald M. Waller²

¹*Centre d'Écologie Fonctionnelle et Évolutive UMR 5175, CNRS, Université de Montpellier, Université Paul Valéry Montpellier, EPHE – PSL, IRD, 34293, Montpellier, France*

²*Department of Botany, University of Wisconsin-Madison, Madison, WI, 53706, USA*

ABSTRACT

Human-driven species annihilations loom as a major crisis. However the recovery of deer and wolf populations in many parts of the northern hemisphere has resulted in conflicts and controversies rather than in relief. Both species interact in complex ways with their environment, each other, and humans. We review these interactions in the context of the ecological and human costs and benefits associated with these species. We integrate scattered information to widen our perspective on the nature and perception of these costs and benefits and how they link to each other and ongoing controversies regarding how we manage deer and wolf populations. After revisiting the ecological roles deer and wolves play in contemporary ecosystems, we explore how they interact, directly and indirectly, with human groups including farmers, foresters, shepherds, and hunters. Interactions with deer and wolves generate various axes of tension, posing both ecological and sociological challenges. Resolving these tensions and conflicts requires that we address key questions using integrative approaches: what are the ecological consequences of deer and wolf recovery? How do they influence each other? What are the social and socio-ecological consequences of large deer populations and wolf presence? Finally, what key obstacles must be overcome to allow deer, wolves and people to coexist? Reviewing contemporary ecological and sociological results suggests insights and ways to improve our understanding and resolve long-standing challenges to coexistence. We should begin by agreeing to enhance aggregate benefits while minimizing the collective costs we incur by interacting with deer and wolves. We should also view these species, and ourselves, as parts of integrated ecosystems subject to long-term dynamics. If co-existence is our goal, we need deer and wolves to persevere in ways that are compatible with human interests. Our human interests, however, should be inclusive and fairly value all the costs and benefits deer and wolves entail including their intrinsic value. Shifts in human attitudes and cultural learning that are already occurring will reshape our ecological interactions with deer and wolves.

Key words: herbivores, carnivores, ecological cascades, human–wildlife conflict, livestock, human health

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* Author for correspondence (Tel: +33 467 613 264; E-mail: jean-louis.martin@cefe.cnrs.fr)

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I. INTRODUCTION

Fear of a major human-driven species annihilation looms as a major crisis (Ceballos, Ehrlich & Dirzo, 2017). However, the restoration of deer (cervid ungulates) to abundant population levels in the northern hemisphere, and the recolonization of lost ground by wolves (*Canis lupus*), their main predators, have not resulted in relief but in conflicts and controversies around their interactions with their environment, each other, and humans. These conflicts challenge us to think hard about what we value in wildlife (for deer: e.g. Nelson, 1998 and Moss, 1999; for wolves: Nie, 2002 and Hermann, Voß & Menzel, 2013). Here, we review the ecological and sociological costs and benefits that have been identified as accompanying the recovery of these species, in a synthetic effort to understand the underlying reasons for conflicts and controversies and to highlight questions to be addressed to help resolve the challenges we face when deer, wolves and people and their livestock live together.

(1) Deer and wolves, the consequences of a shared history

We label deer ‘herbivores’ because they are highly adapted to find, ingest, and digest a range of woody browse and herbaceous species. But viewing deer only as plant consumers ignores millennia of additional selective forces that have moulded them. Historically, deer have shared habitats with wolves, cougar (*Puma concolor*), and other predators. Perceiving deer only as plant eaters seeking to maximize food intake neglects this shared history and its impact on deer bodies and behaviour (Byers, 1997; Geist, 1998). From studies in places where wolves persisted, we know their importance in deer population dynamics through the moulding of their life-history and population growth characteristics (Messier, 1994;

Peterson *et al.*, 2014). We can also infer the strength of these effects from the fact that ‘bottom-up’ effects of ecosystem productivity on deer populations are strongly damped in the presence of wolves (Crête, 1999; Ripple & Beschta, 2012; Letnic & Ripple, 2017). These behavioural adjustments of deer trading off foraging for safety in the presence of wolves (Creel & Christianson, 2008; Chamaillé-Jammes *et al.*, 2014) lead to nutritional costs and reduced impacts on vegetation (Letnic & Ripple, 2017). This may be perceived erroneously as the result of a bottom-up control of the ungulate populations (Christianson & Creel, 2010; Martin *et al.*, 2010).

When predators are present, spatial heterogeneity in predation risk can create a “landscape of fear” (Laundré, Hernández & Ripple, 2010) that affects the distribution and movement of deer, how they forage, and thus the distribution of herbivore-sensitive plants across the landscape with cascading effects on other species. In the absence of predators, deer are more homogeneously distributed resulting in more intensive and widely distributed impacts as well as ecological homogenization (Rooney *et al.*, 2004). Although the historical proposition that predators reduce plant consumption by herbivores (Leopold, Sows & Spencer, 1947; Hairston, Smith & Slobotkin, 1960; Flader, 1974) has been challenged (e.g. Caughley, 1970, 1983; Colinvaux, 1979), recent research substantiated the idea that natural landscapes that have lost carnivores undergo substantial ecological changes (Terborgh & Estes, 2010; Ripple *et al.*, 2014; Atkins *et al.*, 2019). The differences between natural landscapes with or without carnivores may be perceived as positive or negative depending on the particular impact and on the perspective of different human stakeholders.

(2) Wolves and humans, a complex relationship

The relationship between wolves and humans has a long and complex history (Moriceau, 2011; Alleau & Linnell, 2015;

Linnell & Allean, 2016; Treves & Bonacic, 2016; Lescureux, 2018). In many societies, observations of, and interactions with, wolves led to cultural learning in humans (Lescureux & Linnell, 2010, 2013 and references therein), potentially leading to respect (Boitani, 1995; Treves & Bonacic, 2016). Humans also often recognized that, like us, wolves cooperate in hunting and care for their kin (Drompp, 2011). Human attitudes towards wolves also were shaped by the multifaceted interactions among geography, history, beliefs and culture, including the local history of interaction between wolves and people [Boitani, 1995; Mech & Boitani, 2003; Lescureux & Linnell, 2010, 2013; Moriceau, 2011 and references therein]. Hunters, nomadic or sedentary shepherds, farmers, and urbanites have all developed idiosyncratic, and sometimes deeply contrasting, attitudes towards wolves; attitudes that shifted with context, place and time (Lescureux & Linnell, 2013; shifting baseline *sensu* Pauly, 1995). In most human societies sharing wolves' original range, wolves occupied a special place. They were associated with the warrior class among Indo-Germans (McCone, 1987) and Inner Asians (Drompp, 2011). In Roman mythology, a She-wolf nursed and saved Mars' twin sons. In the Caucasus wolves were seen as a symbol of strength, independence and freedom (Layton, 2014). This contrasted with their perception as evil and cruel by the Zoroastrian pastoralists (Drompp, 2011) who nevertheless showed great reverence for its domesticated kin, the dog (Foltz, 2010).

In western cultures, strong attitudes against wolves have been, and still are, prevalent. The status of wolves often contrasts markedly with the status of most other large mammals, and especially with attitudes towards domesticated wolves (Treves & Bonacic, 2016). Indeed, thousands of years ago, the special human–wolf relationship brought wolves into the human family as dogs, for good and bad (Treves & Bonacic, 2016). Since this distant past, the advent of livestock herding motivated the eradication of wolves from many landscapes they once shared with us (see Lescureux, 2018).

Today, wolves are still among the few animals for which National Parks do not necessarily provide a safe haven from legal hunting or culling, even in Europe and North America where they are legally protected (Haber, 1996). In parts of the U.S.A., for example, hunting for wolves can occur over extended hunting seasons, with little bag limit, and no restriction on killing animals with dependent young. Although such practices are widely accepted for many species considered as pests (e.g. corvids, rats, invasive non-natives, etc.), they breach accepted hunting ethics and regulations set for most wild animals (Haber, 1996).

(3) Challenges to be resolved

Across much of Western Europe and North America, cervid ungulates became far more abundant during the 20th and early 21st centuries. In response, wolves, where protected, are making a comeback too. But resurging populations of deer and wolves are coming into increased conflict with

people, especially farmers, foresters, shepherds or hunters. They also generate conflict among segments of increasingly urbanized human societies. We review the ecological and sociological challenges these shifts in distribution and abundance pose, in particular: (i) how and why deer and wolves have shifted in distribution and abundance historically; (ii) the ecological consequences of deer and wolf recovery; (iii) the social and socio-economic consequences of large deer populations and of wolf recovery and, finally, (iv) the questions to be addressed to overcome the challenges posed by deer, wolves and people living together.

II. DEER AND WOLVES, FROM DECLINE TO RECOVERY: HOW AND WHY DID IT HAPPEN?

(1) Historic declines

Between 1450 and 1900, white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) populations in what became the U.S.A. declined from an estimated 40+ million individuals to fewer than half a million in 1900 (see McCabe & McCabe, 1984 ; Webb, 2016 and references therein). This largely reflected unregulated commercial and subsistence hunting fuelled by a growing number of settlers. By the early 20th century deer populations were extirpated, or on the brink of extinction, in many eastern states. In Europe, large ungulate populations including deer had become similarly rare or extirpated in many areas by the 19th century (Boitani, 1995). [Correction added on 13 April 2020, after Online publication: In the preceding paragraph, the scientific name of mule deer has been corrected in this version.]

In year 1500 an estimated 400 000 wolves (Hampton, 1997) probably coexisted with an abundant human population (Mann, 2005) in what became the U.S.A. That number suggests that their prey must have been similarly abundant until European colonists transformed the continent (see McCabe & McCabe, 1984). In Europe, wolves remained widespread and locally abundant until the 18th century. [Correction added on 13 April 2020, after Online publication: In the preceding paragraph, the estimate of wolf population size in the U.S.A. has been corrected and the citation updated in this version.]

In the U.S.A., wolves declined to become extinct in 47 of the lower 48 states by the mid 20th century, remaining only in northern Minnesota. In Europe they were exterminated from most parts by the first half of the 20th century (Delibes, 1990; Hindrikson *et al.*, 2017). Paradoxically, wolves were extirpated earlier in the sparsely settled Nordic countries, yet retained viable populations in many Mediterranean parts of Europe despite a long history of dense human populations (e.g. see Boitani & Linnell, 2015). Thus, habitat loss, scarcity of their natural prey, and human hunting, often organized at the state level, have all contributed to these declines (see Treves *et al.*, 2017 and references therein).

(2) Deer recovery

Today, a mere century later, over 30 million white-tailed deer alone inhabit North America (VerCauteren, 2003). The 20th century also witnessed similar increases in deer abundance and distribution across Europe, (Fuller & Gill, 2001). Over 10 million roe deer (*Capreolus capreolus*) inhabit western Europe, not counting other ungulates which have also increased (Burbaité & Csanyi, 2009). In Scotland, the red deer (*Cervus elaphus*) population has increased to over 300,000 individuals (Clutton-Brock, Coulson & Milner, 2004). The current standing biomass of large ungulates in Europe is estimated at 0.75 billion kg, representing a consumption of approximately 20 million tons/year of green vegetation (Apollonio, Andersen & Putman, 2010).

We are uncertain about the degree to which bottom-up *versus* top-down trophic interactions contributed to these dramatic increases in deer populations. The extirpation of most deer predators certainly alleviated direct pressure on deer populations and altered deer behaviour (see Sections IV.1. and IV.2). At the same time, however, major changes in habitat and human land use occurred (e.g. see Fuller & Gill, 2001, Côté *et al.*, 2004, Milner *et al.*, 2006 and references therein). Active forest management created abundant early successional habitat, edges and fragments which together boosted deer abundance. Changes in agricultural land use, including increased plantings of winter crops and reversion of abandoned fields to forest, supported higher deer densities. Milder winters and developing suburban areas interconnecting un-hunted green spaces also contributed, as has winter feeding of deer (Putman & Staines, 2004).

The result of these changes, together with favourable legal dispositions (e.g. the 1963 law on hunting plans in France, the 1979 Bern Convention and the 1992 Habitats Directive for Europe or the 1937 Pittman-Robertson Act in the USA), has been spectacular, continent-scale, recoveries of deer populations (for a UK historical perspective on legal status and trends in deer populations see Phillip *et al.*, 2009). These count as significant wildlife conservation success stories. Ironically, we now see an excess of success as deer have become ‘overabundant’ across much of their range (Augustine & DeCalesta, 2003). Their abundance has become a challenge to wildlife managers in large parts of North America and Europe (Warren, 1997) and legislation designed to protect deer may today conflict with the recognized need to manage their populations (Phillip *et al.*, 2009). It has also led ecologists to investigate the downstream effects of such recoveries on landscapes and ecosystem functions (e.g. Waller & Alverson, 1997; Fuller & Gill, 2001; Rooney, 2001; Boulanger *et al.*, 2015).

(3) Wolf recovery

The late 20th century saw the restoration and expansion of several large carnivores (Boitani, 1995; Enserink & Vogel, 2006; Chapron *et al.*, 2014). Across Western Europe, we now tally 12,000+ wolves, distributed in 10 populations,

spanning 28+ countries – a major conservation success (Hindrikson *et al.*, 2017). This reflects increased prey abundance (the recovery of wild ungulates) and effective protection in the form of Europe’s 1979 Bern Convention. This recovery took place despite significant increases in Europe’s human population with intensified land use in many regions coupled with large areas where agricultural lands were abandoned. As for their decline, wolves’ recovery has been most successful in rural areas of southern Europe but slower or non-existent in more natural, less roaded, areas of northern Europe (Chapron *et al.*, 2014). As for deer, it resulted from a combination of changes in legal status, hunting regulations, and attitudes (Bern Convention in 1979, Habitats Directive in 1992) (Boitani & Linnell, 2015). In the U.S.A., wolf population recoveries occurred across the western and midwestern U.S.A. while they were protected under the U.S.A. 1973 Endangered Species Act (Fritts, Bangs & Gore, 1994; Mladenoff, Sickley & Wydeven, 1999; Morell, 2008, 2013). However, wolf recovery proceeded at a slower rate and to a lesser degree than deer recovery. In Europe and the U.S.A. it was slowed by legal and illegal hunting and, in places, by major roads and other human disturbances [for the upper midwestern U.S.A. see Thiel, 1985, Mech *et al.*, 1988 and Mladenoff *et al.*, 1995, 1999; for Spain see Blanco & Cortes, 2001].

III. CONSEQUENCES OF DEER RECOVERY

(1) Positive and negative perceptions: an assessment in progress

How has the recovery of deer populations across North America and Europe affected people in managed or non-managed ecosystems? We can categorize perceived consequences of higher deer densities as either beneficial or detrimental (Table 1). How these are viewed often depends on context. Many celebrate the benefits that deer provide. These include opportunities to view and appreciate deer, now the commonest wild large mammal in many areas. In North America observing wildlife has become increasingly popular (Duffus & Dearden, 1990). Deer hunters also exist in great numbers, spending considerable time and money to hunt a game species they cherish (Nelson, 1998; Sharp & Wollscheid, 2009). Most directly, deer provide food to hunters. Venison remains popular especially among a newer clientele of hunters eager to obtain and share supplies of lean, organic meat (Cordain *et al.*, 2002). Many hunters, however, prefer to hunt large bucks for the challenge (and trophies) this provides. Although hunting represents a sizeable industry in the U.S.A. with 11.5 million hunters spending \$25.6 billion, this segment underwent a 29% decline between 2011 and 2016 (U.S. Department of the Interior, 2017). In the same period, wildlife-watching grew rapidly with expenditures rising 28% to \$76 billion.

While hunters and wildlife lovers welcome abundant deer for these obvious benefits, many farmers, foresters,

Table 1. Synthesis of costs and benefits as perceived by society associated with dense deer populations with examples of references

Effects of deer on:	Benefits	Costs
Wildlife	Recreational hunting (Sharp & Wollscheid, 2009) Wildlife viewing opportunities (Duffus & Dearden, 1990)	Reduce forage for other species (Beck & Peek, 2005) Threats from parasites and disease (Schmitt <i>et al.</i> , 1997; Rizzoli <i>et al.</i> , 2011)
Ecological conditions	Deer reduce yew cover, favouring other understorey plant species (Windels & Flaspohler, 2011)	Reduce understorey plant cover and diversity (Côté <i>et al.</i> , 2004) Reduce animal diversity (birds) (McShea & Rappole, 2000; Chollet & Martin, 2013) Biotic homogenization (Rooney <i>et al.</i> , 2004) Facilitate invasions of exotic worms, plants and diseases (e.g. Dávalos, Nuzzo & Blossey, 2015)
Ecosystem processes	Facilitation of native plant dispersal (Myers <i>et al.</i> , 2004; Albert <i>et al.</i> , 2015)	Facilitation of invasive plant seed dispersal (Myers <i>et al.</i> , 2004) and invasive plant establishment (Knight <i>et al.</i> , 2009) Accelerate nutrient cycling and nutrient losses (Harrison & Bardgett, 2004), increasing stream pollution (McDowell, 2008) Soil compaction, reduced infiltration, more erosion e.g. (Shelton <i>et al.</i> , 2014) Declines in soil carbon (Maillard, 2019) Eventual declines in forest tree carbon sequestration and storage (to be studied)
Agriculture and forestry	-	Crop losses, horticultural damage (e.g. Putman, Apollonio & Andersen, 2011) Limit regeneration in many tree species (e.g. Schaap & DeYoe, 1986) Sparse & simplified under- and mid-storey conditions (e.g. Stockton <i>et al.</i> , 2005)
Human health	Food from venison Outdoor pursuits	Deer-vehicle accidents (also involving substantial property damage) (e.g. Gilbert <i>et al.</i> , 2017) Tick-borne diseases (Lyme, babesiosis, ehrlichiosis, etc.) (e.g. Rizzoli <i>et al.</i> , 2011)
Wildlife health		Reservoir for bovine tuberculosis (Schmitt <i>et al.</i> , 1997) Parasites limit abundance of elk, moose, etc. (Lenarz, 2009) Chronic Wasting Disease (Storm <i>et al.</i> , 2013)

gardeners, and public health officials have begun to focus on potentially negative effects of high deer densities (Table 1). Our knowledge of the range and extent of these effects has emerged slowly and remains incomplete. Although often obvious to specialists, many of these effects are far from evident to the general public and correspondingly neglected by those charged with managing deer populations. A complication is the differences in attitude between specialists (favourable to deer management) and the general public (less favourable) even when there is agreement on impacts being negative (Fischer *et al.*, 2014). Finally, it is difficult to find quantitative estimates of likely cumulative ecological and economic impacts of deer and we are not aware of previous efforts to enumerate them comprehensively.

(2) Direct and indirect effects on forest ecology

Several factors can limit deer populations including harsh winters, predation/hunting, and disease. In the hypothetical absence of these factors, deer populations are mainly

controlled by the food available. When deer first colonize a forest devoid of large herbivores, the standing biomass of these resources is likely to be substantial. This biomass decreases if deer consume more than the yearly plant growth, starting with the most palatable species. This can eventually lead to a situation where deer populations remain abundant in strongly altered understories (Horsley, Stout & DeCalesta, 2003; Côté *et al.*, 2004; Baiser *et al.*, 2008; Martin *et al.*, 2010; Le Saout *et al.*, 2014). In such situations, resources are consumed as fast as they appear but little biomass accumulates (Le Saout *et al.*, 2014).

The impacts of abundant deer on vegetation can be dramatic. They include direct impacts on tree regeneration (Tilghman, 1989; Martin & Baltzinger, 2002; Vila *et al.*, 2003a, 2003b) that act cumulatively over successive decades on multiple species to shift overall recruitment and forest composition (Bradshaw & Waller, 2016). Deer also shift forest understories towards less-palatable species that resist or tolerate herbivory while reducing understorey cover and diversity (e.g. Augustine & Frelich, 1998; Rooney & Waller,

2003; Wiegmann & Waller, 2006; Waller, 2014). These direct impacts, in turn, trigger a cascade of indirect effects on invertebrates as diagnosed in several biomes around the world (Baines, Sage & Baines, 1994; Suominen *et al.*, 2003; Allombert, Stockton & Martin, 2005b; Chips *et al.*, 2015; Iida *et al.*, 2016). Vertebrate communities are similarly affected, most noticeably songbirds that nest on the ground or in the understorey and, for most species, depend on invertebrates to feed their young (DeCalesta, 1994; McShea & Rappole, 2000; Fuller, 2001; Allombert, Gaston & Martin, 2005a; Martin, Arcese & Scheerder, 2011; Rushing *et al.*, 2020). The most critical evidence for these effects comes from studies where long-term/historical data are available in areas of contrasting browsing history (Martin *et al.*, 2010). We know less about how deer affect below-ground ecosystems (Wardle *et al.*, 2001). Nevertheless, one survey in the U.S.A. used 2–7-year-old fenced exclosures to document that deer increased soil compaction while reducing mean plant height, cover, diversity, abundance, tree growth and recruitment, and mice and tick abundance (Shelton *et al.*, 2014).

Drastic reductions in deer abundance can reverse many of these effects, although change can be slow. Partial recovery takes decades for the understorey (Balgooyen, 1995; Chollet *et al.*, 2016), and necessarily even longer if the overstorey has been affected. After a time lag, increased cover in the understorey vegetation allows animal communities that depend on such cover to increase as well (Chollet *et al.*, 2016).

(3) Costs to forestry and agriculture

Although the ecological effects of deer on forestry and agriculture have been well documented, aggregate estimates of the monetary costs of deer impacts to economic sectors like forestry and agriculture are scant. The limited information available, however, suggests that costs are significant. In the U.S.A., the cost of protecting seedlings from browsing exceeds \$500/ha (Schaap & DeYoe, 1986). In Poland, the protection of seedlings/saplings against browsing summed to an estimated €11–15 M euros in 2002/2003. Annual deer damage to forestry costs an estimated €218 M in Austria, €3.2 M in Finland and €585,000 in Hungary (in 2005). In Sweden, impacts of moose (*Cervus alces*) on pine wood quality was at least €50 M/year in 2005 (Reimoser & Putman, 2011; McWilliams *et al.*, 2018).

In addition to their impacts on forests, deer often damage agricultural crops, damage that can be significant when their populations are high. In France (28 Mha of cropland) costs to agriculture per year were estimated at about €20 M in 2004, against €0.26 M for Finland in 2006 (2.3 Mha of cropland), and €100–300,000/year in Slovakia (1.4 Mha of cropland) in 2001/2005 (Reimoser & Putman, 2011), representing costs of about €7/10 ha for France and of €1.1–1.4/10 ha for Finland and Slovakia.

(4) Costs to human safety and to human and wildlife health

High deer populations can also compromise human safety and health. As for other sectors, we lack systematic compilations of these costs but the examples below illustrate how varied and substantial these can be.

(a) Deer–vehicle collisions

Every year many people are injured and some killed by hitting deer with their motor bikes, cars, trucks, or even aeroplanes. Deer–vehicle collision risks reflect traffic volume as well as deer densities interacting with local factors (Bashore, Tzilkowski & Bellis, 1985; Finder, Roseberry & Woolf, 1999; Langbein, Putman & Pokorny, 2011; Hothorn, Brandl & Müller, 2012). Across the whole U.S.A. there were an estimated 1.23 million deer–vehicle collisions between July 2011 and June 2012, killing about 200 people and causing more than \$4 billion in vehicle damage (State Farm Insurance 2012 <http://www.insurancejournal.com/news/national/2012/10/24/267786.htm>). In Canada in 2000, 29,000 collisions occurred, 23 people died and 1887 were injured (<https://www.tc.gc.ca/eng/motorvehiclesafety/tp-tp14798-1289.htm>). In Pennsylvania, the U.S.A. state with the most deer–vehicle collisions, 115,000 collisions occurred in 2013 causing about \$400 million in property damage. Individual states in the U.S.A. midwest estimate 40–60,000 such accidents per year, typically injuring over 100 people, sometimes causing deaths, and incurring tens of millions of dollars in medical and property damage. In the U.K., property damage from deer collisions is about €25 M per year (Langbein *et al.*, 2011). In Germany every year 200,000 roe deer collide with vehicles, resulting in 50 people killed and 3,000 injured. The overall cost is about €490 M (Hothorn *et al.*, 2012). Collision costs are estimated at €100 M/year in France and €163 M/year in Finland. For Europe, overall costs to repair damaged vehicles are estimated to be over €1 billion. More unexpected, between 1990 and 2013, there were 1,088 collisions between planes and deer spp., elk (*Cervus elaphus*), moose, or caribou (*Rangifer tarandus*), with most involving deer (FAA and USDA statistics). One person was killed and 29 injured, plus appreciable property damage to the planes.

(b) Diseases associated with high deer density

Diseases associated with high deer densities are increasing in number and severity in both human and livestock populations. Human diseases borne by ticks that feed on deer include Lyme disease, babesiosis, and ehrlichiosis transmitted by black-legged (*Ixodes scapularis*) and lone star (*Amblyomma americanum*) ticks. In North America, Lyme disease is now the most prevalent contagious disease in the U.S.A., with 20,000–30,000 cases reported annually reflecting a probable overall incidence of 300,000 new cases each year according to the Center of Disease Control and Prevention (CDC). Chronic cases are debilitating and require protracted

treatment. In Europe, more than 65,000 cases of Lyme disease are treated per year (Rizzoli *et al.*, 2011). A recent report suggests that Lyme incidence in England may be three times higher than previously estimated (Cairns *et al.*, 2019). Babesiosis, like malaria, attacks red blood cells and can be fatal if not treated promptly. It emerged recently and is now established in seven U.S.A. states that also show high Lyme incidence. Co-infections of Lyme and babesiosis parasites in mice increase the severity of Lyme symptoms in mice (Bhanot & Parveen, 2019). In Connecticut, babesiosis increased sixfold between 2001 and 2008. In Wisconsin and New York (areas with high Lyme incidence), cases of meningoencephalitis related to the spread of deer tick virus increased from around one case per year between 1958 and 2003 to 21 and 12 cases, respectively, in 2008 and 2012. Similarly, human granulocytic anaplasmosis (HGA), related to Rocky Mountain spotted fever and typhus, is now the third most frequent vector-borne disease in North America and Europe (http://www.eurekalert.org/pub_releases/2012-11/bc-lod110612.php).

Do these alarming increases in serious tick-borne diseases reflect, or merely coincide with, rapid recent increases in deer populations? This question raises controversy with different studies coming to different and sometimes conflicting conclusions. Some consider deer populations as inherently unlikely to affect Lyme incidence because deer rarely provide competent hosts for the *Borrelia* bacterium that causes it (Telford III *et al.*, 1988). Because deer boost tick populations, however, with a mature female laying 2000+ eggs, dense deer populations multiply the number of vectors, making tick bites more likely. Similarly, the complexity of *Ixodes* tick life cycles, with multiple mammalian hosts [typically chipmunks (*Tamias* spp.), white-footed mice (*Peromyscus leucopus*), and deer in eastern North America], each responding in its own way to variation in food resources, predators, and *Borrelia* infections, leads to complex interactions, complicating our ability to tease out causal effects (Ostfeld *et al.*, 2006, 2018; Shelton *et al.*, 2014). Fragmented forests can also boost the density of nymphs infected with Lyme disease (Allan, Keesing & Ostfeld, 2003). These complexities generate variation in how deer densities affect Lyme disease prevalence across ecosystems and time (reviewed in Mysterud *et al.*, 2016).

Despite these complexities, several studies suggest that dense deer populations foster higher tick populations, increasing the risk for diseases like Lyme. Many have noted the striking geographical coincidence of high deer and tick-borne disease levels. Because these might be dismissed as correlative and misleading, however, rigorous studies that experimentally reduce deer populations are more definitive. One of these showed that experimentally reducing deer numbers substantially reduced tick abundance with nymphal burdens becoming unrelated to habitat structure once deer were removed (Adler *et al.*, 1992). Several studies have now linked densities of ticks and/or Lyme disease incidence to the abundance of white-tailed deer (Wilson, Levine & Spielman, 1984; Wilson, Adler & Spielman, 1985; Wilson *et al.*, 1988, 1990; Deblinger *et al.*, 1993; Rizzoli *et al.*, 2011; Telford &

Sam, 2017) including at fine geographic scales (Rand *et al.*, 2003). Studies that failed to find relationships between deer density and Lyme incidence tend either to be non-experimental or to involve limited reductions leaving deer above a threshold density (Jordan, Schulze & Jahn, 2007). Such threshold effects do not allow us to conclude that deer abundance is unrelated to disease incidence given the rigorous experimental evidence now available. This includes a study in Connecticut where the incidence of Lyme disease was strongly correlated to ambient deer densities (Kilpatrick, Labonte & Stafford, 2014). A hunt there reduced deer density to 5.1 deer/km², reducing tick abundance by 76%, exposure risk by 70%, and the number of reported cases of Lyme disease by 80%. The studies reviewed suggest that the high deer densities prevalent in most of Europe and North America, even under conditions where deer are not considered competent hosts for the disease (Rizzoli *et al.*, 2011), potentially contribute to the dramatic increases in serious human infectious diseases by increasing parasite vector densities and perhaps the frequency of co-infection. Although fragmented forests and climate change have clearly also played a role, our primary option for ameliorating the 'risk landscape' is to reduce deer density (Telford & Sam, 2017). Telford & Sam (2017) also emphasizes that arguing against deer reduction as a way to control tick-borne diseases conflates its potential efficacy with sociopolitical obstacles to reducing deer numbers.

High deer densities are also associated with disease outbreaks in deer themselves, other wildlife species, and domestic livestock (e.g. Vicente *et al.*, 2006). The first reported outbreak of bovine tuberculosis in deer (in Michigan in the 1990s) was associated with high deer density (Schmitt *et al.*, 1997). Increases in supplemental feeding enhanced epidemic transmission rates (Miller *et al.*, 2003), leading to a ban in that part of Michigan on such practices. Fallow deer (*Dama dama*) and red deer in SW England and Wales have also tested positive for bovine TB (The Deer Initiative, 2009).

High deer densities also negatively affect other species by propagating disease. For example, white-tailed deer sustain reservoir populations of a meningeal parasite (*Parelaphostrongylus tenuis*) that acts as a non-fatal heartworm in deer, but as a fatal brainworm in larger ungulates like elk, moose, and caribou. In northern Minnesota where moose populations declined precipitously since the 1990s, necropsies reveal that this parasite infected 45% of 54 moose evaluated (Wünschmann *et al.*, 2015). Such findings support recommendations to limit deer densities in areas where managers are seeking to reestablish elk and moose (e.g. Peterson *et al.*, 2009).

Finally, Chronic Wasting Disease (CWD) (for review see Escobar *et al.*, 2019), a spongiform encephalopathy similar to 'mad cow' disease and Creutzfeldt-Jacob disease in humans, is spreading rapidly across the U.S.A. and now in parts of Europe (Benestad *et al.*, 2016). It is caused by prions that are taken up in plants and can persist in the soil for long periods (Johnson *et al.*, 2007). In the U.S.A. it was originally endemic to a few western states but has broken out

repeatedly in areas of high deer density usually in association with game farms and/or supplemental feeding. Efforts to contain such an outbreak in Wisconsin in 2002 failed. CWD has continued to increase in incidence and spread to neighbouring counties and states despite intense initial efforts by wildlife managers to reduce local deer densities and ban hunters from baiting and feeding deer. These efforts generated a strong backlash against the agency leading to the reversal of some efforts and continuing spread of the disease (Storm *et al.*, 2013). CWD has also spread to other states and Canadian provinces (Fig. 1). Deer with CWD also pose risks to other deer species [e.g. to wild reindeer (*Rangifer tarandus*) in Europe (Mysterud & Rolandsen, 2018)] and potentially to livestock.

These results make clear that high deer populations in many regions generate high costs in terms of human, wildlife, and livestock health, property damage, agricultural and forestry losses, and a complex set of threats to ecosystem services and biological diversity. True comparisons of costs, especially those related to the loss of life, and benefits are difficult to assess in comparable terms. Nevertheless, the marginal benefits of adding more deer for possible increases in license revenues and commercial activities from hunting – an estimated \$100 billion in the US in 2001 – (Henderson & Moore, 2006) may be less than the cumulative higher costs these high densities now generate.

Despite increasing research in this domain, the full range and significance of deer impacts remain unknown and unquantified. They are certainly obscure to most citizens (and decision-makers) who may only see a few of these. This selectivity of vision is exacerbated by the fact that those with special or limited interests can be expected to emphasize those particular benefits, or costs, of most interest to them (Nickerson, 1998; Mercier & Sperber, 2011).

The fuller accounting of deer costs and benefits presented here should not be interpreted as pointing a finger at deer. Rather, the objective is to highlight the many ramifications of a situation where little top-down control is exerted on an herbivore that evolved in a world with carnivores. This evolution resulted in deer gaining reproductive and foraging efficiencies sufficient to withstand the predation risks faced. To enumerate fully the costs and benefits that populations of wolves and other predators provide to humans, we must include in our reckoning how these predators act to limit deer numbers and their impacts (see Gilbert *et al.*, 2017).

IV. CONSEQUENCES OF WOLF RECOVERY

With abundant prey available and legal protection, wolves have expanded in range and population in many regions.

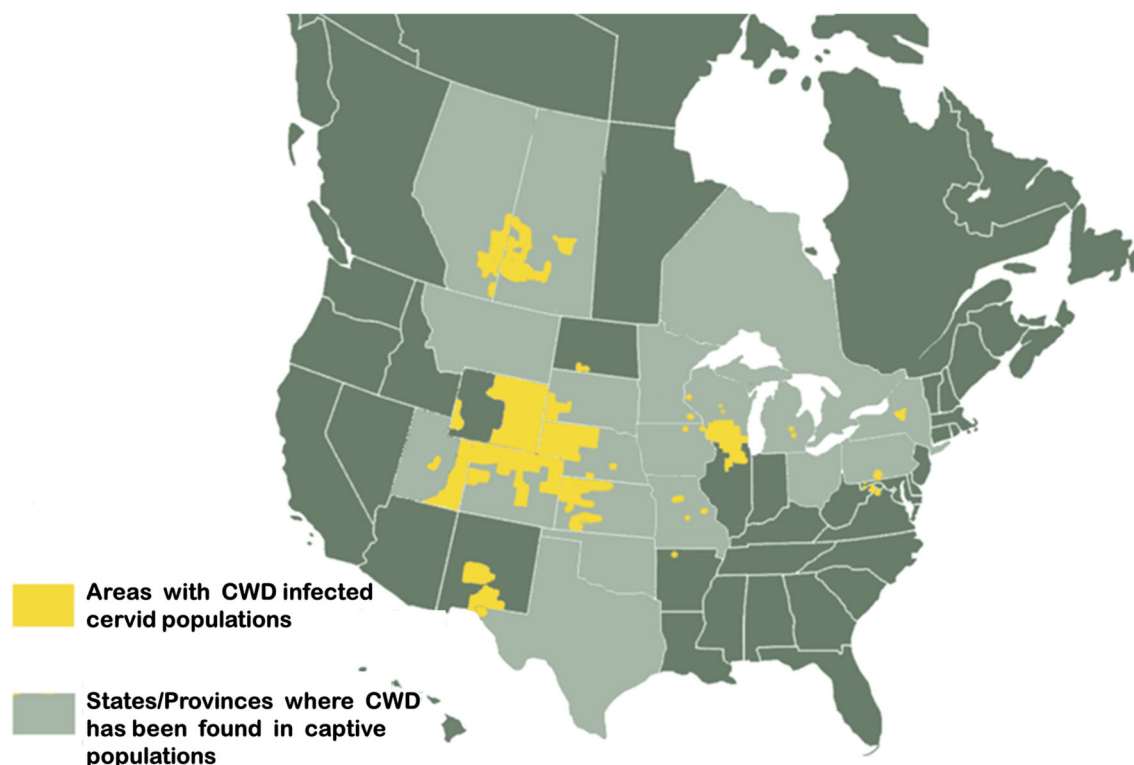


Fig. 1. Map of North America showing the distribution of cervid populations in November 2016 infected with Chronic Wasting Disease (CWD) and the states and provinces where CWD occurs within captive populations. Source: <http://cwd-info.org/map-chronic-wasting-disease-in-north-america/>

Recovering wolves attract public attention for their own sake and for their impact on domestic flocks of livestock. Wolves are also animals that have been and are still able to threaten humans directly (Linnell *et al.*, 2002; Moriceau, 2011; Linnell & Alleau, 2016). By contrast, the public rarely considers how wolves might benefit humans and natural ecosystems by mitigating undesired ecological, agricultural, forestry, and societal (health, accidents) consequences of dense deer populations.

(1) Wolves and biodiversity: hypotheses, facts, and reasons for an ongoing debate

Restored wolf populations can provide important gains for biodiversity by limiting the density of deer or other wild ungulates (Letnic & Ripple, 2017). Positive indirect effects of wolves on understorey vegetation have also been documented in the midwestern U.S.A. (Callan *et al.*, 2013; Flagel, Belovsky & Beyer, 2016). Cascading positive effects on other trophic layers can follow (DeCalesta, 1994; McShea & Ripple, 2000; Smith, Peterson & Houston, 2003; Ripple & Beschta, 2012; Chollat & Martin, 2013) but these have not yet been fully investigated and remain debated (Ford & Goheen, 2015).

Indeed, debate continues to surround the question of whether wolf populations tend to reflect ungulate abundance or whether predation from wolves controls ungulate abundance. The latter hypothesis is gaining support (Donadio & Buskirk, 2016; Letnic & Ripple, 2017; Mech, Fieberg & Barber-Meyer, 2018). This debate parallels the long-standing controversy over whether herbivores control the abundances of individual plant species within a community or whether the plant community controls herbivore abundance (Hairston *et al.*, 1960; Martin *et al.*, 2010). These questions regarding the importance of top-down *versus* bottom-up trophic control have puzzled ecologists since the advent of ecology (e.g. see Colinvaux, 1979).

We think there may be three main reasons why controversies persist over trophic cascades. The first concerns the fact that ecologists often prefer to focus on what they consider equilibrium conditions rather than transient population dynamics. Without changes in population, however, the cause(s) of such perceived equilibria are rarely clear, when they do exist. Regulated populations of deer, for example, could reflect finite resources in the form of woody browse and the forbs and grasses that deer prefer to eat in spring and summer or the presence of human control by hunting, and/or wolf predation. Without a perturbation of some kind, it is difficult to infer why stability persists.

A second reason concerns the need to distinguish just how prey and predators interact. It is easy to see how higher numbers of predators like wolves might directly reduce the number of prey like deer and that lower deer abundance, in turn, could increase plant abundance. It is uncertain however if, when, and where, wolves will recover to densities at which they can have meaningful consumptive effects on their abundant prey in landscapes that are increasingly anthropized

(Kuijper *et al.*, 2016). Consumptive effects can however be complemented, or even outweighed, by non-consumptive effects (also termed risk effects) (Creel & Christianson, 2008). Prey respond to predators, and in particular change how they use the landscape – the places and time they spend foraging; this is the “landscape of fear” idea of Laundré *et al.* (2010). This affects where deer spend their time, which plants they eat, how thoroughly they exploit one patch before moving on to another (Christianson & Creel, 2008; Chamaillé-Jammes *et al.*, 2014), and ultimately their nutritional status (Christianson & Creel, 2010). We can thus envision situations where the presence of wolves protects many plant populations by limiting local and/or total rates of herbivory or by reducing how selectively deer forage. These risk effects, importantly, may depend less on predator densities than on predator presence, and act even when predators remain too scarce to limit prey numbers directly (Schmitz, Beckerman & O'Brien, 1997; Creel *et al.*, 2008).

A third reason for controversy is that plants may increase the amount of chemical defences in their leaves or stems in response to herbivory or the presence of chemical signals associated with herbivory in nearby plants (Tallamy & Raupp, 1991; Karban & Baldwin, 1997). Such induced defences thus reflect a response to the local presence of an herbivore that may or may not translate to a numerical limitation on its abundance depending on the local availability of alternative food sources.

Ford & Goheen (2015) proposed a “gold standard” for accepting when a trophic cascade is acting. This standard requires that one simultaneously shows that wolves constrain or reduce the abundance of deer, that deer constrain or control the abundance of the plants they eat, and that more abundant wolves favour more abundant populations of the plants deer eat. Having to show all three of these effects at the same time sets a high bar for demonstrating a trophic cascade, however, as it will prove difficult to demonstrate the action of all these forces simultaneously. This might still provide a reasonable standard if all three processes are always evident whenever trophic cascades occur. More realistically, however, one or more of these numerical responses could be hidden or difficult to demonstrate due to non-linear and transient dynamics in the system. For example, the impacts that deer are having on many plant populations, or on the understorey as a whole, may be hard to detect for years as deer populations gradually increase, reducing the density and relative abundance of certain species progressively, until a tipping point occurs when herbivory by deer suddenly greatly reduces or eliminates local populations of favoured species (lower curve, Fig. 2). Augustine & Frelich (1998) observed such effects in *Laportea*. Only at this point (B) can we easily observe how sensitive the plant's population is to deer herbivory. Beyond this point, deer impacts would again disappear as these plant species become too scarce to detect deer effects, as noted for palatable tree saplings by Bradshaw & Waller (2016). Deer adjust by shifting to lower quality forage. Recovery of the plant population (upper curve, Fig. 2) rarely retraces the initial trajectory both because depleted

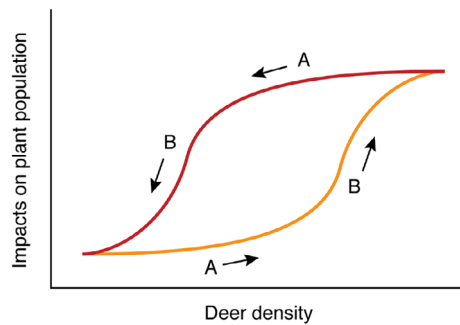


Fig. 2. Non-linear responses to shifts in deer density impede our ability to detect trophic cascades. The lower curve depicts the initial effects of increases in deer on a plant population. These remain subtle and difficult to demonstrate (A) until the plant population is depleted to a threshold density at which point it can rapidly disappear (B). Conversely, the upper curve shows how substantial reductions in deer density (perhaps for an extended time) may bring little apparent effect on the plant population (A) until the plant population escapes herbivory enough to recover rapidly (B). Under such ecological hysteresis, cumulative impacts of deer herbivory act to delay and obscure the effects of deer on plant populations except over particular (and different) short intervals (B).

plant populations provide few seed sources and because selective foraging by deer targets scarce palatable seedlings, impeding recovery. This again narrows our ability to detect deer impacts to a small part of parameter space. Trophic cascades commonly exhibit such ecological hysteresis (Wilson & Agnew, 1992; Augustine, Frelich & Jordan, 1998; Terborgh *et al.*, 2010). Thus, even though all three elements in the cascade could be acting and important, it may prove difficult or impossible to demonstrate all these interactions at once. This greatly constrains our ability to meet Ford & Goheen's (2015) rigorous criteria. This is especially true when we lack observations spanning longer time scales and wider ranges of deer–wolf–plant densities.

(2) The benefits of wolf recovery

Given that dense deer populations threaten the diversity and regeneration of forests, agricultural outputs, and human and wildlife health, we predict that restoring wolf populations would reduce these impacts. That is, if wolves limit deer numbers and impacts, their presence could have high economic value. Lacking integrated economic assessments of deer impacts, we also lack reliable estimates of these potential benefits. The Yellowstone studies suggested that wolves acted indirectly to modify deer behaviour, reducing their impacts on vegetation (Laundré, Hernández & Altendorf, 2001; Ripple *et al.*, 2001; Fortin *et al.*, 2005). These results were challenged (Kauffman, Brodie & Jules, 2010; Winnie Jr, 2012; Middleton *et al.*, 2013) to conclude that the Yellowstone data have been over-interpreted. However, recent studies in the

upper midwest of the U.S.A. documented convincingly, and in their own right, that wolf presence enhances the magnitude and spatial extent of tree regeneration (Flagel *et al.*, 2016) and plant diversity in forest understories (Callan *et al.*, 2013). These studies suggest that year-round stalking and hunting by wolves acts both to reduce deer populations (a numerical effect) and to modify the spatial distribution of deer browsing impacts. Their interpretation was that deer that are wary, clumped, and moving frequently might be browsing less exhaustively on palatable species, reducing impacts on these plant populations. These effects likely also depend on the history and characteristics of local wolf populations (Linnell, Swenson & Anderson, 2001) and on how humans modify the landscapes in which these interactions occur (Melis *et al.*, 2009; Kuijper *et al.*, 2013, 2016; Boitani & Linnell, 2015).

Positive effects of wolf recovery to local economies have also been investigated. In the Greater Yellowstone area, the presence of wolves increased park visitation by about 4%, adding \$35 million to the local economy (Duffield, Neher & Patterson, 2006). Yellowstone, of course, is already a famous national park with many other attractions. Non-park regions that lack clear sight lines and ample wolf viewing opportunities are less likely to benefit to the same degree, especially if the local attractiveness of wolves for tourists declines as wolves become more common. Nevertheless, protecting carnivore habitat has been positively linked to the economic development in several communities (Rasker & Hackman, 1996).

Can predator presence partially mitigate impacts of high deer densities on human safety or property? We have few studies on wolves' influence on deer–vehicle collisions [but see chapter 2 in Raynor, 2017 for a first assessment of a mitigating effect by wolves], but Gilbert *et al.* (2017) assembled evidence that cougars recolonizing the eastern U.S.A. for another 30 years could reduce deer–vehicle collisions by about 22%, preventing over 20,000 human injuries, 155 fatalities, and \$2+ billion in costs. Adding in the value of avoided wildlife and human diseases or of reduced damage to forestry and agriculture that would result from lower deer densities might increase the potential value of predators by several times this. Such benefits of wolf presence on wildlife disease control have been recently documented (Tanner *et al.*, 2019). In Bhutan, a study showed that the presence of an apex predator, the tiger (*Panthera tigris*), had indirect economic benefits through reduced losses in crops or livestock (Thinley *et al.*, 2018). This benefit, however, must be balanced against the losses of human lives tigers can cause (Löe & Röskaf, 2004). Another study in India documented that the presence of leopards (*Panthera pardus*) had indirect benefits to public health (Brackowski *et al.*, 2018). Such savings of life and property should be visible enough to bear on public discussions and decisions about how we manage wildlife. Better assessing the nature and extent of such beneficial effects in the context of recovering wolf populations in Europe and North America is challenging but needed.

(3) The costs of wolf recovery

Wolves have direct economic impacts on livestock farmers but incur little or no costs to urban citizens. The costs of wolf depredation to livestock in the Greater Yellowstone area is estimated to be \$64,000/year for a population of 300 wolves or about \$210/wolf/year (Duffield *et al.*, 2006). Costs to livestock breeding have been estimated in other contexts (e.g. Bostedt & Grahn, 2008). These analyses generally suggest that the direct economic costs of depredation by wolves are minor for the livestock sector as a whole but often substantial for individual livestock breeders (Muhly & Musiani, 2009). These costs also extend beyond the simple market value of losing individual animals to include the sunk costs of past breeding efforts.

Not all livestock breeders are concerned by wolf attacks. Depredation of livestock varies with livestock species and breed. Wolf impacts tend to be relatively more important for sheep breeders grazing extensively in semi-natural habitats, and disproportionately more costly for small-scale sheep breeders whose flocks graze outside in bushy or forested areas (Mech *et al.*, 2000; Treves *et al.*, 2004). Costs are generally higher in places where wolves are coming back where livestock may represent up to half the prey items taken during the grazing season (Pouille, Carles & Lequette, 1997). In other contexts, wolves feed mostly (>90%) on wild prey (Smietana & Klimek, 1993; Meriggi & Lovari, 1996; Sidorovich, Tikhomirova & Jedrzejewska, 2003; Capitani *et al.*, 2004) with livestock representing <5% of the consumed biomass. Once wolves become established, livestock depredation increases when and where wild prey are rare (Papageorgiou *et al.*, 1994). Where hunting and poaching reduce wild ungulate abundance, wolves can consume >35% livestock (Sidorovich *et al.*, 2003). This also increases human–wolf conflict (Linnell *et al.*, 2002; Sidorovich *et al.*, 2003). In extreme cases where wolves have access to free-ranging cattle during the grazing season, the frequency of livestock in wolf scat can reach 45% and >74% of the biomass consumed (Morehouse & Boyce, 2011). Beyond these economic costs is the underlying perception by the rural people affected that the wider society imposes the recovery of a predator onto them and has little regard on their role or function in society and their values (Nilsson Dahlstrom, 2009; Eriksson, 2016a, 2016b).

The size and strength of wolves also make them a potential threat to human lives. Loss of human lives to wolves in the past has been thoroughly and critically examined (Löe & Röskft, 2004; Moriceau, 2011; Linnell & Alleau, 2016). They were often linked to wolves infested by rabies. In contrast to what has been done for other species like brown bear (*Ursus arctos*) (Herrero, 2018), little effort has been made to study the conditions for wolf attacks on humans to occur in the current context, and, even more so, on how to respond in such an event to minimize the risk of a fatal outcome (Löe & Röskft, 2004; Linnell & Alleau, 2016). Part of the reason is the current relatively rare incidence of attacks on humans in Europe and North America compared to fatalities

caused by other wild animals (Linnell & Alleau, 2016), or even by domestic animals such as dogs which caused an average of 17 human death/year in the U.S.A. and in excess of 1 death/year in Canada over study periods spanning two or more decades (Sacks *et al.*, 1996; Avis, 1999; Raghavan, 2008).

As with benefits, wolves have many indirect costs that, in aggregate, could exceed their direct costs. These include the increased costs in time, money and energy that livestock breeders incur to defend their herds from wolves (Widman, Steen & Elofsson, 2017). This additional workload extends to include psychological pressure. When wolves return to an area, livestock breeders must adopt new, or abandon old, practices. If more animals are herded into smaller areas, returning wolves could result in more overgrazing and soil compaction and under-grazing in other areas, influencing both pasture quality and flora (Meuret & Provenza, 2014). Wolf attacks can also cause ewes to abort, decrease milk production, decrease appetite, increase stress, dismantle the flock structure, and result in the loss of herding dogs (Fritts & Paul, 1989).

Financial compensation for livestock destroyed by carnivores is usually met favourably (Naughton-Treves, Grossberg & Treves, 2003), but its effectiveness has been questioned (Boitani, Ciucci & Raganella-Pelliccioni, 2011). For herders accustomed to free-roaming husbandry in semi-natural landscapes, the return of wolves imposes a new external cost rarely acknowledged by those favouring the restoration of wolf populations (Muhly & Musiani, 2009). The uneven spatial distribution of these costs is another level of uncertainty. It could however become an asset to help identify means of coexistence by analysing the mechanisms at work in areas with low or negligible losses (Breck, 2004; Espuno *et al.*, 2004; Rigg *et al.*, 2011).

Hunters often claim that wolves reduce deer harvests. Such claims may be reasonable if wolves act to reduce deer densities substantially (Letnic & Ripple, 2017), or if deer made wary by wolves are more difficult to shoot. Wolves were estimated to reduce deer harvests by hunters by 5–30% in the Yellowstone ecosystem, appreciably less than was anticipated (Duffield *et al.*, 2006). Direct effects of wolf predation on prey abundance has also been studied in Poland's Białowieża forest. There, wolves killed and consumed on average 127 large ungulates per year *versus* 309 shot by hunters (Jędrzejewski *et al.*, 2000). These combined losses reduced ungulate populations by less than 10%, a value deemed unlikely to reduce hunting opportunities (Głowaciński & Profus, 1997). Similar impacts and figures appear for North America (Kolenosky, 1972). Studies that explore the relative effects of wolf predation, climate, and hunting on prey populations often conclude that observed declines in deer populations more often reflect human harvest pressure than predation (Fuller, 1990). The impacts of wolves on deer populations also reflect habitat productivity (Crête, 1999) and the harshness of winters (Melis *et al.*,

2009; Strickland, 2009). An intriguing ecological model (Kirchhoff & Person, 2008) even goes so far as to suggest that despite the tendency for returning wolves to initially depress deer densities, resulting improvements in habitat conditions could boost resource levels enough to favour long-term recovery in the deer population as deer growth and reproduction improve. Thus, deer could recover to densities similar to those without wolves as overall ecosystem productivity improves. Wolves would then check further increases in deer density, preventing excessive browsing and sustaining high productivity. Such exercises emphasize the need for a long-term perspective and a deep understanding of underlying ecological dynamics.

V. CHALLENGES AND WAYS FORWARD

(1) Asymmetries in costs and benefits

Thus far, we have documented that both deer and wolves can be seen as either beneficial or detrimental depending on the context and who is viewing them. Can challenges in living with deer or wolves be overcome by more completely identifying and tallying economic costs and benefits? At the moment, we see little effort to aggregate the economic costs and benefits of deer or wolves to encompass larger scales (county, national) or longer periods (many decades). A search for consensus on how to live with deer and predators is further complicated by the unequal distributions of costs and benefits that individual stakeholders experience. This unequal distribution can accentuate extreme feelings and misunderstandings about deer or wolves. For example, stakeholders directly suffering from deer or wolves (e.g. farmers, foresters, hunters or livestock breeders) see clear benefits in reducing their populations. Farmers or foresters often suffer significant direct economic losses from abundant deer populations (see Section III). However, farmers or foresters who hunt deer or receive revenues from leasing private or public land to hunters can be inclined to accept a trade-off between having more deer and losing more from those deer. The nature of this trade-off deserves further exploration (but see Goodale, Parsons & Sherren, 2015). In the absence of associated benefits, the notion of a trade-off is beyond reach for livestock breeders and/or hunters when it includes direct losses due to wolves or carnivores (Skogen & Krangle, 2003; Goodale *et al.*, 2015).

While direct benefits and costs from large deer populations are easy to perceive, others, such as their direct and indirect impacts on biodiversity or human health and safety, are harder to quantify and reveal. With wolves, this asymmetry in perceiving costs and benefits is radical. Direct costs such as livestock destruction are easy to perceive. They are economical and psychological. Benefits of restored wolf populations for biodiversity, forestry,

tourism, human health and human lives (reduced road casualties through restored carnivore populations) etc. are all indirect, difficult to assess and time-consuming to identify and quantify. They are thus easy to minimize or overlook.

The asymmetry in our ability to quantify and to perceive costs or benefits complicates any assessment of the full scope of the problem by stakeholders and the public. It certainly plays a role in explaining why human attitudes towards deer or wolf recovery tend to be polarized, opposing (easily perceived) benefits of one species against the (easily perceived) costs caused by the other (Fig. 3A, D). This is amplified by the natural tendency of any given group of stakeholders to emphasize evidence that confirms their perspective while discounting or ignoring conflicting evidence (Nickerson, 1998).

(2) Acceptance *versus* conflict, a matter of time, place and species

Deer generally benefit from a broad level of sympathy across the general population (Nelson, 1998). However, situations of high abundance, especially in suburban areas and in areas with deer-sensitive crops, together with an increasing awareness of the potential harm that high deer populations can cause to resources, property, health and lives, has led to more contrasting attitudes towards their presence (Warren, 1997; Storm *et al.*, 2007). Cognitive dissonance emerges starkly in a survey of Pennsylvania hunters (Diefenbach, Palmer & Shope, 1997). A vast majority of hunters (87%) acknowledged that high deer densities impaired forest integrity, meaning that controlling deer populations was necessary to keep deer in balance with their food supply and with local plant and animal communities. Nevertheless, a majority of these same hunters disagreed that deer damage to local forests was a problem, instead expressing the opinion that deer populations were too low and that permits for antlerless deer should be reduced or eliminated.

In the same region, a survey of agricultural producers and homeowners revealed a direct link between the level of damage they experienced and the perception of deer as a nuisance (West & Parkhurst, 2002). Surveys of the general public showed strong support for deer abundance control to avoid threats to human health or safety or environmental damage, but control was judged less acceptable when it was aimed at reducing aesthetic impacts or personal property damage (Fulton *et al.*, 2004). Among Scottish recreational hunters, resistance to regulating soaring deer populations, a reluctance rooted in hunting tradition or personal preferences, was reinforced by antipathy to conservationists (MacMillan & Leitch, 2008).

These examples, related to increasing deer populations, illustrate how personal perspectives influence our ability to envision co-existence strategies based on objective analyses of costs and benefits. Lacking solid numbers for these costs and benefits only amplifies the importance of personal beliefs (*sensu* Dandy *et al.*, 2012).

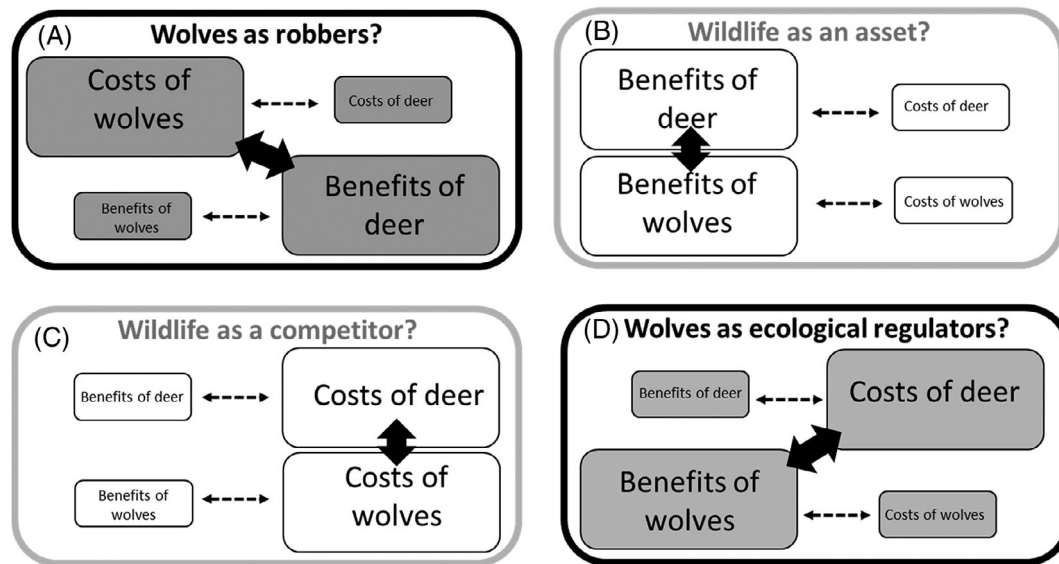


Fig. 3. Schematic illustration of the asymmetry in appreciation (confirmation bias) of relative costs and benefits of recoveries of deer and wolves in a context of deer ‘overabundance’. The two dominant polarized views (A and D) refer to wolf recovery in a context of large deer populations. Minority views are reflected in boxes B and C. The relative size of the boxes within each figure represents the relative importance of costs and benefits within a given category. The size and shape of arrows reflect the relative importance given to specific costs or benefits when developing an argument. Large full arrows identify confirmation biases, dashed narrow arrows identify biases against provided evidence.

When it comes to the presence of wolves, the level of conflict and tension is orders of magnitude more acute. Although a significant fraction of the population perceives their presence as positive (Jacobsen & Linnell, 2016; Treves & Bonacic, 2016), those who most favour their presence are often those who interact the least with them. Positive attitudes towards wolves can decline once wolves become present in an area (Williams, Ericsson & Heberlein, 2002; Dressel, Sandström & Ericsson, 2015). In a context of an increasing wolf population in the midwest U.S.A., attitudes of a selected group of citizens became more negative and fearful over time, independently of having been subjected to wolf impact (Treves, Naughton-Treves & Shelley, 2013). Around Yellowstone National Park, although no net change occurred in the generally positive attitudes people held toward wolves after their introduction, attitudes became more polarized. Support for wolves especially decreased among visitors to the Park who were hunters or ranchers (Duffield *et al.*, 2006). In some instances however, people initially unsympathetic to wolves developed more positive attitudes as their knowledge about wolves increased, often *via* direct interactions with them (Ericsson & Heberlein, 2003; Bisi *et al.*, 2007).

The opposition to wolves, based on livestock depredation, recorded in the midwest U.S.A. contrasts with the tolerance towards black bears in the same region, even though bears caused almost three times as much depredation to livestock (Treves & Karanth, 2003; see also Bangs & Shivik, 2001). Paradoxically, wolves were also the first species listed as endangered in the U.S.A. (Sharpe, Norton & Donnelley, 2001).

(3) Lethal control, a source of conflict

Resorting to lethal control of wildlife is where opposition in opinions seems most acute. Culling wild deer in Europe or North America often triggers strong reactions from stakeholders and the public. Whether individuals support or oppose deer culling often depends on their perceptions and the particular impacts being considered, or on the ultimate cause of deer overabundance (Dandy *et al.*, 2012). Reactions to lethal wolf control are most polarized: lethal control is seen as the only real option for some, yet as totally unacceptable for others (Dandy *et al.*, 2012). On the surface, the rationale is to eliminate a competitor or taker of livestock or game. When livestock depredation is the concern, lethal control is often seen as preferable to prevention measures (e.g. Mech, 2001; but see Musiani *et al.*, 2003, Gehring, VerCauteren & Landry, 2010, Gehring *et al.*, 2011, Urbigkit & Urbigkit, 2010 and Degeorges & Lalo, 2017), although its efficiency as currently practiced relative to non-lethal methods has been questioned (Treves, Krofel & McManus, 2016; but see Redpath *et al.*, 2017) and should be investigated further (Treves *et al.*, 2017; van Eeden *et al.*, 2018). In Sweden, lethal control to reduce impact on livestock was widely accepted, but hunting wolves for other reasons was only advocated by a minority (Ericsson *et al.*, 2004). In herders, the idea of lethal control often correlates with the notion of ‘wolves not in my backyard’ emphasizing the local spatial component. Among politicians, lethal control is often conceived as a means to increase tolerance, but the emphasis can also be on controlling the development of poaching (Doré, 2011; Linnell,

Trouwborst & Fleurke, 2017). The potential for an actual opposing effect on poaching has been proposed but challenged (Chapron & Treves, 2016; Pepin, Kay & Davis, 2017).

For people who favour protecting deer and wolves as a coevolved interacting system, or are in favour of more ethical relationships with non-human life, 'control' is perceived as another instance of abusive interference of humans with 'wild', i.e. 'self-willed' nature, where animals exist for themselves in their own right [see Foreman, 2004; Morizot, 2016].

(4) Differences in values and the value of disagreement

How opposing groups of concerned stakeholders interact will depend on the degree to which each group accepts and understands the challenges, constraints, and value system of other groups (Jacobsen & Linnell, 2016). This can be made more difficult if opinion leaders use human–wildlife conflicts as a vehicle to promote their own political agendas (Pulliainen *et al.*, 1999; Skogen & Krangle, 2003).

Ultimately, resolution of these disputes will hinge on how much trust each group can grant to the knowledge of other groups (Brainerd & Bjerke, 2002; Bisi *et al.*, 2007). Somewhat counter-intuitively, developing such trust fundamentally requires that all stakeholders first agree on their disagreement, rather than trying to resolve their differences in opinion prior to working together. The recognition of fundamentally different viewpoints should be seen as a necessary preliminary step rather than making human–wolf conflict even more unsolvable [assuming that all parties agree to respect their disagreements (Bisi *et al.*, 2007)]. The common ground of accepted disagreement recognizes and bridges distinct world views, providing the basis for working together towards the mitigation of specific and consensual problems posed by living with wild animals. This collaborative process could, over time, erode entrenched emotions and opposing points of view and pave the way to less polarized attitudes by focusing on common visions obscured by distrust or patronizing (e.g. see Skogen, 2003, Redpath *et al.*, 2017 and references therein). For conservationists, 'is lethal control of wolves acceptable if it aims at reducing the propensity of wolves to attack livestock?' could then become a valid question. For herders 'how many losses from wolves, compensated financially by tax money, are acceptable when considering their positive effects on decreasing deer damage to society?' also could become an acceptable question. For hunters it would be about defining an acceptable reduction in game abundance or accessibility in light of the costs of deer presence to agriculture, forestry or public safety or in light of wolf sport hunting opportunities. For politicians it could be to accept that the question is not a binary one as, for example, accepting or not the presence of wolves, but of defining viable terms of coexistence, as they do, for example, for another high-liability component of our societies, the individual car.

(5) A need for a broader perspective?

Controversies, whether concerning living with deer or with wolves, often seem bogged in essentialisms in the sense that species are seen as uniform entities in need of technical 'control', rather than as an ensemble of sentient individual beings. Herders, hunters, environmentalists, scientists tend also to be considered as uniform entities in which individuals are uniform vehicles of simple truths devoid of judgment autonomy (e.g. see Skogen & Krangle, 2003).

To date, the portraying of a radical headlock opposing 'herders' to 'conservationists' about the presence of wolves has occupied the frontstage and front pages while controversies about ungulate abundance were left backstage (Mounet, 2007). Given the wide range of deer impacts, their sometimes dramatic consequences on human lives, and the potential for carnivores to limit these impacts, we wonder why the legitimate concerns and distress of livestock herders or those of hunters so consistently capture the spotlight. At some point, the far-reaching consequences deer have for land managers, foresters, health care providers, the insurance industry, and citizens concerned for their health and road safety must also count, as well as the potential influence wolves may have on the above.

VI. DISCUSSION

(1) Top concerns for a way forward

We have reviewed how the relatively narrow visions that often dominate debates over deer and wolf management neglect the intertwined consequences that concern much broader segments of society. We suggest a corresponding need to consider a far wider set of perspectives as we address the questions of how best to interact with deer and predator populations. The top concerns for future research on these questions should be to approach better in an integrative way: (i) the ecological and sociological mechanisms behind increases in deer populations, (ii) the ecological and sociological mechanisms that drive changes in wolf distribution and abundance, (iii) the full consequences on our lives of these related dynamics, and (iv) how to maximize aggregate benefits and minimize the collective costs incurred when we interact with deer and wolves as parts of integrated ecosystems subject to long-term dynamics. While an integrative approach in concerns (i) and (ii) can build on a broad knowledge base, concerns (iii) and (iv) will pose real challenges even in the acquisition of the basic knowledge needed for an integrative approach.

(2) Obstacles to overcome

This broader and more integrated approach, which, we feel, is still lacking both in the research, political and public sphere, will have to overcome the apparent entrenched

attitudes and conflicting values attributed to what are perceived as opposing homogenous groups. This would allow the ambivalence and mixed feelings running within these groups to emerge and enrich the debate, despite and beyond the perceived need for loyalty towards social boundaries constructed to confront those perceived as adversaries (Skogen & Krange, 2003). It would also bring to the forefront the question of mutual respect and understanding of differences in values and opinions among those involved (Redpath *et al.*, 2013, 2017; Jacobsen & Linnell, 2016). In short, there is a need to (i) make a better effort to cost/quantify the indirect effects of wolves and deer; (ii) encourage conflict resolution by opposing sides respectfully accepting their disagreements; and (iii) understand the cultural motivations of dislikes to work out the causal reason not the proximal reason for conflicts (e.g. people feeling that they are not respected).

(3) From conflict to coexistence

We must acknowledge that people within different groups not only differ in the values they hold most dear but also that they bear different valued elements of knowledge that must be shared as we seek viable solutions. If coexistence is the goal aimed for, we need deer and wolves to persevere in ways that are compatible with human interests. At the same time, human interests would have to be conceived in ways that do not threaten the continued existence of deer and wolves. Morizot (2016) suggests that instead of focusing on one side over another (deer, wolves, sheep herders, hunters, environmentalists, etc.), we could instead focus on how to achieve a workable network of ecological and sociological interactions among these components. Steps towards a more balanced socio-ecological approach are emerging (e.g. Skogen, 2003; Treves & Karanth, 2003; Dickman, 2010). Loud voices will continue to polarize the debate as changes in human attitudes and cultural learning take time, but they do occur. As these emerge, our ecological interactions with deer and wolves will be reshaped.

VII. CONCLUSIONS

(1) Historically, deer (cervid) and wolf populations in North America and Western Europe declined greatly until the 20th century at which point they began to recover dramatically in terms of geographic range and abundance. Deer recoveries reflect scarce predators and dramatic changes in hunting policies and land use. Wolf recoveries reflect both legal protection and responses to rising deer numbers but remain less complete.

(2) Current high deer densities are having many ecological, economic, and social effects but these are perceived differently by different stakeholders. Deer have both direct effects on tree regeneration, natural vegetation, and planted crops

and many indirect effects *via* their impacts on plant and animal communities, diseases and parasites of humans and wildlife, and on vehicular accidents. Where deer populations lack control, these collective and cumulative impacts can be large.

(3) The recovery of wolf populations also has ecological, economic, and social effects that affect various human groups quite differently. Although controversies persist over trophic cascades, wolves have considerable potential to mitigate negative impacts of deer *via* both direct effects on their populations and indirect effects on their movement and behaviour. Top-down beneficial effects of wolves include their ability to mitigate deleterious impacts of deer on forestry, agriculture, tourism, and natural ecosystems and to improve human and wildlife health and safety. Wolves might even relieve deer browsing enough to improve habitat conditions and actually sustain more deer. Such tri-trophic cascades may be common but are difficult to detect and demonstrate, sustaining controversies.

(4) Further controversy results from the fact that benefits from wolves are hard to measure and rarely fully accounted for, meaning they are rarely weighed fairly against the more obvious impacts wolf populations have on certain rural groups dependent on livestock operations or deer hunting. Contrasting views on the relative costs and benefits of deer and wolves sustain strong sentiments and controversy.

(5) We need to aggregate and evaluate the costs and benefits of deer and wolves across larger scales (county, national) and longer periods (many decades). Even this necessary effort, however, is unlikely to yield a consensus on how to coexist with deer and wolves as different stakeholders perceive different costs and benefits. This difficulty is compounded for deer as their direct benefits are easily perceived while the several costs they incur are often indirect, delayed, and dispersed among many parties. By contrast, costs for wolves are easily perceived while their benefits are often indirect and difficult to document. This asymmetry tends to polarize human attitudes. Our review shows that human attitudes towards wolves can shift over time and among regions from conflict to acceptance when conflicts can be resolved through collaborative approaches that respect differences in values.

(6) We face continuing concerns and obstacles as we move forward from conflict to coexistence. Integrative approaches that respect and enumerate a full range of values are more likely to succeed. Although such approaches remain rare, progress is possible if we recognize deer, wolves, and their habitats as a coupled system and highlight the aggregate benefits to be achieved while minimizing costs to affected human groups.

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VIII. REFERENCES

[Correction added on 13 April 2020, after Online publication: The reference Allen & Grosvenor, 1974 has been deleted and the reference Hampton, 1997 has been added in this version]

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