European Bison *Bison bonasus* (Linnaeus, 1758)

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L. Corlatti, F. E. Zachos (eds.), *Terrestrial Cetartiodactyla*, Handbook of the Mammals of Europe,
https://doi.org/10.1007/978-3-030-24475-0_28

Common Names

English	European bison
German	Wisent
French	Bison d'Europe
Spanish	Bisonte Europeo
Italian	Bisonte Europeo
Russian	Зубр

Taxonomy, Systematics and Paleontology

The European bison (*Bison bonasus,* Linnaeus, 1758) is a large herbivore belonging to the order Cetartiodactyla, suborder Ruminantia, family Bovidae, and genus *Bison* that also includes the American bison (*Bison bison,* Linnaeus, 1758) (Fig. 1). Some authors suggest the European bison species to be within the *Bos* genus due to its close association with other species of wild cattle (Groves and Grubb 2011; Soubrier et al. 2016). Despite a rich fossil record, the taxonomy, evolutionary history, and paleobiogeography of the European bison are still being developed and debated (Massilani et al. 2016; Soubrier et al. 2016).

The genus *Bison* experienced several intervals of expansion, contraction, and local extinction during the last 50,000 years in Europe, culminating in reduced genetic diversity during the Holocene (Gautier et al. 2016; Massilani et al. 2016). The oldest skeletal remains of European bison are dated to >50 kya. The temporal distribution of genotyped individuals reveals that European bison mitochondrial lineages are observed before 50 kya and after 34 kya, when steppe bison (*Bison priscus*) appear to be largely absent from the European continent (Soubrier et al. 2016). Paleontological and archeological findings suggest that the species distribution during the Late Pleistocene and Holocene extended east from France to the Ural and Northern Caucasus, and north from Bulgaria to southern Sweden and portions of the North Sea that were unflooded during the Late Pleistocene (Benecke 2005; Soubrier et al. 2016; Hofman-Kamińska et al. 2019) (Fig. 2).

Traditionally, it has been considered that the European bison developed within one single phylogenetic line (including *Bison priscus*, *B. schoetensacki*, *B. bonasus*); or at least two parallel lines, with one being the line of *B. schoetensacki* (Freudenberg, 1910) called also forest bison, which evolved to the recent

Fig. 1 Male (left) and female with calf (right) of European bison (photograph © Rafał Kowalczyk)

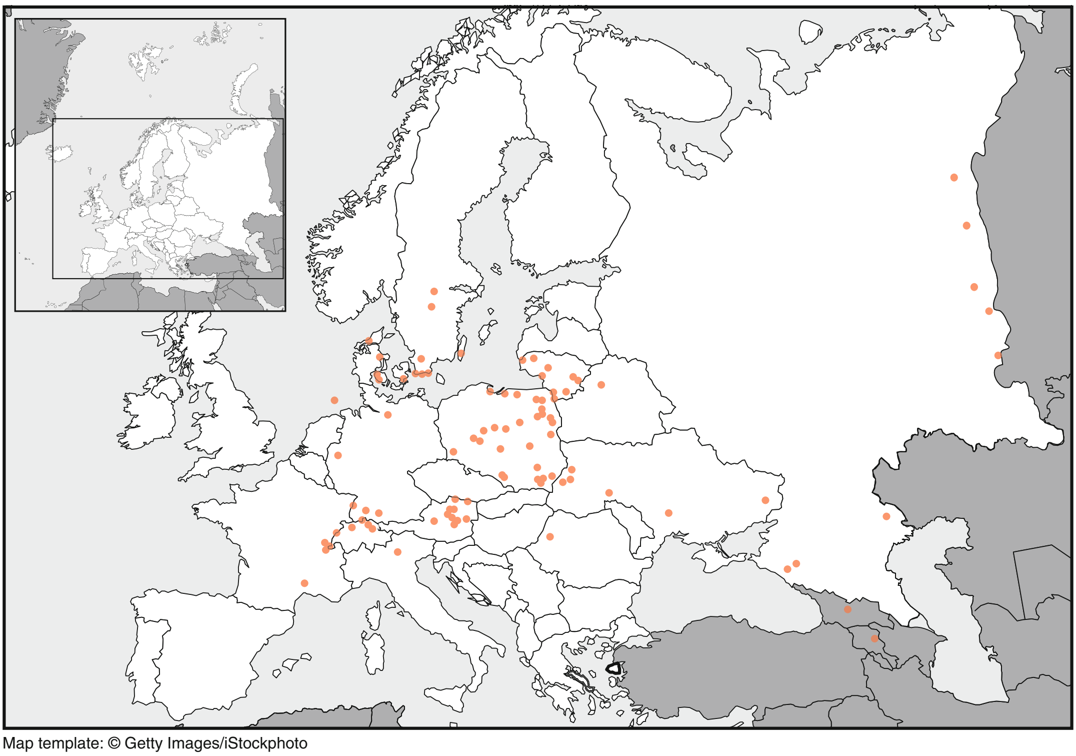


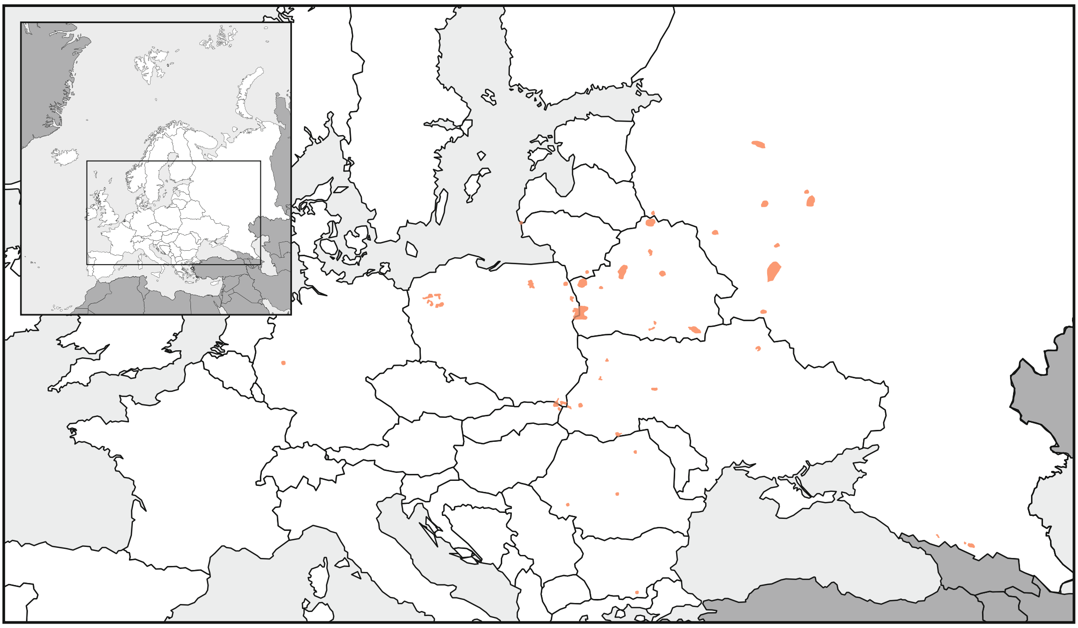
Fig. 2 Historical (Late Pleistocene and Holocene) distribution of European bison in Europe. Dots show locations of historical skeletal remains. (Based on Soubrier et al. (2016) and Hofman-Kamińska et al. (2019)) (Map template: © Copyright Getty Images/iStockphoto)

B. bonasus, and the other being the line of the steppe bison *B. priscus*. However, validity of *B. schoetensacki* is questioned (Drees 2005), and recent genomic analysis place *B. schoetensacki* in one of the *B. bonasus* clades (Soubrier et al. 2016; Massilani et al. 2016; Palacio et al. 2017) and should be renamed accordingly (see details in "Genetics" section). During the Holocene, the species distribution range declined extensively due to meta-population extirpation through an interaction of human persecution and broad environmental change from extensive open landscapes to forested habitats (Hofman-Kamińska et al. 2019). Since the sixteenth century following the medieval period, the European bison persisted in the wild only through royal protection. By the nineteenth century, wild, free-ranging European bison were limited to only the Białowieża Forest of northeast Poland and western Belarus, and Caucasus mountains (Pucek et al. 2004).

Presently, two subspecies are recognized as the Lowland (Białowieża) European bison (*Bison bonasus bonasus*) and the Caucasian (mountain) European bison (*Bison bonasus caucasicus,* Turkin and Satunin, 1904). Some authors earlier recognized the Carpathian (Transylvanian) European bison (*Bison bonasus hungarorum,* Kretzoi, 1946), though that description was based on the morphological identification of only a single bone, and this subspecies has not been recognized in genetic analysis conducted on fossil material (Soubrier et al. 2016; Massilani et al. 2016). Lowland bison were distributed across western and eastern Europe (Węcek et al. 2017; Hofman-Kamińska et al. 2019), while the Caucasian bison occurred only in the northern Caucasus mountains and foothills (Heptner et al. 1966). Compared to the Lowland bison, Caucasian bison morphology included smaller body size, darker coloration, more hairy head and body front, and shorter and more rounded hooves, being attributed to geographical isolation and local adaptation (Flerov 1979). During the nineteenth century, royally decreed translocations ensured that the European bison survived in captivity at several locations across Europe (Krasiński and Krasińska 2017). Yet, by the early twentieth century, the species was increasingly imperiled in the wild, with the Lowland bison becoming extinct in the wild in 1919, and the Caucasian bison extinct in the wild by 1927 (Pucek et al. 2004). As the species was going extinct in the wild, 54 remaining European bison were registered in captivity in the early 1920s (Raczyński 1978; Pucek 1991). A detailed pedigree analysis of these 54 bison indicates that all contemporary European bison are descendants of only 12 founders with individual genotypes (Slatis 1960). Among the bison that survived in captivity there was only one Caucasian male. Captive breeding was then undertaken to create two isolated genetic lines of the European bison, being a Lowland line through seven founders and a Lowland-Caucasian hybrid line with 12 founders (Pucek et al. 2004). Restoration of the species into native habitat started at the Białowieża Forest in 1929 and the history of the many challenges, failures, and successes of this restoration program have been well described (Pucek et al. 2004; Krasińska and Krasiński 2013; Krasińska et al. 2014; Krasiński and Krasińska 2017). In 1950, following sufficient expansion of the Białowieża Forest population, all known individuals of the Lowland-Caucasian hybrid line were removed from the Białowieża breeding center in order to focus only on the Lowland line. Subsequent DNA analysis of the extinct Caucasian bison has shown that some Caucasian bison genetic variants were still detectable in the bison population that occupies the Białowieża Forest in Belarus (Tokarska et al. 2015). This is likely due to an unknown extent of breeding between Lowland and Lowland-Caucasian bison in the Belarusian part of the Forest during initial restoration (Bunevich et al. 2006). The vast majority of European bison herds in Belarus originate from the Belarusian part of the Białowieża Forest with uncertain affiliation to the Lowland line.

Current Distribution

The current distribution of free-living European bison derives largely from multiple reintroduction programs sourced from captive breeding, as well as some recent translocations from wild, free-ranging herds (Fig. 3). In 1952, the European bison was first restored as free-ranging wildlife to the Białowieża Forest in NE Poland, with successive successful reintroductions to locations in Belarus, Lithuania, Poland, Russia, and Ukraine. More recently, free-ranging European bison herds were created in Slovak Republic (2004), Germany (2013), Romania (2014), Bulgaria (2019), and Latvia (2019). In 2019, there were 6244 wild, free-living European bison (EBPB 1987–2020) distributed in 47 herds isolated by geographical distance



Map template: © Getty Images/iStockphoto

Fig. 3 Distribution and ranges of free-living European bison populations (Map template: © Copyright Getty Images/ iStockphoto)

Table 1 Distribution and abundance of 47 free-living populations of European bison (EBPB 1987–2020 and Plumb et al. 2020)

Country	Number of populations	Total population size
Belarus	10	2020
Bulgaria	1	7
Germany	1	26
Latvia	1	5
Lithuania	2	284
Poland	6	2048
Romania	3	107
Russia	16	1381
Slovak Republic	1	48
Ukraine	6	315
Total	**47**	**6244**

or barriers (e.g., border fence) (Fig. 3), with additional new reintroductions being planned. Another 2217 European bison occur at over 200 captive centers and semi-captive herds in nearly 30 countries (EBPB 1987–2020). The Lowland bison line is generally the focus of restoration in Belarus, Lithuania, and northeast Poland, while the Lowland-Caucasian line is the focus in Germany, southern Poland, Romania, Russia, Slovak Republic, and Ukraine (EBPB 1987–2020) (Table 1).

Description

Size and Morphology

The European bison is the largest terrestrial mammal of Europe. A compact body and large head set on a strong neck, combined with a pronounced hump and horns twisted inwards, give the European bison a widely recognized iconic appearance (Fig. 1). The European bison displays a distinct sexual dimorphism, with males 33% bigger than females (Krasińska and Krasiński 2002). Bison cows are characterized by a more delicate construction of the front part of the body, less pronounced hump, narrow head with thinner and more twisted horns, compared to males (Fig. 1). Body mass of mature males is 436–840 kg, and 340–540 kg for mature females (Krasińska and Krasiński 2002). New-born calves weigh an average 26 kg with an observed range of 15–35 kg (Krasińska and Krasiński 2002). Head and body length of adult males vary between 258 and 323 cm, whereas that of females varies between 222 and 292 cm, with shoulder height of mature males reaching 188 cm and 167 cm for mature females (Kowalczyk R., unpublished data on file at zoological collection of the Mammal Research Institute PAS). The tail of both sexes reaches 30–60 cm long and drapes to the heels or below. Black horns are on the sides of the head for both sexes, and become increasingly worn with age for males, and increasingly twisted for females. Maximal distance between horn curves reaches 87 cm with horn length reaching 65 cm (Krasińska and Krasiński 2002, Kowalczyk, unpublished data on file at zoological collection of the Mammal Research Institute PAS). The muzzle is wide and dark gray. At a glance, the European bison closely resembles the American bison, though with smaller and less sloping hindquarters, and some differences in hair coverage and coloration (Krasińska et al. 2014).

Pelage

European bison have a dense, dark brown to golden–brown coat, with some individual variety of coloration shades. The sides of the head and legs are darker in both sexes. In males, the top of the head, chin, neck, shoulders, hump, upper parts of front legs, and prepuce are covered with longer hair. The longest hairs (up to 50 cm) form the tuft at the end of the tail. The rest of the body is coated with short fur; however, the border between the coat covering forequarters and hindquarters is not so distinctly marked as in American bison. New-born calves are red-brown, and after first moulting (3–4 months after birth) their coat coloration change to dark brown. Adult bison begin to moult at the end of winter, usually in March and continues for next 4–5 months (Kiseleva 1974). Both sexes of the European bison intensively rub against trees, broken trunks, and stumps to enhance moulting. The winter coat begins to develop in September and is complete by early November.

Head and Dentition

The skull is wide and massively built, with pronounced protruding bony rims around eye sockets. Males have a greater cavity volume, and the skull is narrower in females. Mean length of the skull is 500 mm (maximum of 542 mm) in males, and 417 mm (maximum of 458 mm) in females. The mean width is 298 mm (maximum of 342 mm) in males, and 240 mm (maximum 277 mm) in females (Szara et al. 2003). Both sexes exhibit two teeth generations: milk teeth 0.0.3.0/3.1.3.0; permanent dentition 0.0.3.3/3.1.3.3, in total 32 teeth. Milk teeth are replaced between 22 and 44 months of age, while molars erupt over a relatively long period between 6 and 43 months of age (Węgrzyn and Serwatka 1984).

Physiology

Physiology of European bison (reproductive cycle, ruminant physiology of an intermediate feeder, etc.) is similar to that of other temperate European ungulates. Body temperature range is 38.1–38.4 °C. Mean heart rate is 106 ± 19/min. Respiratory movements are 10–18/min. Blood pressure (systolic/diastolic) is 132 ± 13/117 ± 7 mmHg (Gill 1999). Main blood parameters and their values are presented in Table 2.

Genomic analysis of genes under selection showed adaptation of European bison to colder climate conditions, which is confirmed by development of thick pelage and lack of historical occurrence in warmer environments of southern Europe (Gautier et al. 2016; Hofman-Kamińska et al. 2019).

Table 2 Hematologic values of European bison in the Białowieża Forest (Anusz et al. 2007)

Parameter	Unit	Mean ± SE	Min–Max
Erythrocytes	T/l	7.4 ± 1.7	2.1–11.1
Hematocrit	l/l	0.3 ± 0.0	0.1–0.5
Hemoglobin	g/l	128.9 ± 25.2	51.00–177.0
Leukocytes	G/l	4.7 ± 1.4	1.3–9.1
Lymphocytes	%	72.1 ± 13.5	34.0–95.0
Monocytes	%	1.3 ± 0.4	1.0–2.0

Genetics

Chromosomes

$2n = 60$ chromosomes, of which 58 are acrocentric autosomes, and two are the sex chromosomes (Melander 1959; Fedyk and Sysa 1971).

Phylogeny and Phylogeography

While some genomic, paleogenomic, morphometric, and paleoecological studies have elucidated large parts of the evolution of bison populations during the Late Pleistocene and Holocene in Eurasia (Soubrier et al. 2016; Massilani et al. 2016), the origin of European bison remains an ongoing subject of scientific debate, with some data interpreted contradictorily (Soubrier et al. 2016; Massilani et al. 2016; Wang et al. 2017; Grange et al. 2018). The first interpretation of ancient mitochondrial genomes and genome-wide nuclear DNA surveys suggests that the European bison is a hybrid between the extinct steppe bison (*B. priscus*) and the aurochs (*Bos primigenius*), the ancestor of modern cattle (Soubrier et al. 2016). The second interpretation of metagenome data proposes that *B. bonasus* mitogenome lineage is more closely related to the *Bos p. taurus* lineage than to the *B. priscus–B. bison* lineages. The lineages maintained parallel evolutionary paths with gene flow during a long period of incomplete speciation. Genetic affiliation between the European bison and cattle mitogenomes results from incomplete lineage sorting (Massilani et al. 2016; Grange et al. 2018). Time for the node separating the *Bos p. taurus–B. bonasus* and the *B. priscus–B. bison* lineages was estimated at 927 (1064–790) kya, and the node separating the *B. p. taurus and B. bonasus* lineages at 768 (886–657) kya (Massilani et al. 2016). It is agreed that the *B. bonasus* mitogenome lineage can be subdivided into two sublineages: Bb1 also named BisonX, which went extinct at the onset of the Holocene, and Bb2, which gave rise to modern-day European bison (Soubrier et al. 2016; Grange et al. 2018). The divergence between BisonX and modern bison lineages occurred at 120 (92–152) kya, likely during the last (Eemian) interglacial.

Genetic Diversity

Contemporary genetic variability of European bison is relatively low, being an effect of population bottleneck due to species extirpation in the wild in the early twentieth century and subsequent restoration from limited number of captive survivors (Pucek et al. 2004; Wójcik et al. 2009; Tokarska et al. 2011). Descendants of only 12 individuals were successfully used in the recovery of the Lowland Caucasian line, while Lowland line derives only from seven founders. Furthermore, the share of genes of individual founders is extremely unequal in the two lines, with domination of a pair of bison (named Planta and Plebejer) constituting over 80% of those in Lowland line, and 50% in the Lowland-Caucasian line (Olech 2003). There is only a single male line in the Lowland bison line, and only three males in the Lowland-Caucasian line (Tokarska et al. 2011). Mean expected heterozygosity, calculated on the basis of microsatellite data, has been estimated as 0.29 (29%) for the Lowland line and 0.35 (35%) for the Lowland-Caucasian line (Tokarska, unpublished). Of more than 52,000 analyzed cattle SNP (single nucleotide polymorphism) loci amplified in European bison, only 900 were found to be polymorphic (Pertoldi et al. 2010). Despite the low genetic variability, deleterious signs of inbreeding depression are rarely observed in European bison. Some slight skull (elongation and narrowing of splanchnocranium) and fore limb shape modifications were found in Lowland-Caucasian line (Kobryńczuk 1985). In general, the lack or limited impact of inbreeding depression on European bison vitality and viability may be due to rapid demographic recovery of the species after the bottleneck, which minimizes the negative impact on the genetic variability by purging the genetic load. It is also possible that genetic depletion took place before the founder event, or because the founders' genomes were, by chance, free from significant genetic load (Tokarska et al. 2011; Tokarska 2013).

Hybridization

European bison may readily hybridize with American bison, which is privately farmed in Europe, to produce fertile offspring. It is unclear to what extent privately farmed European-American hybridized bison could impact the genetic integrity of ongoing and future wild, free-ranging European bison restoration efforts. A hybridized population of European-American bison originating from Askania-Nova, with 95% gene pool coming from *B. bonasus*, was translocated to the wild at the Caucasian Biosphere reserve in 1940, and thrived and increased to approximately 1500 by the 1990s (Sipko et al. 2010). Crossing of European bison and domestic cattle through artificial insemination has proved to be difficult and of very low efficiency (Krasińska and Krasiński 2013). European bison x cattle hybrids are distinguishable from bison on the basis of body mass (>1000 kg) and variable coloration related to the breed of cattle used (Krasińska 1988). First-generation (F_1) male hybrids are infertile, and further crossing only possible by having hybrid females covered by back-crossing (Krasińska 1988). Cross-breeding of bison with domestic cattle has never been observed in the wild, despite close encounter of bison with cattle when moving from forested areas onto adjacent agricultural lands.

Life History

Growth

At birth, the mean body mass of male bison is 28 ± 6 kg (mean $\pm$ SD), and 24 ± 4 kg in females, with no significant difference between sexes (Krasińska and Krasiński 2002). Calves double their body mass by 3 months age, and do not differ significantly between sexes during the first two years of age. As observed in the field, the age of bison may be determined by the combination of body size, and horn size and shape. For both sexes, there is strong growth of body mass and markedly inward-curving horns by year 3 of age, with female bison fully grown by 5 years, and males fully grown by 7 years of age (Krasińska and Krasiński 2002). Sex-related differences in both size and shape of horns are pronounced earlier than differences in body structure. Male horns grow continuously until full development by 7–8 years age, with horn tips then frequently becoming worn down and rounded, due to rubbing against trees and aggression with other males. Female horns grow longer and more curved with age, with 20+-year-old females retaining sharp horn tips (Krasińska and Krasiński 2013).

Reproduction

In wild, free-ranging populations, age at primiparity is generally 3 years, with two-day estrus intervals repeating across the annual rut during August to October (Krasiński and Raczyński 1967; Daleszczyk 2002; Krasińska and Krasiński 2013). In captivity, age of primiparity ranges between 2 and 5 years (Jaczewski 1958; Daleszczyk 2011). Average gestation lasts for 264 days (range: 254–270) (Jaczewski 1958; Krasiński and Raczyński 1967; Kiseleva 1974). Parturition usually lasts 1–2 h, with up to 3.5 h observed (Daleszczyk and Krasiński 2001; Zięba 2007). Wild free-ranging European bison males generally begin to exhibit sexual activity at 3 years age (Korochkina 1971), with fully developed spermatogenesis at 4 years age (Czykier et al. 1999). Free-ranging European bison cows almost exclusively deliver a single calf (Krasińska and Krasiński 2013), with only one case of twin calves reported in a wild, free-ranging population in the Vologda region of Russia (Tyapougin and Gusarov 2004; Gusarov 2011). Twin calves are also very rare in captivity (Kelterborn et al. 2009). Nearing parturition, a cow typically leaves the group, and delivers a calf in a relatively secluded place. A newborn calf stands up after 20–45 min and thereafter follows the mother, that is a behavior trait adapted to open habitats, and the cow-calf pair then rejoins a group with a 1–2 days (Daleszczyk and Krasiński 2001). Also like the American bison, the European bison exhibits birth synchrony with a majority of calves (70–80%) born between May and July (Krasiński and

Raczyński 1967; Krasiński 1978); however, births during early and late months of the year have also been observed (Krasiński 1978; Kelterborn et al. 2009), especially in supplementary fed herds (R. Kowalczyk, unpublished).

Sex ratio at birth may differ between populations. In the Białowieża Forest it was found that increased population density and reduced female body mass led to increasing female-biased calf sex ratios, whereas years with oak *Quercus* sp. seed masting (abundant food resources) corresponded to male-biased sex ratios (Hayward et al. 2011), suggesting alignment with the Trivers-Willard hypothesis that offspring sex ratio is responsive to maternal condition (see Rutberg 1986; Hewison and Gaillard 1999). Calves follow their mothers for the first year of their life, and thereafter may remain in a mother's group for several years (Krasińska et al. 1987).

Survival

European bison are generally long-lived, with females reaching 25 years age and males rarely exceeding 20 years (Pucek et al. 2004; Krasińska and Krasiński 2013; Krasińska et al. 2014). Main sources of mortality are diseases and parasitic infections, and injuries due mainly to traffic collisions (Krasińska and Krasiński 2013). Locally, poaching may play important role. Mortality is higher during severe winter (Mysterud et al. 2007). Mysterud et al. (2007) also reported that generally low adult natural mortality in the Polish Białowieża population increases when reduced oak *Quercus* sp. masting combines with increased winter severity. Daleszczyk and Bunevich (2009) reported low but variable age-sex structured mortality rates up to 3 years age between the adjacent Polish and Belarusian Białowieża Forest populations (Krasińska and Krasiński 2013; A.N. Bunevich and Białowieża National Park, unpublished data), with variability in sex structured mortality between the populations then diminished after 4 years of age. Most recently, overall adult annual survival rate of 0.88 ± 0.09 (mean $\pm$ SD) was estimated for the Polish Białowieża population from radio-tracking data, being lower for males (0.85 ± 0.14) compared to females (0.91 ± 0.07) (R. Kowalczyk, unpublished data).

Habitat and Diet

Habitat

Like the American bison, the European bison is well adapted to foraging in open and mixed habitats, with a wide muzzle, hypsodont (i.e., high-crowned) teeth, and functional length of the anterior part of the jaw that facilitate consumption of a large volume of herbaceous primary production (Mendoza and Palmqvist 2008). At the beginning of Holocene (10–12 kya), bison roamed in open habitats across Europe as indicated by stable isotope analysis (Bocherens et al. 2015; Hofman-Kamińska et al. 2019). Isotopic signatures indicate subsequent shifts in habitat use from open landscapes to forests at the Mezolithic to Neolithic transition 7.5–6 kya years ago (Hofman-Kamińska et al. 2019). Kerley et al. (2012) have argued that replacement of open tundra-steppe by forest cover after the last postglacial period and increasing human pressure related mainly to development of Neolithic agriculture, forced bison into forests as a refuge habitat. As described earlier, royal protection of wild European bison following the medieval period focused on forested habitats (Pucek et al. 2004). Following upon this historical pattern, initial European bison restoration efforts focused mainly on forested habitats in Eastern Europe (Pucek et al. 2004; Krasińska and Krasiński 2013; Krasińska et al. 2014). Restoration continues to focus primarily on forested habitats across Europe including mixed and deciduous forests intersected by abandoned agricultural lands/open river valleys/forest glades, coniferous forests with little herbaceous understory, foothills, and higher elevation transition habitats of mountainous areas, as well as southern taiga (Krasińska and Krasiński 2013).

The Refugee Species Hypothesis proposed by Kerley et al. (2012) suggests that the European bison is not an obligate forest specialist, and that continuation of restoration emphases on forested habitats alone risks confining the species to sub-optimal or marginal habitats, with important density-dependent consequences for species fitness and long-term recovery. Stable isotope analysis showed strong plasticity and variation in habitat use and preference among modern bison populations in response to the proportion of forest cover (Hofman-Kamińska et al. 2018a). When reintroduced into forested habitats, supplementary feeding provides incentive for forest habitat association by bison (Kuemmerle et al. 2018), yet free-ranging bison exhibit habitat selection preference for open and wet/open habitats and abandoned fields over the proportionally (in relation to available area) less-preferred forest habitats (Kuemmerle et al. 2010, 2018; Zielke et al. 2019). Among mixed-forest habitats, coniferous forests are avoided, while alderwoods are preferred in summer and autumn due to higher humidity and persistence of lush vegetation when compared to other forests (Daleszczyk et al. 2007). In some populations, movement from forests into adjacent open habitats increases in winter (Kowalczyk et al. 2013). Kerley et al. (2012, 2020) suggest that supplemental feeding during winter seriously disrupts the species natural habitat ecology and thus reinforces an unsustainable refugee cycle for the European bison.

Foraging and Diet

The European bison is adapted to uptake large amounts of different plants, including fodder with lower digestibility such as senescent graminoids and fibrous plants (Hofmann 1989; Gautier et al. 2016) with daily fresh matter intake of 23–50 kg (Gębczyńska and Krasińska 1972; Holodova and Belousova 1989). Despite their morphological adaptations to grazing, stomach content analysis, DNA metabarcoding of feces, and teeth microwear analysis indicate that European bison are mixed feeders or browsers (Gębczyńska et al. 1991; Kowalczyk et al. 2011, 2019; Bocherens et al. 2015; Merceron et al. 2015; Hofman-Kamińska et al. 2018b). In the Białowieża Forest, European bison diet consists of 454 vascular plant species, including naturally browsed and delivered with supplementary fodder (Korochkina 1972; Jaroszewicz and Pirożnikow 2008; Kowalczyk et al. 2019). DNA-based analysis of feces showed that during growing season Europe bison diet consists mainly of woody species (30% trees, 30% shrubs), followed by herbaceous forbs (34%), graminoids (4%), and cryptogams (2%) (Kowalczyk et al. 2019), with red raspberry (*Rubus idaeus*), European hornbeam (*Carpinus betulus*), wood avens (*Geum* sp.), stinging nettle (*Urtica dioica*), and meadowsweet (*Filipendula ulmaria*) being among the most highly consumed species (Kowalczyk et al. 2019). In winter bison diet is strongly influenced by access to supplementary feeding. With increasing supplementary feeding, European bison decrease intake of woody materials (65% in non-fed bison utilizing forest habitats to 16% in intensively fed herds) and increased intake of herbaceous forages (32% in non-fed bison utilizing forest habitats to 82% in intensively fed herds) (Kowalczyk et al. 2011). The species of trees mainly browsed by bison are of lower economic importance for forest management, including hornbeam (*Carpinus betulus*), birches (*Betula sp.*), and willows (*Salix sp.*). Thus, the supplementary winter feeding that occurs for many reintroduced European bison populations has a strong influence on foraging ecology (Kerley et al. 2012; Hofman-Kamińska et al. 2018a).

In the Carpathian Mountains, the most important forage species during winter is the bramble (*Rubus fruticosus*) (Pčola et al. 2006; Aleksandrowicz et al. 2009; Mazurek 2010). In natural conditions of Dutch dunes, bison predominantly fed on grasses across all seasons with only 20% of diet consisting of woody forages (Cromsigt et al. 2018). The mixed foraging ecology of the European bison facilitates cascading ecological process such as dispersal of seeds in forest ecosystems (Jaroszewicz et al. 2009). The total number of plant species dispersed by bison is approximately 2–3 times higher than for wild or domestic large ungulates (Jaroszewicz et al. 2013). This is particularly important for plant species with no specific dispersal adaptations. Dung deposition may result in increase in species richness, especially in coniferous forest patches, by introducing new species not recorded previously (Jaroszewicz 2013).

Close to 25% of the species registered on bison dung piles has not been previously registered locally (Jaroszewicz et al. 2009).

Home Range

Home range sizes of European bison females and mixed groups are influenced by the distribution and availability of forage resources, while home range for mature males is more related to reproductive behavior and activity than food-related factors. During the growing season in the Polish Białowieża Forest, home ranges of mixed age and sex groups covered 69 km^2 on average (range: 45–97 km^2) and were similar to those of bulls (70 km^2) (range: 29–152 km^2) (Krasińska et al. 2000). Younger males (4–6 years old) occupy smaller home ranges (44 km^2), while fully mature males (≥6 years) occupy much larger home ranges (84 km^2) due to increased mobility during the breeding season (Krasińska et al. 2000). The Knyszyn Forest of northeast Poland is dominated by coniferous tree stands with reduced understory forages, and thus bison occupy larger home ranges (130 km^2) than in mixed deciduous forests of Białowieża (Kowalczyk 2010, Kerley et al. 2020). In the Bieszczady Mountains of southeast Poland, individual bison home range size varies between 59 and 123 km^2 in winter and 1 and 62 km^2 in summer (Perzanowski and Januszczak 2004). Summer home ranges of bison introduced to the German highlands reached 42.5 km^2 (Schmitz et al. 2015). Within a mixed forest landscape such as the Białowieża Forest that includes also open habitats (forest glades, meadows, river valleys), European bison disproportionately use their home ranges, with core areas overlapping with open habitats, which indicate their natural preference (Kowalczyk 2010).

Migration, Dispersal, and Range Expansion

Consistent with the *Bison* genus (see Plumb et al. 2009), European bison exhibit a complex and dynamic movement ecology underpinned by multiple interactive drivers across multiple spatial and temporal scales, including seasonal variation in forage quality and availability, weather (ambient temperature, snow depth, and ice-crusting), competitive mate selection during the seasonal rut, and density-dependent intraspecific competition (Krasińska et al. 2000; Kowalczyk et al. 2013). This complex movement ecology includes extensive ongoing intra-season local movements, seasonal migrations, and dispersal tied to range expansion. Although all free-ranging bison populations will exhibit dynamic local movement with some preference for open habitats as discussed above, not all bison populations exhibit clearly defined seasonal migration. Dispersal generally occurs by individual male bison (usually in age of 3–7 years) that may disperse over large distances ranging up to 700 km (Krasińska and Krasiński 2013). In expanding populations, dispersal by mixed age-sex groups is observed as the result of density-dependent intraspecific competition (Kowalczyk et al. 2013; Krasińska et al. 2014; Plumb et al. 2014). In complex mixed forest-open landscapes with little elevation variation, bison seasonally move between summer and winter areas, whereas in more simple landscapes of suboptimal forest habitats, bison often attempt to move to open habitats in winter leading to agriculture depredation (Hofman-Kamińska and Kowalczyk 2012). In mountainous area, bison seasonal migrations respond to changes in weather and habitat quality along elevational gradients (Krasińska et al. 2014; Plumb et al. 2014). In the Carpathian Mountains, seasonal migrations by European bison are triggered by significant changes in ambient temperature (decrease in late autumn and increase in early spring) and by the appearance of first snowfalls in autumn, with maximum migration distances of 13–19 km for mixed herds, and 5–23 km for old males (Perzanowski et al. 2012). There is evidence of attempts at range expansion in 70% of free-ranging European bison populations, where this density-dependent process is driven by mixed age-sex groups attempting to utilize open habitats in the vicinity of forests, but where management interdiction otherwise prevents such use of open habitats (Kerley et al. 2012). Daily movement distance of mixed age-sex groups ranges between 1.8 and 9.1 km (Rouys 2003; Schmitz et al. 2015); however, during rut bison males can move several kilometers a day.

Behavior

Group Size

The European bison exhibits a well-developed and dynamic social organization (Krasińska et al. 2014). The primary social unit is a mixed age-sex class group of up to 20 individuals generally, including adult cows, 2–3-year-old subadults, and calves. The size and composition of mixed groups are dynamic and change seasonally, with regular rotation and frequent exchanges of some individuals (Krasińska and Krasiński 2013). Generally, the number of groups decreases as average group size increases during the annual rut and in winter, and the number of groups then increases as average group size decreases during spring-summer. Within any season, groups' size tends to be larger in open habitats than in forests. The mean size of free-ranging mixed groups in the Polish Białowieża Forest was 13 animals (maximum 92, Krasińska and Krasiński 2013), and 21 animals (maximum 120) in the Belarusian Białowieża Forest (Kozlo and Bunevich 2009). In the Bieszczady Mountains of southeast Poland, regardless of the season, mixed groups included either 3–10 individuals (29–64% of observations) or 11–20 individuals (16–32% of observations) (Perzanowski et al. 2015). Mixed groups are led by mature cows who lead the group's local movements in search for optimal foraging conditions. Outside of the breeding season, adult males and females are separated; in most populations bulls and mixed groups occupy distinct ranges for majority of the year. Mature males join mixed groups during the rut, but also in winter, when bison aggregate in supplementary feeding sites at fixed locations in the Białowieża Forest. Sexually mature bulls (4–5 years old) often abandon mixed groups after the rut and remain in bachelor groups consisting of 2–8 individuals. Bachelor groups change their size and composition frequently, with 60% of adult bulls greater than six years old remaining solitary or in pairs (Krasińska and Krasiński 1995).

Activity

European bison exhibit multi-phasic rhythm of activity typical of large ruminants, with foraging bouts of 15–315 min alternating with resting bouts of 15–255 min devoted primarily to rumination (Caboń-Raczyńska et al. 1987). In the growing season, bison spend *c.* 60% of their daily activity on feeding, 30% for resting, and 10% on movements (Caboń-Raczyńska et al. 1987). Observations in the Białowieża Forest identified four feeding bouts coinciding with dawn and dusk, and two periods during mid-day (Caboń-Raczyńska et al. 1987). European bison exhibit limited activity during night, especially between 2300 h and 0200 h (Rouys et al. 2001). Winter supplemental feeding essentially inverts the typical activity budgets of free-ranging European bison populations so that daily time spent resting (60%) is twice as much as time spent feeding (30%) (Caboń-Raczyńska et al. 1983, 1987).

Mating Behavior

The annual rut typically starts in August and ends by mid-October, with some initial increase in time spent by mature males by mid-July in beginning to search for receptive females. A tending-bond mating system is polygynous and based on non-territorial males courting individual estrous females (Krasińska et al. 2014). The highest intensity of rutting activity is observed in August–September. Winter supplementary feeding can influence mature female body condition and alter typical estrus patterns, resulting in disrupted birth synchrony with parturition occurring as late as October–November (Krasiński 1978; Caboń-Raczyńska et al. 1983). During the rut, non-territorial males actively search for receptive estrous females roaming between mixed groups or follow a specific herd. A male bison uses chemical cues in the urine to detect females coming into early heat. The male sniffs the urine and performs a lip curl (flehmen behavior) standing for several seconds with raised head and opened mouth. If a female is in heat, the male will follow and court her. European bison exhibit competitive mate selection in which mature males typically dominate younger, smaller subordinate males, and thus mate more successfully. Mate competition typically includes mature males testing younger rivals with aggressive behaviors, including encircling a rival, hoofing the ground, wallowing, shaking the head, and damaging young trees. If the other male does not retreat or display submissive posture, and rather tries to re-demonstrate aggressive behavior, then the probability for a direct contest increases, though physical fights between males during the rut are observed only rarely in the wild (Krasińska and Krasiński 2013). Aggression is rarely observed among free-ranging cows, subadults of either sex, or calves, though some mild aggression has been observed during unnatural aggregations at winter feeding sites (Krasińska and Krasiński 2013).

Communication and Senses

The call of European bison is best described as grunting, and they never roar like mature American bison males. The call of males is lower and hoarser than that of females. Females grunt usually when communicating with calves and males during the rut (Gill 1999; Krasińska and Krasiński 2013). Gill (1999) notes that the olfactory sense of bison is very well developed and essential in detecting danger and in reproductive communication, including locating other animals or groups by smelling tracks of cows left on the ground. Like many other ungulates, bison have an auxiliary olfactory sense organ (vomeronasal or Jacobson's organ) located between the roof of the mouth and the palate, with the flehmen behavior facilitating the organ function (Gill 1999). The European bison is a near sighted animal, yet is able to distinguish larger objects from a distance of several hundred meters (Gill 1999, Kowalczyk, pers. obs.). They have a well-developed sense of hearing. European bison are able to run quite fast, but only for a short distance.

Parasites and Diseases

Endoparasites

Karbowiak et al. (2014a, b) described 88 species of endoparasites in European bison, with species richness, prevalence, and intensity of infections increasing in multiple populations (Drożdż 1995). Endoparasite species richness and individual animal loads have also been documented to increase when bison are unnaturally aggregated in winter at fixed locations for supplementary feeding (Radwan et al. 2010; Kerley et al. 2012; Karbowiak et al. 2014b; Kołodziej-Sobocińska et al. 2016a, b). Endoparasites often found in bison include the liver fluke *Fasciola hepatica* (prevalence of 44%), the lungworm *Dictyocaulus viviparus* (prevalence of 58%) (Demiaszkiewicz et al. 1999), several species of the round worm *Ostertagia* (*O. ostertagi, O. lyrata, O. leptospicularis, O. kolchida, O. antipini*), and multiple *Nematodirus* species (*N. helvetianus, N. roscidus, N. europaeus*) (Demiaszkiewicz et al. 2012). Endoparasites can sometimes infect up to 100% of individuals (Karbowiak et al. 2014a). One of the most pathogenic parasites in European bison is the blood-sucking nematode *Ashworthius sidemi* (Schulz 1933) that was first found in free-ranging bison in Bieszczady Mountains in Poland in 1997, then in Białowieża Forest in 2000, in Knyszyn Forest in 2009, and in Borki Forest in 2016 (Dróżdż et al. 1998; Demiaszkiewicz et al. 2009, 2018). Another blood-sucking nematode *Haemonchus contortus* was initially described in captive breeding bison in the Białowieża Forest in the 1960s (Dróżdż 1961, 1967). The prevalence and intensity of *A. sidemi* infection in European bison in the Polish Białowieża Forest increased rapidly and reached 100% prevalence in tested animals four years after detection, with maximal median intensity of 8200 nematodes per animal and significant deterioration of blood parameters (Kołodziej-Sobocińska et al. 2016c). Among the factors that influenced infection intensity were the number of years since introduction, herd size, age and sex of bison, suggesting that management practices can also have a strong influence in the spread of a newly detected parasites (Kołodziej-Sobocińska et al. 2016b).

Infectious Diseases

While several diseases are known to occur in European bison, including blue tongue virus, foot-and-mouth disease, respiratory viruses, and bovine tuberculosis (Larska and Krzysiak 2019), they are not as broadly distributed within or across free-ranging populations as the infectious endoparasites described above. The bluetongue virus (BTV) was first detected in a captive group of European bison in 2007 (strain BTV-8) resulting in substantial mortality (Glunz 2008). The virus is transmitted by blood-sucking *Culicoides* spp. midges, and, surprisingly, a different strain (BTV-14) was detected soon thereafter in both cattle and European bison in Northeastern Poland (Orłowska et al. 2016). Clinical signs of BTV include fever, salivation, nasal discharge, edema of the head, congestion and ulceration of the oral mucosa, weakness, depression, and sometimes cyanosis of the tongue (hence the name bluetongue), with morbidity dependent on animal age and the BTV strain involved (Schwartz-Cornil et al. 2008). Although BTV is not common in European bison, it is a mandatory reportable disease that can trigger prescriptive management (OIE 2008). Foot-and-mouth disease (FMD) in European bison in the Polish Białowieża Forest was described in the early twentieth century, but has been absent in the species since 1950s (Krasińska and Krasiński 2013). Following a 2011 outbreak of FMD in cattle in Bulgaria, there is no evidence for the maintenance of FMD in wildlife in Europe (Weaver et al. 2013). Surprisingly high seroprevalence of respiratory viruses such as bovine adenovirus type 3 (BAdV-3), bovine parainfluenza type 3 (PIV-3), and bovine respiratory syncytial virus (BRSV) have been detected in European bison resulting in pathogenesis of the lungs or upper respiratory tract (Salwa et al. 2007; Krzysiak et al. 2018). These respiratory viruses seem to be circulating more freely among free-ranging bison than captive bison, suggesting possible spillover from domestic livestock (Larska and Krzysiak 2019). Likewise, potential spillover of domestic ruminant diseases such as bovine herpesvirus 1 (BHV-1) and the Schmallenberg arbovirus (SBV) are also an emerging concern for European bison (Urban-Chmiel et al. 2017; Kęsik-Maliszewska et al. 2018). Bovine tuberculosis *Mycobacterium bovis* is not a common disease in European bison, and was detected in European bison for the first time in the 1990s at the Bieszczady Mountains (Poland), with some spillover into cattle (Żurawski and Lipiec 1997). This disease was then not detected again in European bison until 2010–2011 through a necropsy of one cow and culling of one bull (Welz et al. 2005; Brewczyński and Welz 2011). It was also detected in one of Polish breeding centers in 2013 (Krajewska et al. 2016). Larska and Krzysiak (2019) make a compelling argument that continuing changes in climate and land use will drive the prevalence of emerging and re-emerging diseases in wild, free-ranging European bison and that comprehensive, effective, and efficient long-term disease monitoring is therefore crucial to the long-term recovery of the European bison.

Population Ecology

Population Dynamics

Many restored European bison populations are now subjected to periodic culling to remove sick or injured animals, and more commonly to reduce population size (Kerley et al. 2012; Krasińska and Krasiński 2013). Annual mortality rarely exceeds 6% in larger populations such as the well-studied Białowieża Forest population (Krasińska and Krasiński 2013) (see details in "Survival" section). As such, established free-ranging European bison populations in Poland are characterized by relatively high annual growth rate of 3–12% (Kowalczyk unpublished data); however, demographic stochasticity underpins highly variable annual growth rates in small populations (EBPB 1987–2020; Krasińska and Krasiński 2013). Long-term data indicates negative density dependence in free-ranging European bison populations (Jędrzejewska et al. 1997; Mysterud et al. 2007; Samojlik et al. 2019). Historical data from Białowieża Forest shows that European bison annual population increase was ~3%, and was negatively correlated to bison density and total biomass per unit area of other wild ungulates

(Jędrzejewska et al. 1997). Contemporary data from the Polish Białowieża Forest showed that recruitment rates were best predicted by population density, with recruitment rates declining as population size increase (Mysterud et al. 2007). Additional factors that influence annual growth rate include spring temperature, Oak forest mast pulses (cyclic increased acorn production by oak tress) in the previous year, and winter severity (Mysterud et al. 2007). Historically, large predators are not thought to have affected European bison density nor population increase rate (Jędrzejewska et al. 1997).

Competition with Other Ungulates

Little information is available on competition of bison with other ungulates. At high ungulate densities observed in the Białowieża Forest in the nineteenth century, the growth rate of the European bison population was negatively correlated to its own density and to the total biomass (per unit area) of other wild ungulates, including (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and fallow deer (*Dama dama*) (Jędrzejewska et al. 1997), but there is little information available on niche separation and dietary overlap between European bison and sympatric wild ungulates. Other species of ungulates generally avoid close encounter with bison, though aggression by bison against wild boars and domestic horses has been reported (Krasińska and Krasiński 2013).

Conservation Status

In 2000, the Red List of the International Union for Conservation of Nature (IUCN) Species Survival Commission (SSC) included the European bison as an Endangered species, and based on extensive restoration activities, the IUCN Red List status was upgraded in 2008 to Vulnerable D1 (Olech 2008). The species Red List status was further upgraded in 2020 to Near-Threatened (Plumb et al. 2020). The European bison is listed as a Protected Fauna Species in Appendix III of the Bern Convention (Council of Europe 1979), and as a Priority Species in Annexes II (including animal and plant species of community interest whose conservation requires the designation of special areas of conservation) and IV (animal and plant species of community interest in need of strict protection) of the European Union Habitats and Species Directive (European Union 2013). The European bison is also included in the European Endangered Species Programme (EEP) for zoos established by the European Association of Zoos and Aquaria (EAZA) in 1996. One of the important tools in conservation management is the European Bison Pedigree Book (EBPB) that has been published annually since 1932 and includes lists of all known European bison individuals in captive and wild-living populations. The species abundance and distribution are increasing both in captivity and in the wild with a total of 8461 bison registered in 2019, including 1738 captive, 479 semi-free-living, and 6244 free-living individuals (EBPB 1987–2020). Despite increase in total abundance, there is also concern about long-term population viability. In 2019, only 2518 mature individuals occurred in eight isolated wild free-living sub-populations greater than minimum viable population (e.g. 150 mature animals), and no sub-population was greater than 500 mature animals (Plumb et al. 2020).

In 2004, the IUCN-SSC-Bison Specialist Group (BSG) published a report entitled "European Bison Conservation Status and Action Plan" (CAP, Pucek et al. 2004). With the overall population growing from ~3000 in 2003 to >8000 in 2019, there is now a clear need to undertake collaborative conservation planning in order to update the 2004 CAP. Key issues to be examined include climate and environmental change, science advances and needs, increased interest in restoration programs involving large mammals, meta-population dynamics, conservation genetics, disease ecology, habitat availability and shifting land use practices, restoration and translocation priorities, human dimensions, in situ and ex situ management, and variable national and European Union legal and policy status. Indeed, an updated CAP will be an important milestone for its potential to empower new initiatives and result in better alignment of multinational conservation strategies and actions. Accordingly, the IUCN-SSC-BSG has formally launched a collaborative multi-stakeholder conservation planning process with the explicit objective to develop an updated CAP that adopts the "One Plan" approach has a very strong scientific basis for actionable consensus developed through transparent multi-stakeholder deliberations (Plumb, pers. comm.).

Management

In general, the European bison has been, and continues to be, intensively managed as a forest specialist (Kerley et al. 2012, 2020). Within many of these forested locations, the species dietary needs and distribution are managed through supplementary winter fodder. Supplemental feeding is a management practice dating to times of royal protection that is aimed at reducing damage to regenerating forest stands and agricultural crops, while also limiting bison dispersal to open habitats (Hayward et al. 2015; Samojlik et al. 2019). Winter supplemental feeding also results in unnatural bison aggregations that subsequently elevates parasitic prevalence, and disrupts natural animal behavior, habitat selection, social organization, and movement ecology (Krasińska et al. 2000; Kołodziej-Sobocińska et al. 2016a; Haidt et al. 2018). Experimental introduction to a coastal dune area in which forest patches intertwine with open grasslands and shrubberies shows that European bison can live in natural environment without provision of additional food (Cromsigt et al. 2018). Many free-ranging populations, including small ones, are controlled by culling to reduce population size, regulate sex-age structure, and remove sick and aggressive individuals (Kerley et al. 2012). In lieu of management culling, some commercial hunts for bison are being organized in Belarus and Poland, and it is currently unclear how bison hunting may affect individual population viability or long-term recovery of the species. Despite active management interventions intended to disrupt dispersal and range expansion, restored bison are beginning to exhibit preference for open grassland and agricultural croplands adjacent to traditional forest habitats (Kowalczyk et al. 2013).

Impact on Agriculture and Forestry

The increasing number of bison and the expected expansion of bison populations out of forest habitats, as well as the potential creation of new free ranging herds, is expected to increase risks of human-bison conflict (Hofman-Kamińska and Kowalczyk 2012). Farm crop depredation by bison in areas neighboring forest habitats is emerging as a key human-bison conflict. Incidences of crop damage increase with decreasing distance from the woodland patches in northeast Poland, with 69% of cases of crop depredation adjacent to the Białowieża Forest, and 80% of cases adjacent to the Knyszyn Forest occurring within 0.5 km from nearest woodland patch (Hofman-Kamińska and Kowalczyk 2012). The majority of crop depredation in Lithuania and Poland occurs during winter (December–March) and focuses on cereals, hay, maize, and rape (Hofman-Kamińska and Kowalczyk 2012; Kibiša et al. 2017). Poland and Lithuania have established crop depredation compensation programs funded by state environmental agencies, with annual compensation levels reaching 300,000 euros in Poland, and 100,000 euros in Lithuania (Hofman-Kamińska and Kowalczyk 2012; Kibiša et al. 2017). Bison damage to tree stands generally has low economic impact, and includes mainly browsing and debarking, though increased debarking has been recorded around feeding sites during winter aggregation (Krasińska and Krasiński 2013). While the amount of woody materials consumed by bison in winter changes with access to supplementary fodder, preferred tree species browsed by bison in the Polish Białowieża Forest are hornbeam *Carpinus betulus*, birch *Betula* sp., and willow *Salix* sp., that are of lower economic importance for forest management (Kowalczyk et al. 2011, 2019).

Future Challenges for Research and Management

The European bison narrowly escaped extinction almost 100 years ago, and through multiple examples of personal perseverance and determined national effort, the species has increased in numbers from 54 animals in captivity to over 8000 animals across the European continent in an array of captive situations and free ranging herds. Yet, evidence is accruing that simply continuing within the scope of recent restoration activities is unlikely to achieve full ecological recovery for the species. Rather, it is more likely that sustainable long-term ecological recovery of the European bison across the historic range will be achieved through innovative collaborations among a broader forward-looking coalition of conservation actors that comprehensively address the full suite of emerging science, threats, and opportunities. As noted by Kerley et al. (2020), the European bison has already gone extinct in the wild once, and it would be a tragedy if we were to place it at risk again through incomplete conservation planning, deficient conservation science, or absence of adaptive management.

Conservation Planning

It is clearly time to undertaking a new collaborative multi-stakeholder conservation planning process to produce an update to the 2004 CAP that includes a long-term conservation action plan with a very strong scientific basis and actionable consensus. The IUCN-SSC-BSG is formally partnering with an array of collaborators to undertake this conservation planning to produce an updated IUCN CAP that will serve as an innovative, efficient, and effective milestone for its potential to empower new initiatives and result in better alignment of multinational conservation strategies and actions.

Science Needs

There is now a critical need to formally organize and inaugurate a European Bison Science Network to enhance levels of collaborative and comparative science. Enhancing the effectiveness and sustainability of restoration activities should include testing of alternative hypotheses about landscape ecology, analyzing habitat availability for optimal restoration designs, and comparative analyses of population viability and potential meta-population management strategies (see Daleszczyk and Bunevich 2009; Hartway et al. 2020). Comparative analyses of the effects of interventionist management such as hunting, culling, and supplemental feeding will be important for improving the efficiency and effectiveness of local conservation management. Also needed are comparative analyses of bison ecology across the historic range (e.g., population ecology, stress physiology, foraging ecology, competition with sympatric wild ungulates, ecological cascades, ethology), comprehensive disease and parasitology monitoring, and innovative social science that addresses the human dimensions of bison recovery.

Adaptive Management

Successfully achieving the full ecological recovery of the European bison conservation will require collaboration of researchers, managers, and policymakers to develop and implement science-based adaptive management (Kerley and Knight 2010). Improved ecological knowledge is needed to devise appropriate management regimes counteracting actual and potential threats to the bison and resulting in the wider naturalization of the species. Adaptive management will be essential to learn from emerging science, as well as restoration and management successes and failures. As an example, recent evidence now recognizes the European bison as a refugee species being managed as a forest specialist despite its evolutionary background as a mixed-feeding species inhabiting open or mosaic habitats (Mendoza and Palmqvist 2008; Kerley et al. 2012, 2020; Bocherens et al. 2015). Adaptive management is the widely recognized approach that would purposefully examine emerging science and alternative hypotheses to critically address the extent to which interventionist management actually contravenes long-term conservation of the species and its evolved ecology. There is a need to institutionalize the capacity to learn and adjust management as needed to restore bison to optimal habitats that secure the needs of the species throughout the year and spacious enough to maintain viable populations (estimated minimum 250 individuals). It is very important to adaptively manage for an effective and efficient balance of interventionist management (e.g., supplementary feeding and culling) with conservation of the full extent of the species naturally evolved ecology. Adaptive management can also serve as a framework to restore large heterogeneous landscapes that include forests, meadows, and open habitats for both existing and future bison herds; to gain and employ improved understanding of the human dimensions of bison recovery and thereby implement effective communication efforts to improve social understanding and acceptance; and to strive for effective genetic conservation and population viability by establishing sufficiently large meta-populations that link isolated populations across regional geographic ranges.

Acknowledgments We thank Tomasz Kamiński from Mammal Research Institute PAS for distribution map preparation

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