Mammal Research Institute, Polish Academy of Sciences
BIAŁOWIEŻA

EUROPEAN BISON

Bison bonasus:

Current state of the species and an action plan for its conservation

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Preface

The struggle to rescue the European bison from extinction began about 80 years ago, immediately after World War I. Although the species no longer existed in nature, a few bison remained in European zoological gardens.

Today the danger of extinction to this the largest mammal of the European Continent seems to have been averted; however, there remain many problems, as detailed in this report. European bison breeders appear to have been very lucky; with little knowledge of the species genetic structure, and using conservative breeding methods, they have managed to rescue the species from extinction. This is a great success for nature protection in Central European countries, particularly in Poland.

Despite of the unquestionable success in rescuing European bison from extinction, there are however many problems concerning its future conservation and recovery in contemporary human-managed ecosystems of Europe; in particular, the incorporation of European bison into communities of large herbivores managed by hunters. Until recent history, the European bison was regarded as a game animal; therefore, its recovery to this status could be regarded as another (further) conservation goal.

The main task of the European bison Action Plan and its Conservation Strategy is to conserve this large mammal as an integral part of Europe's native fauna, to preserve its genetic variability, and enable free-ranging viable populations to function as a natural component of European ecosystems. This goal can only be achieved with international co-operation between those countries possessing bison on their territories and support from those international organisations responsible for nature conservancy in Europe. Financial assistance from relevant funding bodies is essential.

The purpose of this report is to present up-to-date knowledge concerning the status of the European bison and especially its origin, taxonomy, phylogeny, genetic structure, historical and recent distribution, population biology and ecology. Furthermore, we discuss the most important actual and potential threats and research needs. These were prerequisite for outlining the global conservation strategy and necessary action plan for the species future protection and management.

During the creation of this report we referred to the IUCN Status Survey and Conservation Action Plan guidelines, and adapted them to the specific problems of the European bison. The first steps towards preparing an Action Plan for the European bison were undertaken long ago. The Bison Specialist Group SSC/IUCN initiated the project in 1990. Soon after, a draft of An Action Plan for North American bison was prepared by the late Dr C.G. van Zyll de Jong – deputy chair of the Group, at that time. The IUCN had intended to publish both plans for *Bison bison* and *Bison bonasus* in one book. It appeared, however, that further work on an Action Plan for European bison was required, as well as increased international cooperation as political situations in central eastern Europe and countries of the former USSR were rapidly changing; a factor that continued to seriously affect the completion of the work.

However, in the meantime, some ideas concerning the European bison conservation strategy have already been outlined in a number of publications, concerning the World population (cf. Pucek 1991, 1992, 1994, Pucek *et al.* 1996a), and more recently in regional aspects (Balčiauskas 1999, Kozlo 1999, Olech and Perzanowski 2002), but never completed with full details. In relation to this, the workshop on "Population and Habitat Viability Assessment for the European Bison (*Bison bonasus*)" was very important. The workshop was organized in Poland (Woliński National Park) in June 1995 by the Bison Specialist Group SSC/IUCN and Conservation Breeding Specialist Group SSC/IUCN, together with the European Endangered Species Programme (EEP) and Poznań Zoological Garden (cf. Pucek *et al.* 1996b). The report resulting from this assessment has been also translated into Polish and Russian. Many results of this workshop are included in the present Action Plan. During the last few years, conservation strategies for the European bison have also been developed in most of the countries where free-ranging herds exist. We therefore have the possibility to use these documents when published or available.

The team of compilers divided their roles as follows: Irina P. Belousova and Wanda Olech responded for Chapters 6 and 7 ("Genetic structure of the species", and "Origin and genetic characteristics of breeding lines"), and related sections in other chapters, Zbigniew A. Krasiński and Małgorzata Krasińska drafted Chapter 11 ("Biology and population ecology"), Wanda Olech offered statistics concerning European Bison Pedigree Book (EBPB) and European Endangered Species Programme (EEP). Zdzisław Pucek wrote the rest of the report and has edited all the text. As the report is a collective work, authors' credits in each chapter or section are not given. An appendix is included to explain origin of the hybrids of North American and European bison in the Caucasus Mountains (Appendix I) and their contemporary status as.a new subspecies*,* *Bison bonasus montanus* is reported in Chapter 8.

The international workshop of the Bison Specialist Group SSC/IUCN (European part) held in Białowieża in April 23–26, 2002 discussed the draft of the report. Twelve members of the Group and four guest scientists attended the meeting, representing Belarus, Lithuania, Poland, Russian Federation and Ukraine. All participants took part in the open discussion and many detailed corrections and additions to all the chapters were included as a result. Their valuable comments and time are greatly appreciated.

We may regard opinions expressed in this report as those that are generally accepted by the Bison Specialist Group SSC/IUCN (European part). Exceptions include, the different views concerning the problem of necessary temporal isolation between genetic lines of contemporary European bison and their strict separation from European and North American bison in Caucasus. We decided not to present these different attitudes in the report concerning the whole species. Thus, the group of compilers is responsible for the final text of the document.

Białowieża, July 2002 Zdzisław Pucek

Editor

Acknowledgements

As the former Chair of the Bison Specialist Group SSC/IUCN, the IUCN proposed that I start work on an Action Plan for North American and European bison. Recently, however, the Large Herbivore Initiative for Europe (LHI) of World Wide Fund for Nature (WWF) selected the European bison as a priority species for which a Species Action Plan should be prepared. Special consultancy project No.9E0154.01 granted by WWF to Z. Pucek in 1999 made it possible to complete this task and co-ordinate bilateral visits and meetings of specialists from East European countries. This assistance is greatly appreciated.

Many thanks is due to all members of the compilers team for their work on the draft of the report, stimulating discussions, and also to participants of the international workshop of the Bison Specialist Group SSC/IUCM (European part) for their ideas and comments added during the meeting and in the final phase of editing of the document. Responsibility for the final draft belongs to the editor.

Thanks are also due to Stephanie V. Prior (Leverhulme Trust scholar) for her kind revision of English. Iwona Ruczyńska (MRI PAS, Białowieża) offered technical help, particularly during the Action Plan workshop and Michalina Pucek read proofs of several versions of tables and the whole text. Karol Zub (MRI PAS) helped in preparation of figures.

Z. Pucek,

Editor

1. Executive summary

The history of extinction in the wild and present status of the European bison, *Bison bonasus*, is briefly summarised. Reasons for the extinction of this species include the overabundance of other large herbivores, cattle grazing in forests, war, and other political instabilities negatively correlate with European bison numbers and densities.

Restitution of the species began with 54 animals, 39 of which originated from the Białowieża population. The process started with the reproduction of bison in Zoos and reserves, increasing population numbers and distribution as wide as possible, and resulting in release into the wild (1952). The European Bison Pedigree Book (EBPB) played a very important role in maintaining the purity of European bison herds and the separation of genetic lines (i.e. Lowland, Lowland-Caucasian).

Present (year 2000) numbers and distribution of the species in enclosed (191) and free-roaming herds (31) is larger than shortly before its extinction in the wild; a situation that would seem to assure the bisons' better survival. At least 2,864 European bison have been registered by the EBPB (2001) globally, of which ca. 60% were free- or semi-free ranging. The actual world population is a few hundred larger, but those animals remain outside the pedigree book, as not all breeding centres reported data to EBPB. Free-ranging herds are mainly distributed in Poland (5), Byelorussia (7), Lithuania (1), Ukraine (9) and Russia (8).

Many threats remain which could seriously influence the future development of European bison populations.

Re-introductions were somewhat chaotic and increasing slowly. Established free-ranging herds are often small and isolated from each other, and tend to be subject to human influence, including use of traditional management methods, as well as supplemental feeding during winter. As yet, a viable population within a continuous range has not been established. Recent simulations have indicated that free-ranging European bison populations need a minimal population at least 100 individuals to be demographically safe. There are only four such herds (or larger) within the contemporary range of the species.

Recent European bison are the descendants of 13 animals, representing a recombination of only 12 diploid sets of genes; those of the Lowland line originate from only 7 founders. The world herd is highly inbred (F=20.2%), especially the Lowland line (F=32.4%), as found in the 1980s and those indices are still increasing. Inbreeding affects life span, viability of young animals, and the interval between calving and skeletal growth, to a higher degree in the Lowland-Caucasian line than in the Lowland line.

Many indices suggest that the European bison has lost its genetic variability and this process is still in progress. The genetic contribution of founders is uneven; fortunately remaining unaltered over the last decades. Two founders dominate; another two participate to a lesser degree.

Ecology of the species has been reviewed, including available habitats, food, reproduction, population structure and organization, based mostly on studies concerning the largest population of European bison present in Białowieża Forest. Natural mortality has considerably decreased due to a reduction in the natural forces of selection. However, diseases have recently appeared in several herds which may pose a serious threat to European bison populations. Furthermore, the species exhibits a particular sensivity to foot-and-mouth disease (e.g., Polish reserves were decimated due to this infection in 1950s). Balanoposthitis of unknown aetiology has appeared in a few herds, as well as tuberculosis (observed in one herd in Bieszczady Mountains, Poland). Both diseases may exert a deleterious effect on European bison herds.

Future goals in conservation and management of European bison are recommended.

Captive breeding and re-introduction to natural ecosystems should continue. The propagation of captive animals with known pedigrees is also very important for preservation of the species and serves to maintain its genetic purity. The establishment of the European bison Gene Resource Bank could be very important for the future of the species.

In the wild, numbers should increase to attain the management goal of creating self-sustaining populations of both genetic lines. Regulated culling in local populations would be necessary for managing optimal bison habitat. Attention should however be given to the chosen scheme of elimination according to the sex and age of the groups.

Further introductions to the wild are necessary to establish a 'continuous' range and ensure the long-term survival of viable populations. There are proposals to

create such populations in the Eastern Carpathians (Poland, Ukraine and Slovakia, and on the border of Ukraine and Romania), as well as in Russia (Brjanskij Les – Orlovskoe Poles'e NP.). Lowland European bison are well distributed in Belarus, 7-8 herds form one 'meta-population'; together with Lithuanian and Northern Polish populations they may create another region within the bisons' contemporary range. These populations should be monitored, allowed to increase in size, and ecological corridors between them established or a programme for assisted migration (translocations) developed.

Pure Lowland and Lowland-Caucasian lines should be separated in the wild, as well as in enclosed breeding centres, up to the time of their likely natural contact. This isolation is of particular importance for preserving the genetic variability within Lowland-Caucasian line. Genetic studies to determine if these lines could be merged should be undertaken. Pure animals should be separated from European × North American bison hybrids within the Caucasus Mountains and elsewhere.

Current genetic management of the contemporary species should involve a more balanced genetic contribution of founders to the genome. Animals representing founder genes, which are currently under-represented or not present in free-ranging herds, should be identified and included in European bison populations.

The aethiology and epidemiology of European bison diseases, especially of the male genital organs, should be determined and their effects on the risk of extinction assessed.

The place of European bison in ungulate communities and the species effect on the carrying capacity of contemporary forest ecosystems in Europe should be determined.

A review of the European bison's status clearly indicates that its recent numbers and distribution are much better than before its extinction in the wild at the beginning of the XX. century. The European bison is classified as an Endangered (EN) species on the IUCN List of Threatened Animals, mainly due to the many continued threats. While these threats exist, the European bison's full recovery and re-naturalisation in the wild cannot be guaranteed. It should therefore also be included in the Habitat Directive and in Appendix II of Bern Convention.

2. Introduction

European bison (*Bison bonasus* Linnaeus, 1758) is the largest herbivore in Europe. Historically it was distributed throughout western, central, and south-eastern Europe. The species undoubtedly had an important role in the formation of the pre-historic European broad-lived forest and forested steppe ecosystems. This mighty and beautiful animal was honoured by many early-history nations of Europe as a symbol of natural power and homeland. At the same time, European bison was always a game animal. Habitat degradation and fragmentation because of agricultural activity and forest loggings, and unlimited hunting and poaching, were the primary reasons for the decrease and extinction of European bison populations.

By the end the XIXth century, there were only two populations of European bison left in the wild: in Białowieża Forest (B. *b. bonasus*) and in the West--Caucasus Mountains (B. b. *caucasicus*). Pucek (1991, 1994) has summarized the history of their extinction.

Doubtless among the primary reasons for the rapid decrease in the European bison population in Białowieża Primeval Forest at the beginning of XIX century was the over-population of deer species, and the drastic reduction of natural food resources for herbivores, which followed (Wróblewski 1927). World War I completed the inevitable, making it impossible to avoid the final disaster of 1919. During the period of World War I, the Revolution of 1917, civil war episodes and heavy poaching became directly responsible for the complete liquidation of European bison in the West-Caucasus region before 1927 (Bashkirov 1940; Heptner *et al.*, 1966).

Reconstruction of European bison population dynamics during the last two centuries in Białowieża Forest (Jędrzejewska *et al.* 1997) has indicated that bison population density depends on: (1) mean annual temperature, which may limit food resources, and (2) political instability, administrative chaos, wars and other military actions. These two factors, however, explain only 9 % of the total variation in bison numbers.An increase in bison populations numbers depends upon the level of political stability, (if wars are excluded) and is negatively correlated with bison population density, and the total biomass of other wild ungulates (including cattle), which could mean intra- and inter-specific competition. These two factors explained 70% of the total variation in the bison population increase (Figs 2.1 and 2.2). Changes in bison numbers were shaped predominantly by human activity, including chaos and poaching during war times, and to lesser degree by intra-and inter-specific competition (Jędrzejewska *et al.* 1997). These seem to be the most important factors shaping the European bison dynamics in Białowieża Forest before its extinction in the wild at the end of World War I. The effect of political instability on wild animal populations has recently been proved in Caucasus, where the few free-living, re-introduced herds have been decimated and finally made extinct.

After the World War II the species survived only in a few European zoological gardens (Sztolcman 1924).

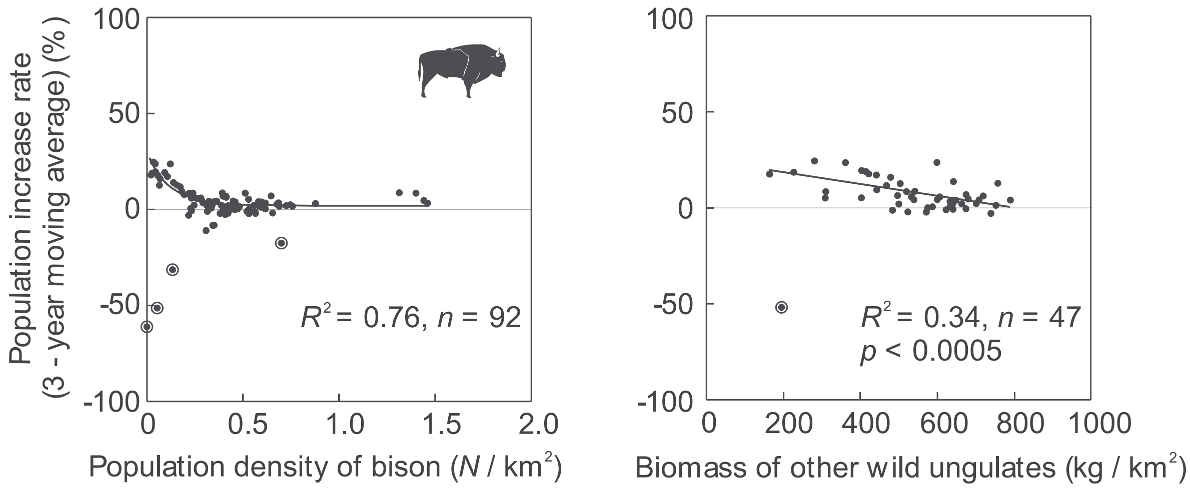


Figure 2.1.
Rates of annual population increase (3-year moving average) of European bison in relation to the density (left) and biomass of other wild ungulates (acc. to Jędrzejewska *et al.* 1997).

Together there were only 54 (29, 25) European bison with proved pedigrees (Raczyński 1978, Pucek 1991), originating from 12 ancestors (or founder animals) (Slatis 1960).

The concept of restoring the European bison using animals kept in zoos originated in several countries and was publicly presented for the first time by Polish zoologist J.Sztolcman at the 1st International Congress of Nature Protection in Paris, 1923 (Sztolcman 1924, 1925). The Congress supported the appeal and expressed a desire to establish an international society for the protection of the European bison. "Actes du Congres International pour la Protection de la Nature, Paris 1923, (p. 93) states that " …an international society should be created, in the shortest possible time, among those countries on whose territory European bison still exist", as well as, "… other nations should offer them financial assistance and that the League of the American Bison make its experience available to the new assembly". By August 25–26, 1923, the International Society for Protection of European Bison [Internationale Geselschaft zur Erhaltung des Wisents] was founded in Frankfurt on the Main. It included 16 countries. Dr K. Primel, the managing director of the zoological garden in Frankfurt was elected as President. The statute of the Society included the maintenance of the European bison by planned breeding and distribution, followed by introductions to large forest complexes. These goals are still valid, although the major task today is to restore the species to the wild within a reduced area of its former range and without. After World War II, the Society was not re-established in its previous form and activity, although its name was used in Poland until 1965 on the cover of the European Bison Pedigree Book.

A particular accomplishment during the period of European bison restitution was the maintenance of the

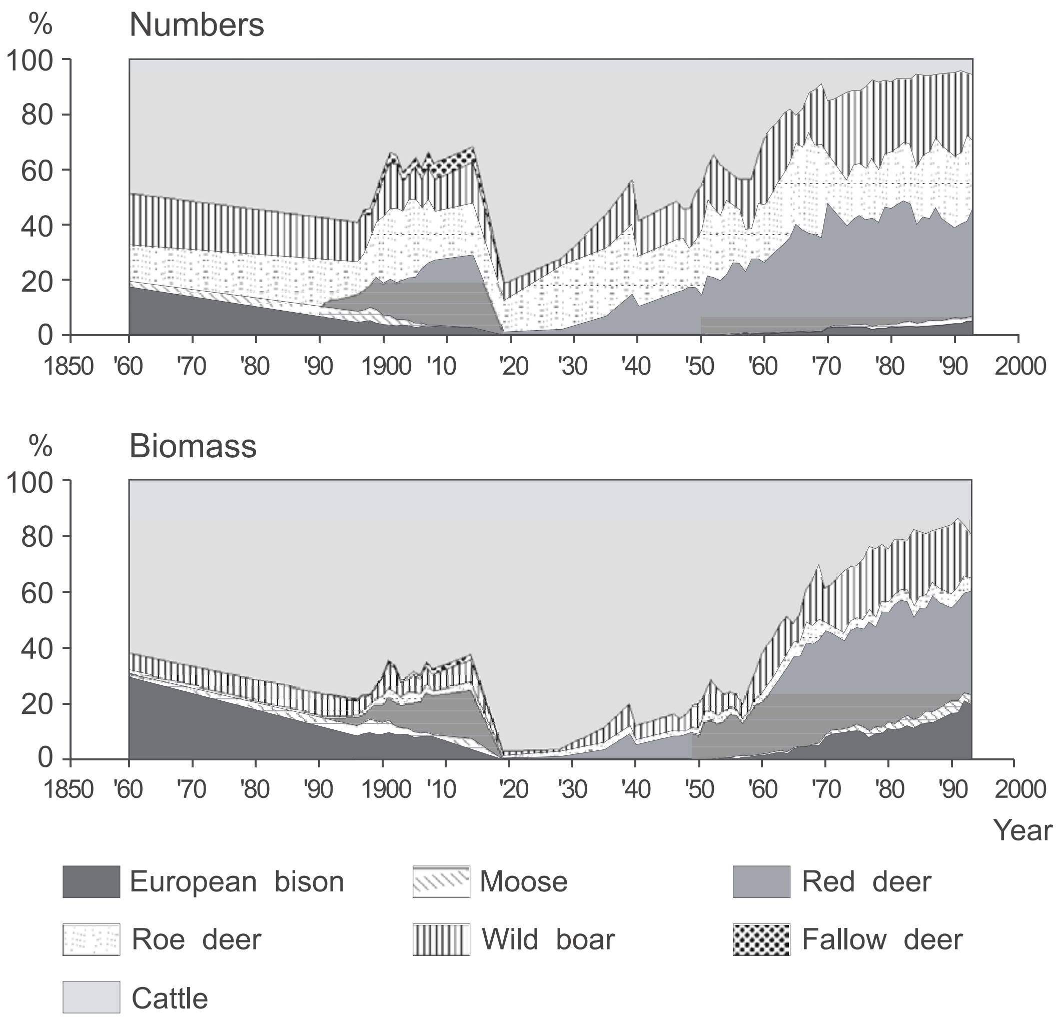


Figure 2.2.
Species structure of ungulate community in the whole Białowieża Primeval Forest (acc. to Jędrzejewska *et al.* 1997).

species' genetic purity, especially in the early period when there were numerous hybrids with North American bison and cattle produced in various zoos. For this purpose, a studbook was created – the European Bison Pedigree Book (EBPB). The first registers of all European bison living in the world (at first also of their hybrids) were published in Germany, in the Society series of "Berichte..." (Groeben 1932; Mohr 1933, 1937). With great effort by the first editors of the EBPB, all crossbred animals were eliminated from breeding with pureblood European bison. An attempt to 'increase' the production of European bison by crossing them with European and American bison hybrids in Schorfheide near Berlin, propagated by Nazi officials of the III Reich, was successfully avoided by killing all these animals during the final phase of World War II (1945) (Wernerowa 1969). No issue of EBPB was published during this time. After WWII, hybrids remaining in Munich (Hellabrunn) were carefully verified by Dr Erna Mohr. Another attempt to produce such hybrids took place in Russia and was aimed at restoring the Caucasian subspecies (*Bison bonasus caucasicus*) by, so called, backcrossing with European bison. Unfortunately, hybrid animals were later released in the Caucasian Biosphere Reserve and are now an established free-ranging herd (see Appendices I).

After World War II, the EBPB was edited in Poland under the auspices of the State Council of Nature Protection. The merits of J. Żabiński, who in cooperation with E. Mohr (Germany) and M.A. Zablotsky (USSR), edited the Book until 1964 and later patronized this enterprise until his death in 1974. Undoubtedly, E. Mohr (Germany) and J. Żabiński (Poland) deserve special credit for twice rescuing the genetic purity of the world population of European bison by introducing only pure blood animals to the EBPB (at the beginning of bison restitution and at the end of WW II). At this time, successive assistant editors issued the EBPB. Starting from 1965 J. Raczyński introduced a new style and form (including the title) of EBPB. From its very beginning the EBPB served as an example of pedigree books for other animals. Since 1993 Białowieża National Park, Poland has published the EBPB.

EBPB is the only official document of the species registration. It is an important source of data about the numbers of European bison in different locations. The EBPB editorial office is used by breeders for making contacts and finding information about the species.

The structure of data included in the Pedigree Book has not changed for almost 70 years. All animals from enclosed breeding centres are registered individually and only the size (sometimes divided by sex) of free-ranging herds is included. Every individually registered animal has a pedigree number, name, numbers and names of parents and the name of breeder or actual owner. The name of each animal usually starts with two or three letters characteristic for the breeding centre. Every issue of EBPB is divided into seven parts:

1. World register of purebred European bison living at the end of a particular year, which includes the number of males and females in every breeding centre (captive and free-ranging) listed according to alphabetical order by country and owner;
2. Official register of purebred European bison born before a particular year, which includes all animals registered by breeders born in previous years listed by pedigree number;
3. Additions and corrections of former lists, which includes animals born or registered after former removal from the list classified by pedigree number;
4. Official register of purebred European bison born in a particular year, which includes all animals registered by breeders born in the last year sort by pedigree number;
5. Changes in European bison in a particular list, which includes information relating to deaths and transfers between breeders in the last year sorted by pedigree number;
6. List of all living European bison on 31 December in a particular year, which includes all animals in enclosed breeding centres arranged alphabetically by country and breeder name;
7. Index of owners.

Animals, which are individually registered, are divided into two genetic lines: animals from the Lowland line are printed in bold letters and those from the Lowland-Caucasian line – in normal fonts.

During the process of European bison restitution , two periods can be distinguished. The first, lasting til 1952, involved the intensive breeding of European bison in zoological gardens, parks, and specially created reserves. A second period commenced with the creation of free-living herds. Now (year 2000) the total number of European bison globally is about 2900 individuals, including about 1700 animals in free and semi-free populations. These figures represent pure blood bison, registered in the European Bison Pedigree Book (EBPB). At least 700 animals remain outside this inventory because of a lack of reliable information from owners. Turnover involving these animals and attempts at including them in the pedigree system, without necessary documentation, may cause a serious threat to the world population of European bison.

3. Conservation status

For centuries the European bison was under special protection as it was considered the property of Polish kings, Lithuanian princes and Russian Tsars. One of the first legal acts concerning bison protection was the so-called "Lithuanian Statutes", declared by Polish King Sigismund the Old in 1553. The death penalty was imposed for killing European bison by Sigismund August (1520–1572). Vladislaus IV introduced strict protection of royal forests in Poland and their game (1641). From 1803, the Russian Tsar Alexander I ordered the special protection of European bison in Białowieża Forest. For at least two centuries, European bison were fed during the winter here (cf. Karcov 1903) and in other places. However, no measure of protection helped stop the species extinction in the wild at the end of WWI.

Today the danger of extinction to the largest mammal of the Eurasian Continent remains; however, in many respects (number, distribution) the situation for the species seems to be better now than at the beginning of the 20th century. Yet, further bison restitution efforts encounter numerous unsolved problems. Many threats still faced by the species indicate the necessity for its active protection and special care. Such actions might include legal protection by law in every country, according to its current status on red lists or red data books, and the creation of free-ranging populations within the territories of national parks or reserves.

On the continental scale, the European bison is included in Appendix III (protected fauna species) of the Bern Convention on the conservation of European wildlife and natural habitats and is treated as an endangered species (EN, A2ce, and C2a) by the 2000 IUCN Red List of Threatened Species. The overview presented below indicates that European bison should be in Bern Convention, Appendix II – strictly protected fauna species. It should be also included in the Habitat Directive of the European Union (Appendix II and IV) as suggested by several European countries (e.g. Poland, Romania, and others).

There is no international strategy on captive breeding for the European bison world population and we know that some regional strategies have only been recently prepared. The European Association of Zoos and Aquaria (EAZA) started the European Endangered Species Programme (EEP) in 1996. In the year 2000, 405 animals in 62 breeding centres (35% of world captive population) participated in this programme. The rules of the programme included: (1) evaluation of genetic value of animals using pedigree information, (2) transfers of animals between participants, (3) preparation of management guidelines for the species.

It is necessary to emphasize the importance of the European Bison Pedigree Book (EBPB), which not only registers and publishes lists of European bison, but also keeps an eye on the genetic purity of the species. EBPB is the only source of information about the genealogy of the species' global population from the beginning of its restitution (beginning of XX century) to the present day. Nevertheless, not all owners of captive bison groups sent information to the EPBP editor annually, and some do not co-operate with EBPB at all. Of course, these groups are usually very small (1–4 animals), but also larger groups exist. [In 1987–1992 three German owners of large captive groups terminated all contact with EBPB: Bayreuth (14 animals), Hohenstand (24 animals), and Krechting (41 animals). EBPB has no information about semi-free ranging herds in Gurley, USA (28 animals), Preslav, Bulgaria (73 animals), Voden, Bulgaria (75 animals), Bucşani-Neagra, Romania (45 animals), and others.] Animals from such breeding groups with no contact with the EBPB editor risk losing their pedigree status and will not have the possibility of introductions to other herds of pureblood European bison. The same is true for animals bought by dealers, who are unable to supply precise information regarding the fate of the animals they are buying and selling. The EBPB should publish some genetic guidelines (e.g. list of genetically important animals) for owners and managers of captive groups. In any case, the EBPB is a necessary tool for successful restoration of European bison, and the Editorial Office of EBPB and the Bison Specialist Group SSC/IUCN are very thankful to all owners and breeders of European bison captive and free-living groups for their information and co-operation.

4. The origin of the European bison

The general assumption is that genus Bison H. Smith, 1827 has it origin in southern Asia. From the late Pliocene of India (Sivalik) deposits of Probison dehmi Sahmi *et* Kahn, 1968 are known, while Protobison kushkunensis Burtschak-Abramowitsch, Gadziev *et* Vekua, 1980 comes from late Pliocene of Trans-Caucasia. According to Flerov (1979) *Bison sivalensis* Lydekker (ex Falconer, 1878) can be traced from the first of these forms. Late Pliocene *Bison paleosinensis* Teilhard *de* Chardin et Pivetau, 1930 is probably a representative of *B. priscus* Bojanus, 1829 (McDonald 1981).

During the late Pliocene and early Pleistocene bison were widely spread throughout the temperate zones of Asia and Europe (cf. Fig. 4.1). They also penetrated through Bering Strait to North America (Flerov 1979).

Forms reaching from Asia to Eastern Europe (near the Black Sea and the south Ukraine) during Villafranchium were relatively short-horned. Longhorn forms (*B. priscus*) developed in large areas of Europe and Asia, from England to Manchuria during the mid-Pleistocene. With the cessation of glaciation bison became smaller in size, especially in Western Europe, with shorter horns (cf. *B. priscus mediator*) as compared with east Europe and Asia (*B. priscus. gigas*). During the early Holocene bison were still widespread but still did not inhabit northern Europe. At the end of the Würm, a transitory form appeared between *B. priscus* and *B. bonasus*, described as *B. bonasus major* Hilzheimer, 1918. *B. bonasus* did not occur in central Europe until the late Holocene. During the last glaciation, perhaps in Caucasian region, it appeared, spreading to the west and north (cf. review in Pucek 1986).

Flerov (1979) claims that both the European bison *Bison bonasus* and the wood bison *Bison bison athabascae* come from Palearctic *B. priscus*. McDonald (1981) and some other authors claim, that the European bison may be derived from late Pleistocene re-emigrants from North America. Craniometrical research by van Zyll de Jong (1986) reveals a great similarity between

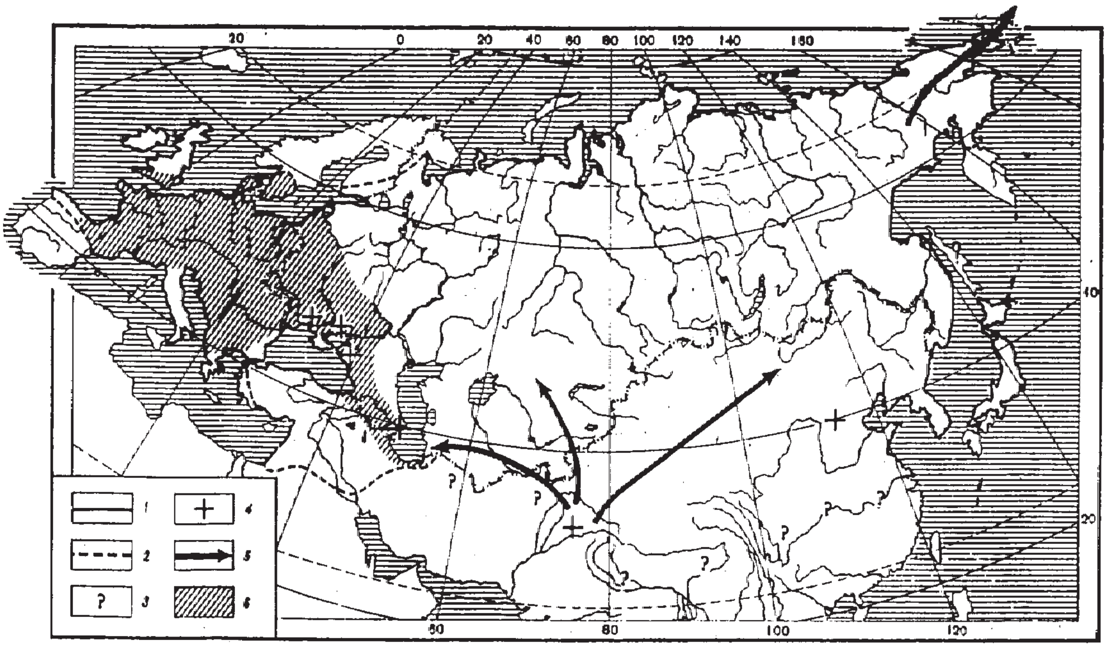


Figure 4.1.
Distribution of *Bison* in Europe and Asia.
1 – Geographical range of genus *Bison*, 2 – probable range, 3 – range unknown, 4 – sites of discovery for the representatives of *Eobison*, 5 – routes' of bison migration in Pliocene and Pleistocene, 6 – range of *Bison bonansus* in Holocene and early historical times (from Flerov, 1979).

Holocene and late Pleistocene bison of Eurasia and North America, which makes an earlier hypothesis of a common ancestor very probable (cf. Skinner and Kaisen 1947; Bohlken 1967). Most recent authors, on the base of significantly different morphotypes and extreme disjunctive distribution continue to give the European bison and North American bison the status of a separate species, disregarding their interbreeding (cf. Wilson and Reeder 1993). In this review, European bison *Bison bonasus* is treated as a separate species. This conclusion is significant when considering problems of genetic purity of Lowland European bison, *B. b. bonasus* and its crossbreeds with Caucasian subspecies *B. b. caucasicus* (Lowland-Caucasian line) as well as their hybrids with North American bison *Bison bison*.

5. Taxonomy

European bison *Bison bonasus* (Linneus, 1758) belong to the Family *Bovidae* Gray, 1872, Subfamily *Bovinae* Gray, 1821, Genus *Bison* H. Smith, 1827. Sometimes it is treated as a synonym of *Bos* Linnaeus, 1758 according to Groves (1981). Three subspecies are recognized (but see Rautian *et al*. 2000):

B. b. bonasus (Linneus, 1758) – (from Białowieża Forest)

B. b. hungarorum Kretzoi, 1946 – Carpathian Mountains and Transylvania, **extinct**

B. b. caucasicus Turkin *et* Satunin, 1904 – Caucasus region, **extinct**

6. Genetic structure of the species

All pure-bred European bison are the descendants of a basic group of 13 animals and represent a recombination of only 12 diploid sets of genes (Slatis 1960). 11 of the 12 founder animals (all of *B. b. bonasus*) originated solely from the Białowieża Primeval Forest, from the Berlin and Budapest zoos and Pszczyna. One bull of *B. b. caucasicus*, born in 1907 in the Caucasus Mountains, was brought to Germany in 1908. Therefore, genetic problems can have a strong influence on the preservation of European bison, on long-term viability, and the adaptability of its populations.

Two genetic lines are distinguished in recent population of the species:

Lowland line (L or Białowieża line) originates from only 7 founders (4 males, 3 females) and includes pure animals of B. *b. bonasus* subspecies. A small, but important, part of this Lowland line included a group derived from a few animals brought from Białowieża to Pszczyna in 1865 (1 bull and 3 cows) and supplemented throughout 1909 by 5 cows from Białowieża and 3 other bulls. Three animals (1 female, 2 males) survived until 1922 (Czudek 1930, Pucek 1991). This group was later mixed (after World War II) together with original Białowieża animals.

The Lowland-Caucasian line (LC), (B. *b. bonasus* × B. b. *caucasicus*) originate from all 12 founders (5 males, 7 females) including the bull of the Caucasian subspecies. Several studies proved small levels of genetic variability in Lowland European bison from free-living population in the western part of the Białowieża Forest (Poland). The average heterozygosity of proteins coded by 20 loci was indicated as 3.5 % (Gębczyński and Tomaszewska- -Guszkiewicz 1987). Similar studies using electrophoresis of many more proteins at 69 structural loci showed the average heterozygosity equal to 1.2 % and only 5.8% loci was polymorphic (Hartl and Pucek 1994). Genetic variability of European bison of the Lowland line from Białowieża Forest (Belarus and Poland) and captive herds of Lowland-Caucasian line (Prioksko-Terrasnyjj and Oka reserves) were studied. Variability and differentiation of proteins (22 loci, Sipko *et al.* 1997), blood group systems (9 systems, 57 antigens, Sipko *et al.* 1995), kappa-casein gene (Sipko *et al*. 1994; Burzyńska and Topczewski 1995), and the major histocompatibility complex class II DRB and DQB gene (Udina *et al.* 1994) were investigated. These studies generally show that genetic diversity within and among European bison lines is considerably lower in comparison to that within and among cattle breeds. From 57 antigens stated for European bison 28 (the half) were widely distributed (in 94.6 %) but the rest of the 29 antigens were found only in 5.4% of all animals tested (Sipko *et al.* 1996). The evidence of high inbreeding is conneced with very small polimorphism of molecular and biochemical markers, especially for the Lowland line (Sipko *et al*. 1997, 1999). In all studies, observed genetic diversity was lower in the Lowland line than the Lowland-Caucasian line. Sipko *et al.* (1997) calculated the level of heterozygosity for both lines, and for the Lowland line it was equal to 1.2–3.8% but for the Lowland-Caucasian was higher 4.4%.

Asymmetry of non-metric characters of European bison skulls from different recent and sub-recent populations of European bison indicates an increase in indices of asymmetry with time. This increase of asymmetry is parallel with higher inbreeding values. The Lowland-Caucasian line shows lower indices of asymmetry than Lowland line. The highest symmetry was observed in pure wild B. b. *caucasicus* whose skulls are preserved in museum collections (Rautian *et al.* 1998).

It is obvious that genetic variation in the European bison has been seriously decreased by the historical population bottleneck; however, the presented studies were only conducted on a small part of European bison population (10 % of free-living, and 1% of captive animals).

Genealogical analysis can be an effective source for more complete information, because most captive European bison have known pedigrees (cf. European Bison Pedigree Book), including those released animals which founded free-living herds. This pedigree data enables the procurement of parameters, which explain the genetic structure of populations. One such parameter is the inbreeding coefficient, which shows the homozygosity of an individual. Mean kinship *(mk)* presents the relation of the individual within a population. The founder genome contribution and retention explain the gene pool structure. The values of those parameters for different herds are presented in tables 7.1–7.4.

Data sources for the European Bison Pedigree Book indicate that the world population of European bison is highly inbred. As found during the 1980s the average value of inbreeding coefficient for world population was equal to 20.2%. The average inbreeding coefficient for live animals with full pedigree in late 1990s was equal to 43.98% for the Lowland line; for the Lowland-Caucasian line it was much smaller and equal to 26.28% (Olech 1998). It is known, of course, that the Białowieża population was isolated for a long time (at least since XVII century) and these calculations can be made for the last 5–6 generations. The inbreeding depression has been shown to be very small in this species, but can influence stability of development and the demographic characteristics of the herd (Sipko *et al*. 1999). The only negative influence of inbreeding found up to now is in the viability of young animals (Slatis 1960; Olech 1987; Belousova 1993). Recent studies show significant positive correlations between the level of inbreeding and the mortality of young animals existing in the Lowland-Caucasian line. For living animals from the Lowland line with a much higher level of inbreeding, a relation between inbreeding and mortality was not found (Olech 1998). The estimated number of lethal equivalents in the captive group is very low (0.16 – Belousova 1993, 0.3 – Pucek *et al.* 1996) and lower than for other species (from 1.4 to 30.3 with median 3.1 – Ralls *et al.* 1988). Successful breeding of a species can be strongly associated with the maintenance of genetic diversity in a population. In the studies made in the Prioksko-Terrasnyjj reserve the harmful effect of low levels of genetic variability (founder genome equivalent /fge/ < 1.3) was shown in female fertility, the viability of calves, and young animals (Belousova 1999).

Inbreeding has a depressive effect on skeletal growth, more expressed in females. Inbreeding in particular affects the skeletons of Lowland-Caucasian animals (Kobryńczuk 1985). Increased inbreeding causes neurocranium shortening and elongation of the skull basis, which results in elongation and narrowing of the splanchocranium. Furthermore, the skeleton of the distal appendage elements is also elongated, while the scapula is shortened. All these changes indicate that the skeleton of Lowland-Caucasian bison approaches that of pure *B. b. caucasicus*, as inbreeding towards the founder of this subspecies increases.

Table 7.1.
Genetic characteristics of the Białowieża line population (acc. to data of Belousova 1999, Olech 2002). Pedigree number and name of founders are given in decreasing participation.

Genetic characteristics	Captive population						Free-living population*	
	1945		1995		2000			
Number of founders	7		7		7		7	
Founder genome surviving	3.9		2.8		2.75		3.3	
Founder genome equivalent (*fge*)	1.7		1.4		1.37		1.6	
Mean kinship (*mk*), %	30.3		36.3		36.5		31.7	
Founders allele participation (%) – 1 Founder allele retention (%) – 2	1	2	1	2	1	2	1	2
45 Plebejer	56.4	97.9	55.0	86.1	54.5	87.5	44.8	92.4
42 Planta	28.8	70.9	29.6	59.9	29.4	61.2	36.3	64.4
16 Plavia	4.2	57.8	4.7	37.8	5.5	34.0	4.6	43.9
87 Bill	3.0	43.7	2.9	29.0	2.6	28.4	5.2	39.9
89 Bilma	2.8	43.6	2.9	29.9	2.6	28.2	5.1	39.7
15 Begrunder	2.6	37.2	2.4	19.3	2.7	17.1	2.6	23.6
147 Bismarck	2.2	38.0	2.4	20.9	2.7	18.4	2.4	25.1

* – the situation at the initial moment of a free-living population.

Table 7.2.
Genetic characteristics of the Lowland-Caucasian line population (acc. to data of Belousova 1999, Olech 2002).

Genetic characteristics	Captive population						Free-living population*	
	1945		1995		2000			
Number of founders	12		12		12		11	
Founder genome surviving	7.9		7.0		7.0		4.6	
Founder genome equivalent (*fge*)	4.5		3.5		3.1		2.0	
Mean kinship (*mk*), %	11.2		14.6		16.1		24.9	
Founders allele participation (%) – 1 Founder allele retention (%) – 2	1	2	1	2	1	2	1	2
45 Plebejer	25.1	97.3	21.2	90.1	22.9	92.2	31.6	89.5
42 Planta	14.8	69.3	16.7	65.1	18.3	66.3	24.5	66.5
16 Plavia	10.5	88.5	8.9	77.9	8.2	78.5	5.3	46.5
87 Bill	6.1	71.5	7.6	65.6	9.0	66.2	10.5	60.5
89 Bilma	10.0	86.1	10.2	81.6	11.7	81.2	11.9	73.0
15 Begrunder	9.7	81.1	8.5	69.9	7.7	71.0	5.2	36.5
147 Bismarck	0.8	38.0	0.6	24.2	0.5	25.3	0.1	11.5
100 Kaukasus	7.5	67.2	8.7	62.8	7.1	62.6	2.2	19.5
96 Gatczina	6.8	65.8	6.5	56.9	6.4	56.8	6.2	37.0
95 Garde	4.0	39.0	4.8	34.0	3.8	33.8	2.3	15.5
35 Plewna	3.4	47.3	4.7	43.6	3.2	43.4	0.1	5.5
46 Placida	1.3	35.1	2.0	28.3	1.3	26.2	–	–

* – the situation at the initial moment of a free-living population.

7. Origin and genetic characteristics of breeding lines

The Lowland line (L, or Białowieża line) originates from Białowieża Primeval Forest and includes animals of *B. b. bonasus*. It is managed as a separate (closed) population. This line, derived from seven founders, lost the majority of its genetic diversity during the first period of the species restitution (Table 7.1.). The effective founder number decreased rapidly at the beginning of the restitution and in 1945 was very small (*fge*=1.7). Presently the level of genetic diversity is lower in the captive world population (*fge*=1.37) than it

Table 7.3.
Genetic characteristics and founder allele participation and retention (%) for chosen free-ranging herds of the Lowland line (the situation on the initial moment of a free-living population) (Bielousova 1999, Olech 2002). All measures estimated in comparison with all founder group (7 founders = 100 % of genome).

Genetic characteristics:	Puszcza Białowieska		Belovezhskaya Pushcha		Puszcza Borecka		Borisovskij leskhoz *		Panevezys-Pasiliu stum. *	
Founder genomes surviving	2.8		2.9		2.6		1.8		1.9	
Founder genome equivalent (*fge*)	1.4		1.4		1.4		1.2		1.2	
Mean kinship (*mk*), %	36.4		35.0		35.4		42.4		40.8	
Founder allele participation (%) – 1 Founder allele retention (%) – 2	1	2	1	2	1	2	1	2	1	2
45 Plebejer	41.9	84.7	48.2	90.5	51.8	83.7	50.1	77.3	49.9	77.7
42 Planta	33.2	61.5	33.6	61.4	30.7	61.9	33.0	51.7	32.9	53.1
87 Bill	6.0	35.2	5.9	36.6	2.2	22.1	5.9	16.8	6.7	21.5
89 Bilma	6.0	37.5	5.5	34.7	2.4	22.3	6.9	19.3	7.1	22.8
15 Begrunder	3.2	21.0	1.6	16.4	3.2	18.2	1.2	4.8	0.8	4.5
16 Plavia	6.4	45.3	3.4	34.1	6.4	36.8	1.8	7.6	1.7	9.4
147 Bismarck	3.2	25.3	1.8	19.3	3.3	20.2	1.1	4.4	0.9	4.6

* – The herds had lost, very likely, an essential part of the genetic variability and have it on extremely low level (*fge* = 1.2) (Estimated by VORTEX model simulation).

Table 7.4.
Genetic characteristics and founder allele participation and retention (%) in free-ranging herds of the Lowland-Caucasian line (the situation at the initial moment of a population). Herds are arranged from west to east (Bielousova 1999, Olech and Perzanowski 2002).

Genetic characteristics:	Bieszczady (west)		Bieszczady (east)		Majdanska		Nadvirnjanska		Bukovynska		Cumanska		Danivska		Cejjskijj zakaznik		Sknjatinskoe		Teberdin. Zapov.	
Number of founders	10		10		9		9		10		10		10		10		10		9	
Founder genomes surviving	2.8		3.0		2.5		2.5		2.9		2.9		2.5		3.5		3.0		2.4	
Founder genome equivalents (*fge*)	1.5		2.0		1.7		1.6		1.7		1.7		1.6		1.9		1.6		1.5	
Mean kinship (*mk*), %	34.2		24.4		28.7		32.8		28.5		28.5		28.5		26.2		32.8		32.8	
Founder allele participation (%) – 1 Founder allele retention (%) – 2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
42 Planta	26.3	56.4	18.6	46.8	24.0	46.6	27.0	53.1	26.2	54.1	23.7	52.4	27.8	53.4	26.5	61.2	25.9	52.1	26.7	48.8
45 Plebejer	52.2	82.8	22.0	57.9	27.0	59.2	35.5	71.7	36.0	77.9	31.6	71.9	37.7	77.8	36.0	85.9	23.3	70.9	33.2	64.2
87 Bill	4.4	28.6	12.2	45.5	11.7	36.8	9.7	34.2	9.9	44.3	10.7	38.7	9.2	33.8	9.3	51.7	9.8	37.5	9.9	33.5
89 Bilma	6.6	39.8	18.3	57.8	10.6	33.2	9.6	34.5	8.7	40.3	9.9	35.5	9.5	33.9	9.1	50.8	9.7	44.2	10.4	34.9
15 Begrunder	2.1	14.6	5.6	18.6	6.6	17.6	4.8	16.1	5.6	22.8	6.2	21.6	3.9	13.0	4.6	24.9	8.1	24.5	4.9	13.4
16 Plavia	2.5	18.9	5.7	18.7	6.7	17.6	4.1	14.4	4.2	19.0	6.0	15.0	4.1	14.8	4.9	30.6	8.4	25.4	4.8	15.5
147 Bismarck	–	–	–	–	–	–	–	–	0.1	1.0	0.4	4.7	0.1	1.4	0.2	6.3	–	–	–	–
100 Kaukasus	1.8	10.9	5.3	16.2	3.7	9.2	2.9	7.4	1.8	7.3	2.8	10.0	1.8	6.1	2.6	10.3	2.7	12.9	2.6	7.1
95 Garde	1.2	7.0	3.6	11.0	3.3	9.1	1.9	6.0	2.4	9.2	3.3	10.5	1.9	6.7	2.5	10.4	2.7	10.2	2.7	7.3
96 Gatschina	2.4	14.5	7.2	22.1	6.3	17.8	4.5	14.0	5.1	19.2	4.8	16.8	3.9	13.6	4.5	20.0	5.2	24.2	4.9	14.8
35 Plewna	0.6	3.7	1.5	5.4	–	–	–	–	–	–	–		–	–	–	–	0.1	1.8	–	–
46 Placida	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

was in free-living herds at the moment of their creation (*fge*=1.6). Over 55 years (between 1945 and 2000) the loss of genetic variability within captive groups continued. This is not only expressed by the founder genome equivalent (*fge*) which changed from 1.7 in 1945 to 1.37 in 2000, but also by the fact that the relationships between animals increased (average mean kinship *mk* changed from 30.3% to 30.5 %) (Belousova 1999, Olech 2002). The value of mean kinship for animals within recent populations ranges from 26.7% to 65.9% (Olech 2002) and shows how homogenous the Lowland line is.

Genes of two founders (45 Plebejer and 42 Planta) are over-represented; their genetic contribution in the Lowland line gene pool is higher than 84%. The rest of the founders made a very small contribution; for four founders, it was no higher than 3%. The same situation concerns the retention of founder genes. Only two founders (Nos 42 and 45) saved more than 50% of their genotype in the living Lowland line. Between 17% and 34% of the other 5 founder's genes were saved in the actual population. The contribution of founder's genes is fairly stable, but the retention of each of the founder's genes is decreasing (Table 7.1).

Due to the bottleneck between 1940 and 1945, the present world population of Lowland line has copies of the same Y-chromosome from the founder No 45.

The number of European bison of the Lowland line living **in free-ranging herds** is close to 900 distributed in 12 herds over the territories of Poland, Belarus, and Lithuania (Table 10.1). The genetic variability of those herds, at the time of their founding (starting in 1952), was very low (Belousova, 1999). The highest initial variability was found in European bison herds in Białowieża Forest (*fge*=1.4) which were created during the first re-introduction. In the Polish part of the Białowieża herd the participation of founders is very interesting because of the lower contribution of founders 45 and 42. Two herds in Borisovskijj leskhoz (Belarus) and Panevezys-Pasiliu Stumbrynas (Lithuania) went through very serious founder bottlenecks and had very low genetic variability (*fge*=1.2) (Table 7.3). Other small herds, such as those in Wałcz forest (Poland) could be in a very similar situation from a genetic point of view. Only 3 herds (Puszcza Białowieska, "Belovezhskaya Pushcha", Puszcza Borecka, about 630 animals in total) are estimated to be genetically and demographically successful populations. In fact, no free-living herd is safe (genetically or demographically) in the long-term because of the low level of variability from the start.

The captive part of the Lowland line population is about 295 animals dispersed throughout 43 breeding centres and zoos. In half of the herds (240 animals in 22 herds) animals of only the Lowland line can be found, but in other herds' animals of both lines are kept together. Animals of the Lowland line are found in all captive herds in Poland (ca 170) (EBPB 2001). All Polish captive herds are treated as one population by a special breeding programme that includes a system of animal exchange (Olech 1997). Genetic variability estimated on pedigrees has decreased very slowly in the last few years (Table 7.1).

The Lowland-Caucasian line (B. *b. bonasus* × B. b. *caucasicus*) (LC-line) [in older Russian literature called also Caucasian-Białowieża line] has always been managed as an unclosed population and sometimes mixed with the Lowland line. The LC-line contains genes of one bull of *B. b. caucasicus* (No 100, Kaukasus) and of all 11 founders of *B. b. bonasus* (4 males and 7 females). The main part of the line's gene pool and genetic variability were lost at the beginning of the species restitution, a process continuing to this day (Table 7.2). The founder genome equivalent for the captive part of the Lowland-Caucasian line is decreasing rapidly, from *fge*=4.5 in 1945 to 3.1 in 2000. The contribution of No 100 Kaukasus and four females (Nos 96, 95, 35, 46) which did not participate in the other line is decreasing because of the Lowland line influence. At the same time, the contribution of seven founders common for both lines is increasing. The value of mean kinship has increased, especially in the last five years. The level of genetic diversity is much lower in free-living herds (*fge* = 2.0) than in the captive part of the world population (*fge*=3.5) (Belousova 1999). Not all twelve founders are represented in free-living herds. Founder No. 46 has not contributed to any herd, and in some herds the genes of founders Nos 35 or 147 are not found. Consequently, the number of founders for free-ranging herds is less than for those animals in captivity. The retention and participation of the genes of five founders characteristic for this line is very small for free-living herds. This was due to the practice of mixing of both lines when these herds were created. For example, one part of the Bieszczady herd is closer to the Lowland line in its genetic characteristics (Olech and Perzanowski 2002). The contribution of founders 147 and 35 and their allele retention in some herds are very small. In the gene pool of some herds, there only exists genes from 9 of the 12 founders and a pair (42 and 45) is over-represented.

The founder's Y-chromosomes are not equally spread in the recent world population. The Y-chromosome of founder No 45 is most common in both free-living herds and captive groups. The Y-chromosome of founder No 100 can be found in the Bieszczady free-living herd and in some captive groups.

The Y-chromosome of founders No 15 and No 147 were lost during the breeding process during 1945–1997. The last male descendant of founder 87 died childless in 1935 (Sipko *et al*. 1999). In conclusion three of five Y-chromosomes were lost.

The free-living part of the world population is about 700 animals forming 19 isolated (free or semi-free) herds in the territory of Poland, Russia and Ukraine (Table 10.2) (cf EBPB 2001). None of these free-living herds is safe (genetically or demographically) in the long-term During the last few years, the Nadvirnjanska and Zalisska herds (Ukraine) have probably lost an essential part of their genetic variability because of the very small number of animals. Only one herd (Bukovynska 138 animals) can be regarded as a genetically and demographically successful population (Table 10.2). The Cejjskijj herd (west-north Caucasian region, Russia) is rapidly disintegrating because of poaching and its future is unclear. Because of the unstable situation in this region, two other herds (about 60 animals in total) were exterminated in the last years. There are 7 very small and unstable herds and 4 herds undergoing the first steps of re-introduction.

The captive part of the lowland-Caucasian line population is about 860 animals dispersed throughout 169 breeding centres and zoos. The captive population has lost a significant part of its gene pool in the first part of the species restitution and this process is continuing (Table 7.4). There is a successful breeding process in 71 larger captive groups (630 animals), 98 zoos have small groups (up to 4 individuals) only for demonstration purposes (225 animals) and 48 zoos did not send information to the European Bison Pedigree Book (EBPB) annually. In the last 10 years, more than 100 breeding centres and zoos were excluded from EBPB because of the lack of any contact. That means that 730 animals from these breeding centres are out of the only official register of pure European bison.

8. Hybrids of European bison

(European × American bison hybrids and European × American bison × Cattle hybrids)

A particular problem concerning the management of extant populations of European bison is the existence of hybrid herds, and first – European American bison hybrids living in the Caucasus.

In 1940, 5 (1, 4) European American bison hybrids (*Bison bonasus Bison b. bison*) were introduced from Askania Nova reserve (Ukraine) and settled in the Caucasus Mountains, in the area of presently known as the Caucasian Biosphere Reserve. At first, they were kept enclosed and mated with each other. Then (since 1949) they were crossbred primarily with males of the Lowland-Caucasian line bison (including 15 bulls that had been brought in 1948–1957, but only eight of them successfully bred). In 1954, these animals were released and progressively the free population developed. At the end of 1965, there were 449 (Kalugin 1968) so-called “pure-bred” or “mountain” bison in the Caucasus Biosphere Reserve and in neighbouring territories (See, Appendix I for details).

It was estimated that in 1960 this free-living population contained 5.24% of North American bison blood (Sipko 1990). The population had 1300 animals in 1984 (Yazan and Nemtsev 1985) and was growing until 1993 when poachers began to disturb it. In 1999,there were only about 550 individuals.

Quite recently these hybrids have been formally described as a new subspecies [!] of European bison *Bison bonanus montanus* Rautian, Kalabushkin *et* Nemtsev, 2000 and included in the Red Data Book of Republic Adygea and protected as a species in the reserve (see Rautian *et al*. 2000).

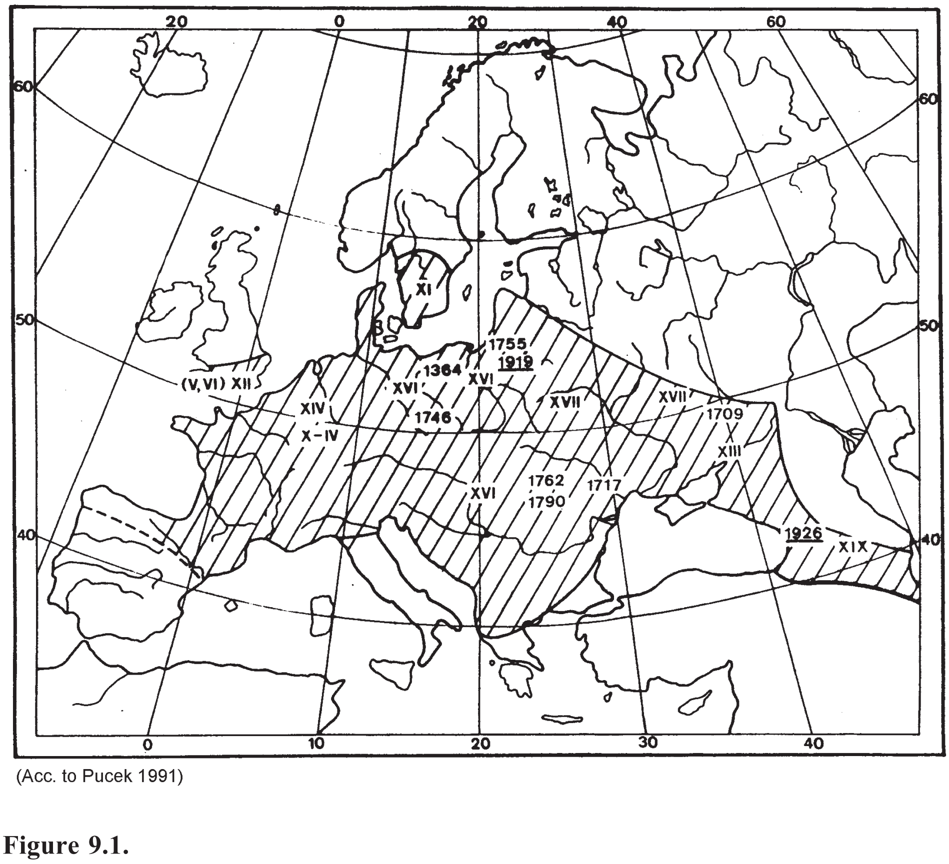
In 1959–1967 a new mixed free-living herd of European American bison hybrids was organized in that region, near Nalchik, East of Caucasus Biosphere Reserve. There were about 250 animals in 1993, but in 2001 only 18 remained. Simultaneously with the acclimatization of these hybrids, free-ranging herds of pure blood Lowland-Caucasian European bison were established in the Caucasus Mountains, not far from hybrid herds. Fears are that all these animals will cross-bread, creating a mixture of various genotypes. According to Russian authors, distances between the herds are not so great, but mountain conditions unable the contact between them.

There are also two other semi-free herds of hybrids: one herd, European American bison hybrids, is in Toksovo Forest Park, near St.Petersburg (10 animals); the other herd, European American bison cattle hybrids, lives in the 200 ha fenced territory in Mordovia Wildlife Reserve (ca 15 animals in 2001).

9. Distribution

9.1. Distribution of the species in historical times

In historical times the range of European bison covered Western, Central and Southeastern Europe, extending up to the Volga River and the Caucasus (Fig. 9.1). European bison probably also occurred in the Asiatic part of Russian Federation, but reconstruction of this range requires further research (Strategy… 2002). There is a consistent opinion that the shrinkage of the European bison range on the continent was caused by the progress of civilisation and that protective actions could not effectively protect the species. The process proceeded from the West, the South and the North. Bison in Gallia were the first to die (VIIIth century). In the north of Sweden bison only survived until the XIth century, and until the XIIth century in the south of England (according to some authors, only to the 5th–6th century, Szalay 1943). In the VIIth century, the European bison's existence was reported from the northeast of France. In the Ardennes and in the Vogues these animals survived until the XIVth century. In Brandenburg by the XVIth century, they were already kept, and bred in enclosures. At the end of the XVIIth century (1689) an attempt was undertaken in Mecklenburg to release European bison from enclosures, however, this was unsuccessful. In the XIIth century, the existence of European bison was reported from the Usocin Forest on the Oder River, near Szczecin. Bison existed in West Pomerania until the year 1364. Thanks to the protective actions of Wilhelm



(Acc. to Pucek 1991)

Figure 9.1.
Range of European bison in Holocene and early historical times (shaded area). Roman and Arabic numerals mean respectively century or year of the last bison record in a given part of the range. (Source: compiled from Hepther *et al.* 1967, Flerov 1979, Kirikov 1979, Pucek 1986 and others).

I, bison survived relatively long in eastern Prussia. In 1726, their number was estimated at 117 individuals (Genthe 1918), but in 1755 the last two animals were killed by poachers between Labiau (today Polesk) and Tilsit (today Sovetsk) (Karcov 1903, Heptner *et al.* 1966). From Prussia and Poland, European bison were transported to Saxony in the XVIth century, and kept in enclosures. In the years of 1733–1746 these animals were set free. They survived in enclosures in Kreyern and later in Liebenwerda until 1793. In the XVIth century bison became extinct in Hungary, although free animals survived a relatively long time in Transylvania. The last individual was poached in 1790. In Romania, the last European bison was killed in the Radnai Mountains in 1762.

In Poland, by the XIth and XIIth centuries bison populations were limited to larger forest complexes, where they were protected as the royal game. In the XVth century, they were found in Białowieża Forest, Niepołomicka Forest, Sandomierska Forest, near Ratna on the Pripet River and in Volhynia (Sztolcman 1924). In the Kurpiowska Forest, they became extinct in the XVIIIth century. The last European population in Białowieża Forest was protected until its extinction in spring of 1919 (Genthe 1918, Sztolcman 1924, Wróblewski 1932, Okołów 1966, Krysiak 1967).

There is direct and indirect evidence of the European bison's existence within the former Soviet Union until the XVIIth and XVIIIth century. Along the River Don, European bison was preserved until 1709, in Moldova up to 1717. The last free population survived in the Caucasus until 1927 (Heptner *et al.* 1966, Kirikov 1979).

It can be assumed that in historical times the European bison was subject to gradual shrinkage and fragmentation of the range, decreasing numbers and isolation of sub-populations leading to extinction.

An interesting theory refers to the effect of climate on the range of bison. According to Heptner *et al.* (1966), the depth of snow cover (50cm-thick snow cover was limit the species' spread to the north) determined the northern border of the species range (see also Vereshchagin and Baryshnikov 1985). In many regions inhabited by bison in historical times, the thickness of snow cover exceeded that value (e.g. within the last 50 years in the Białowieża Forest the monthly maximum depths of snow cover approached that value in five years, exceeding it considerably in two years – 1970 and 1979). This could be a significant factor hindering the bison's survival in that part of range.

9.2. Recent distribution

9.2.1. Captive breeding

European bison are kept in enclosed breeding centres (EBC), zoological gardens, and specially created reserves (191 in the year 2000). The number of bison breeding centres was growing rather slowly and as was the number of animals kept there until the beginning of the last decade. However, only 11.5% of EBC have groups larger than 10 individuals, and 23% of centres keep animals of one sex (7.4% of bison world population). (Fig. 9.2, Table 9.2). These small groups

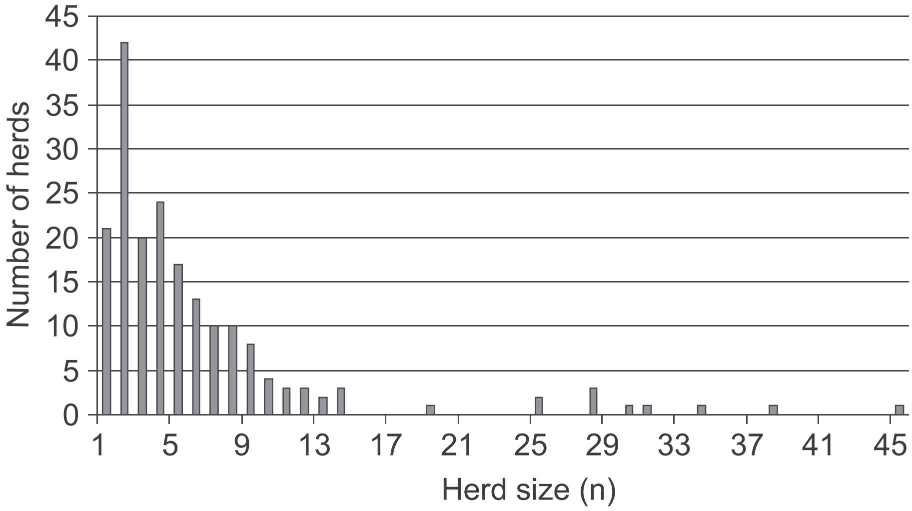


Figure 9.2.
Number of herds in Enclosed Breeding Centres (EBC) according to size. Source: EBPB 2000.

are held in zoological gardens mainly for the purpose of demonstration and less for the propagation of a threatened species. It is of little surprise that during the 1970s, 8–10 of the larger breeding centres with 20–50 bison provided over 50% of the population increase (Woliński 1984). Recently (EBPB 2001) only 27% of world population live in large herds of 25 to 45 animals (Fig. 9.3). During the last decades, a dramatic decrease in the number of breeding centres and animals being bred has been observed (Table 9.1).

European bison EBC's are well distributed in 30 countries of the world (Table 9.2). Most of the herds are from the Lowland-Caucasian line (148) and only 22 are from the Lowland line and of those 16 are located in Poland. Unfortunately, for about 55 herds unproved data has been published in European Bison Pedigree Book in the year 2000.

9.2.2. Free-ranging and semi-free herds

The first re-introduction of European bison to forest ecosystems started in Białowieża Forest in 1952. From about 1960, a reproducing population was established (Krasiński 1983). Similar attempts were also made in the Byelorussian part of Białowieża Forest (Korochkina and Kochko 1982). During the following period, further

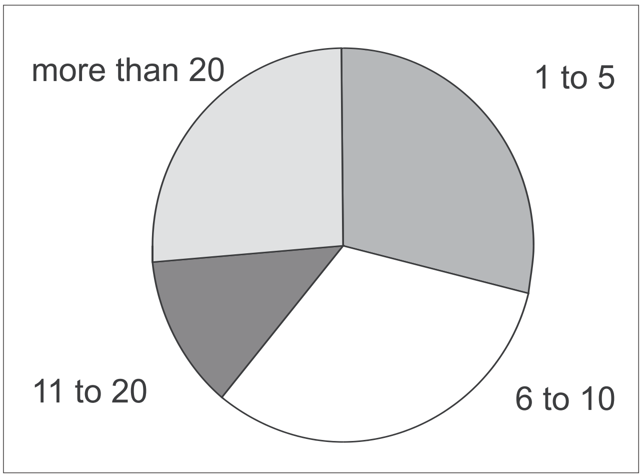


Figure 9.3.
Number of captive European bison according to herd size. Source: EBPB 1999.

Table 9.1.
Total number of captive European bison registered in European Bison Pedigree Book on 31 December.

Year	1960	1970	1980	1990	2000
Number of countries	18	24*	30*	40**	30**
Number of breeding centers	44	144	225	266	191
Number of animals	422	700	1247	1477	1153

* both German countries treated together,
** independent countries of former USSR treated separately.

Table 9.2.
Distribution of number of herds representing two genetic lines in different countries (EBPB 2000).

Country	Total	With one sex	Only L line	Only LC line
Austria	6	5		5
Belgium	2			2
Belarus	1	1		1
Brasil	7	3	1	4
Canada	6	2		6
Croatia	1	1		1
Czech Republic	7	2		6
Denmark	3	1	1	2
Estonia	2	5		2
Finland	2			2
France	11		1	9
Germany	73	11	1	61
Great Britain	4			4
Hungary	1			1
Ireland	1			1
Italy	5	1		5
Japan	2	1		2
Lithuania	2		1	
Netherlands	3			2
Poland	16	2	16	
Portugal	2	1		2
Russia	9	4		8
R.P.A.	1	1	1	
Romania	2	1		2
Slovakia	2	1		2
Spain	5			3
Sweden	8	1		8
Switzerland	3			3
Ukraine	2	1		2
U.S.A.	2			2
Total	191	45	22	148

free-ranging herds were formed in Poland, Lithuania, Belarus, Ukraine, Russia and Kyrgyzstan, some of them outside the historical range of the species. At the end of 2000 there were 30 such herds registered in EBPB, (including two semi-free in large enclosures) (Fig. 9.4 and Tables 10.1, and 10.2).

There were further initiatives to create free-ranging herds, but they failed to be successful due to different reasons, including the extinction of 2 herds in the Caucasus and a lack of information about other ones (e.g. Sary-chelekskijj Reserve, Kyrgyzstan). (Table 10.2). Nearly all free-ranging bison herds are distributed within the eastern part of the historical range of the species (Fig. 9.4). In the main, Lowland line bison occupy the northern part of this range and in the southern part, Lowland-Caucasian animals (Fig. 9.4). Unfortunately, the suggested separation between the genetic lines has not been strictly observed in all areas throughout the reconstructed range. This idea of separation between L and LC lines is one of the basic points outlined since the establishment of the EBPB. Today, this general principal is maintained, and will remain so until more facts are known about the genetic structure of the species as a whole and the lines distinguished (cf. Pucek *et al.* 1996b).

Summarising this chapter, we can say that the recent distribution of European bison is much more advantageous when compared to that prior to their extinction in the wild. During the last decades, the number of bison breeding centres has been increasing, as has the number of countries where this species can be found (Pucek 1991). During the last 10 years, or so, however, progress appears to be slowing down (cf. EBPB 2001).

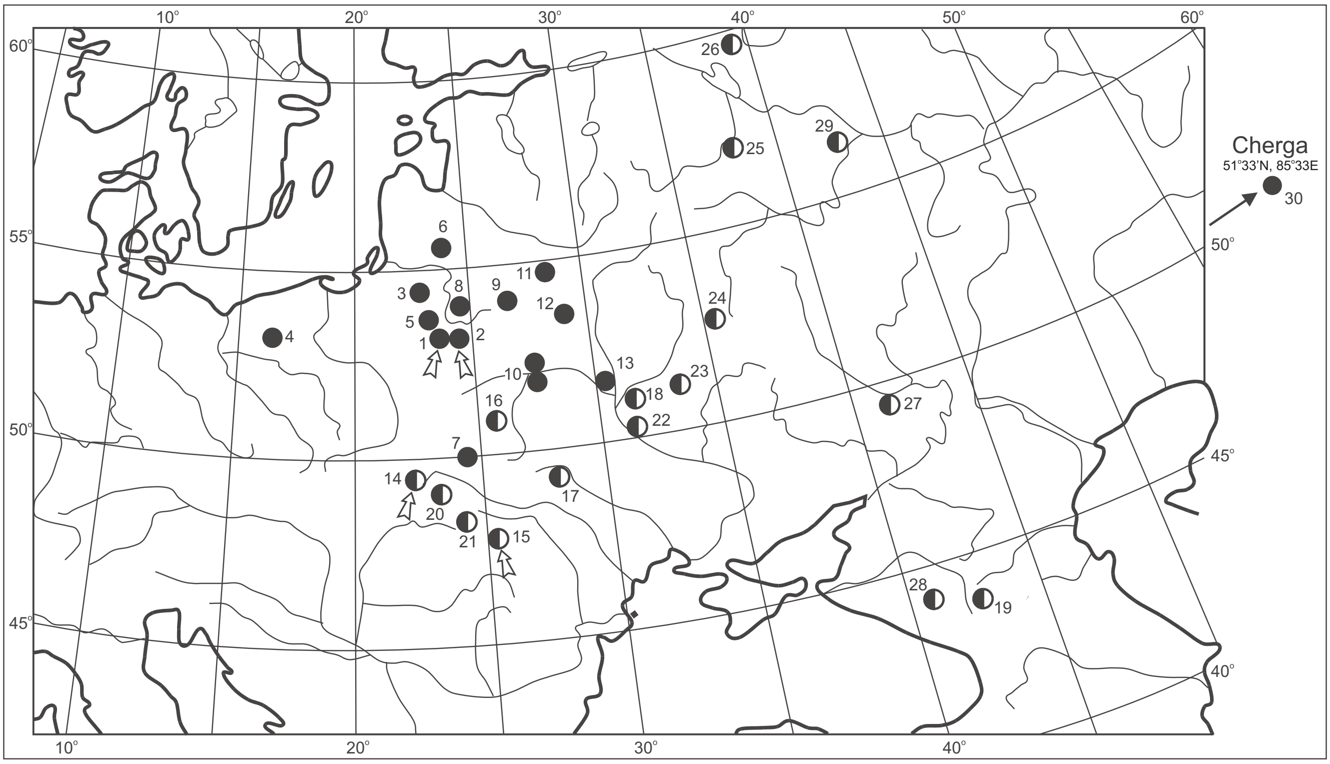


Figure 9.4.
Distribution of free-ranging and semi-free herds of European bison at the end of 2000.
Black points – represent herds of Lowland line listed in Table 10.1., black and white points – animals of Lowland-Caucasian line, listed in Table 10.2. Arrows indicate herds larger than 100 individuals.

10. World population numbers

Dynamics of the world population of European bison is illustrated in Fig. 10.1. The total number of bison registered in EBPB in the world at the end of 2000 was estimated at approximately 2 860. In the first period of restitution, the number of bison was growing very slowly, the rate of growth being seriously disturbed at the end of World War II. In the years 1943–1946, the number of bison declined by 42% [from only 160 animals in 1943 to 93 (43, 50) at the end of 1946!]. This was the second dramatic decrease of bison population in its history (Raczyński 1980, and European Bison Pedigree Book).

In the subsequent years, the European bison population was gradually increasing, doubling every 5–6 years in the 1950s and 1960s. Then the number of bison doubled only every 11–12 years. A slowdown in the enlargement of the bison population has been observed in enclosed breeding centres (EBC) and in free-ranging herds, as well as in particular countries. The increase in European bison numbers in recent years is slower than could be expected on the bases of its reproductive potential.

The possibilities of the progressive enlargement of the European bison population seem to be gradually reducing. Bison numbers are subject to regulation, in several countries, at a low level due to habitat or economic constraints and/or maintained at a definite level, particularly during last decade. However, during the last 3–5 years (1996–2000) a significant decrease in numbers has been observed. In addition, birth rates have become fixed in some free-ranging herds (e.g. in the Białowieża Forest) at a lower level compared to the first years of the intensive population increase following introduction (Krasiński *et al.* 1994a). Beside these factors, some small free-living herds have been exterminated (cf. situation in Caucasus Mountains and Table 10.2) or heavily poached. (In Lithuania, for example, 20% of European bison have been lost during the last two years!). Finally, a number of animals are no

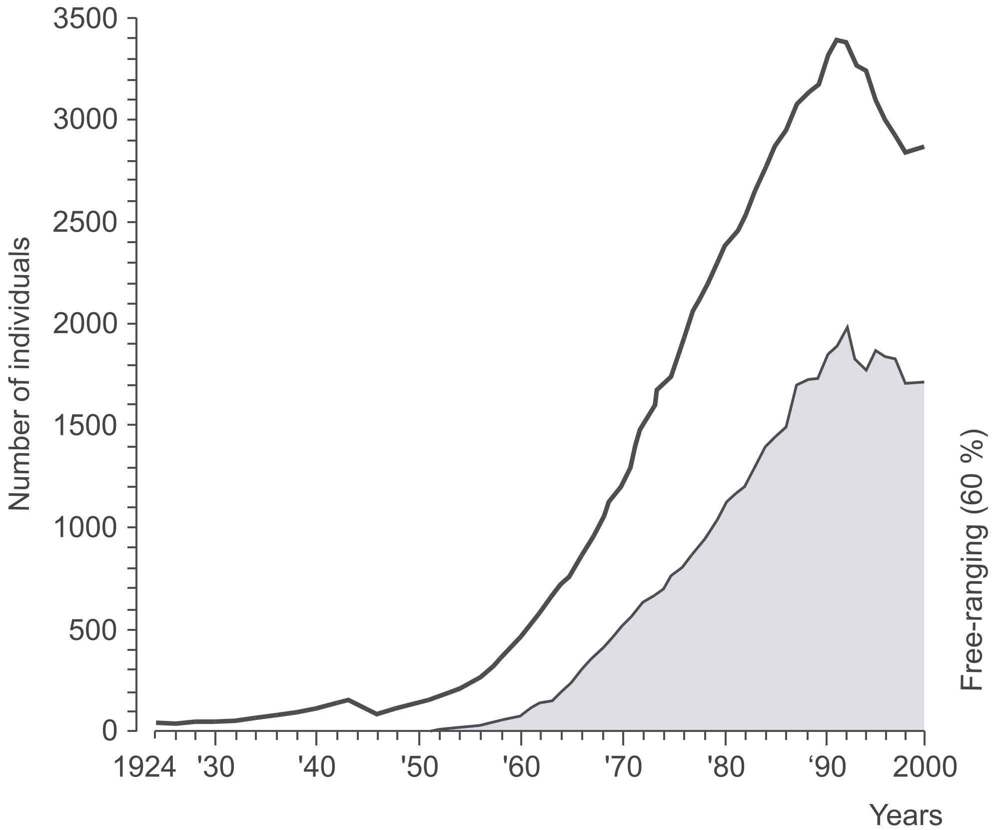


Figure 10.1.
Dynamics of World population of European bison registered in EBPB 1924 – 2000. Shaded area represent animals in free-ranging and semi-free herds.

Table 10.1.
Population size and potential estimates of free-living herds of the European bison of the Lowland line.
Herds ware arranged in three size categories and from west to the east in recent European bison range (cf. Fig. 9.4). Names of herds are consistent with those in European Bison Pedigree Book. Numbers are given on the 31 December of particular years. * Origin of founders are determined by the name of breeding centre or a free-living population: PBP – Białowieża Forest (Puszcza Białowieska), or Pszczyna, Poland; BPB – Białowieża Forest ("Belovezhskaya Pushcha"), Belarus; PTZ – Prioksko-terrasnyjj Biosphere Reserve, Russia.

No	Owner, country	Population size						Foundation		Area of forest complex (occupied by bison), km^2	Protection status	References
		Initial	1970	1980	1990	2000	Potential	Origin of founders *	Year			
	I. Demographically stable, with low risk of genetic variability losses in near 100 years											
1	Puszcza Białowieska, Poland	28 (9, 19)	197	242	272	306	250	PBP	1952–1966	580 (190–400)	National Park and managed forest	Scientifically managed, regulated; supplementary feeding during winter
2	"Belovezhskaya Pushcha", Belarus	41 (25, 16) 2 (2, 0)	63	169	315	265	200	BPB, PBP, Pszczyna, PTZ PTZ	1961–1967 1991	870 (520)	State National Park	Scientifically managed, regulated; supplementary feeding during winter
	II. Populations functioning at risk to the loss of genetic variability											
3	Puszcza Borecka, Poland	15 (7, 8)	7	60	66	60	70	PBP, Pszczyna	1970–1971	180 (107)	Managed forest	Scientifically managed, regulated; supplementary feeding during winter
	III. Populations consisting of < 50 animals, not ensuring normal population functioning											
4	Nadleśnictwo Wałcz, Poland	8 (4, 4)	–	–	13	26	15	PBP	1983	(67)	Managed forest	Little supplementary feeding
5	Puszcza Knyszyńska, Poland	6 (3, 3)	–	8	14	16	30	PBP	1973	840	Managed forest	Supplementary feeding during winter
6	Panevezys-Pasiliu stum., Lithuania	5 (2, 3)	–	–	20	30	?	PTZ	1973, 1974	?	?	?
7	Lopatynska, Ukraine	12 (7, 5)	–	8	10	9	60	Panevezys-Pasiliu	1980–1981	400 (160)	Managed forest	Unmanaged
8	Kolkhoz "Ozery", Belarus	18	–	–	–	35	50	BPB	1998	?	Protected forest	Supplementary feeding during winter
9	Volozhinskijj leskhoz, Belarus	15	–	–	–	39	50	BPB	1994	?	Managed forest	Supplementary feeding during winter
10	Pripjatskijj Natl. Park, Belarus	8	–	–	14	30	50	BPB, PTZ	1987–1988	?	National Park	Supplementary feeding during winter
	Liaskovici	13				13	?	BPB	2000		Incl. Pripiatskijj	?
11	Borisovskijj leskhoz, Belarus	7	–	15	25	33	34	PTZ	1970–1976	100	?	Unmanaged
12	Osipovichskijj leskhoz, Belarus	15	–	–	–	28	50	BPB	1997	?	Managed forest	Supplementary feeding during winter
13	Polesskijj zapovednik, Belarus	17	–	–	–	26	50	BPB	1996	?	Wildlife Reserve	Supplementary feeding during winter
30	Cherga, Russia	12	–	–	41	15	?	PTZ	1982–1984	–	400 ha enclosure, semi-free herd	Winter feeding
	Sub-total (L line)		267	502	790	931						

Table 10.2.
Population size and potential estimates of free-living herds of European bison of the Lowland-Caucasian line. Arrangement of herds, origin of founders and symbols used are the same as in Table 10.1. for Lowland line (cf. also Fig. 9.4). OZ – Okskijj zapovednik (Oka Reserve), Russia.

No	Owner, country	Population size						Foundation		Area of forest complex (occupied by bison), km^2	Protection status	References
		Initial	1970	1980	1990	2000	Potential	Origin of founders *	Year			
	I. Demographically stable, with low risk of genetic variability losses in near 100 years											
14	Bieszczady, Poland	34 (16,18)	38	105	97	164	150?	Different Polish reserves	1963–1976	500 (300)	Managed forest, and National Park	Scientifically managed,
	Western herd	15 (6, 9)		–	–	49		”	1976, 1980	(190)	Managed forest	
	Eastern herd	19 (11, 8)		–	–	115		”	1963–1966	(110)	Managed forest and Natl. Park	
15	Bukovynska, Ukraine	19 (8, 11) 4 (1, 3)	19	57	148	138	240	BPB, OZ, PTZ	1970	590	Managed forest	Experimental hunting
	II. Populations functioning at risk to the loss of genetic variability											
16	Cumanska, Ukraine	14 (9, 5)	37	64	200	56	160	BPB	1965–1967	390	Managed forest	Experimental hunting
17	Uladivska, Ukraine	6	–	12	54	91	60	Cumanska	1976	120	Managed forest	Experimental hunting
18	Danivska, Ukraine	13 (6, 7)	–	–	51	70	80	PTZ	1979–1980	312	Managed forest	Experimental hunting
19	Cejjskijj zakaznik, Russia	46	71	128	235	25	170	BPB, PTZ	1964–1968	150	Protected forest	Unmanaged
	III. Populations consisting of < 50 animals, not ensuring normal population functioning											
20	Majdanska, Ukraine	10 (4, 6)	11	31	32	15	?	BPB	1965–1967	270	Managed forest	Experimental hunting
21	Nadvirnjanska, Ukraine	14 (7, 7)	–	8	26	4	0	PTZ, OZ	1976, 1979	600	Protected forest	Unmanaged
22	Zalisska, Ukraine	8 (4, 4)	8	14	8	11	50	BPB	1967	(150)	Semi-free herd	?
23	Konotopska, Ukraine	14 (3, 11)	–	–	26	32	50	Zalisska	1985	140	Protected forest	Experimental hunting
24	Orlovskoe Poles’e, Russia	32	–	–	–	42	500	PTZ, OZ, BPB Zoos of EU	1997–1999	?	National Park	Beginning of reintroduction
25	Sknjatinskoe, Russia	29 (14,15)	–	–	29	30	30	PTZ, OZ	1986	175	Protected forest	Experimental hunting
26	Ust’-Kubenskoe, Russia	5	–	–	–	10	1000	PTZ	1991, 1994	?	Protected forest	Beginning of reintroduction
27	Fominskijj zakaznik, Russia	9	–	–	–	6	30	PTZ	1993, 1994	?	Protected forest	Beginning of reintroduction
28	Teberdinskijj zapovednik, Russia	12 (4, 8) 7 (4, 3)	12	32	43	18	40	PTZ, OZ	1968–1969 1978	80	Wildlife Reserve	Unmanaged
29	Velikoozerskoe, Russia	9 (2, 7)	–	–	9	15	?	PTZ	1989–1990, 1994	?	Protected forest	Beginning of reintroduction

Table 10.2. (continued)

	IV. Recently extinct herds											
31	"Russkij Les", Russia	7 (4, 3)	–	–	7	0	?	?	1987	–	–	Extinct up to 1997
32	Sunzhenskoe, Russia	17	–	17	8	0	?	OZ	1987	–	–	Extinct
33	Checheno-ingushskij zapovednik, Russia	49 (23, 26)	–	–	44	0	?	BPB, OZ, PTZ	1971–1975	158	–	Extinct
34	Sary-chelekskij zapovednik, Kyrgystan	13 (7, 6)	11	15	18	?	?	PTZ	1962–1964	80	?	?
	Sub-total, LC line		207	483	1035	694						

longer registered in EBPB due to the lack of contact from particular breeders (owners) with the office of the pedigree book. It means that not all European bison are registered and the total world population of the species is about a few hundred larger Fig. 10.1 demonstrates this.

Slightly more than 80% of all captive European bison inhabit eight countries mainly in Central and Eastern Europe (Germany, Poland, France, Russia, Sweden, Czech Republic, Great Britain and Spain). About 60% live in free and semi-free herds, distributed mainly within the historical range of the species (Fig. 9.4). Nowadays, the largest population of bison exists in Białowieża Forest, on either side of the state border between Poland and Byelorussia (571 individuals at the end of 2000). Unfortunately, the border is reinforced by a physical barrier and thus contacts between the bison herds are impossible. This population is similar in size to the last one at the beginning of the 20th century. This is the only population of lowland European bison (*Bison bonasus bonasus*) of this size, and the needs of this species should be given priority (Pucek 1993). The numbers of other ungulates, particularly of red deer should be maintained at a level that would allow the existence of a large population of the European bison. It was not so long ago that high numbers of deer in the Belarusian part of the Białowieża Forest caused a reduction in food supply and a subsequent decrease in the reproduction parameters of European bison (Bunevich and Kochko 1988).

A further two herds larger than 100 individuals exist in Bieszczady (Poland) and Bukovynska (Ukraine) and five herds >50 individuals are in Poland, Ukraine and Russia (Table 10.1 and 10.2).

With regard to free-ranging or semi-free herds (30 in the year 2000), only about 30% of them contained more than 50 animals (cf. Tables 10.1 and 10.2). The free-ranging part of the European bison population (now 60% of the total – Fig. 10.1) was almost doubling each decade from 1970–1990, but recently was found to be sharply decreasing, especially in the case of the Lowland-Caucasian line. Lowland line bison continue to increase (cf. Tables 10.1. and 10.2.). Only four herds are larger than 100 individuals (including 2 in Białowieża Primeval Forest) which according to earlier simulations (Pucek *et al.* 1996b) might have a lower risk of extinction in the near future. Unfortunately, some other herds recently decreased in size or are already extinct (Table 10.2.).

The stability of European bison numbers seems to be affected to some extent by elimination practices and hunting exploitation, which are regulated by the institutions responsible for nature protection in each country holding herds (for details see "Culling").

11. Biology and population ecology

Knowledge of European bison ecology is mainly based on data obtained from the Białowieża Primeval Forest (BPF), but also in Prioksko-Terrasnyjj reserve and Cejjskijj zakaznik. Data concerning the functioning of a medium-sized population (50–70 individuals) in Borecka Forest and a small population (10–18 individuals) in Knyszyńska Forest has been used for comparison. In Białowieża Primeval Forest, European bison have always been treated in a specific way and are subject to special protection. However, their role in the ecosystem has to be considered in relation to other ungulates.

All five elements of the ungulates community, characteristic for continental Europe – European bison (*Bison bonansus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), moose (*Alces alces*) and wild boar (*Sus scrofa*) – should be preserved in Białowieża Forest. The problem is how to establish adequate proportions between the herbivore species and determine what numbers are optimum for the forest habitat conditions.

11.1. Environment and habitat (Relationship between European bison and its habitat available)

During the initial stages of re-introduction, all free-ranging European bison populations occupied small ranges that gradually enlarged until the number of animals in the population reached the optimal level. In no forest complex have European bison used the whole territory (cf. Tables 10.1 and 10.2). In BPF, European bison occupy about 60% of its area (Krasiński *et al.* 1999). For their ranges, European bison select the most favourable forest types (Korochkina 1973, Krasiński 1978a, 1983, Bunevich and Kochko 1988, Kazmin and Smirnov 1992). For long periods, they inhabited limited ranges, with increased density (e.g. Białowieża Forest). Sometimes the area of a population was spontaneously enlarged (Krasińska and Krasiński 1994). In other cases, European bison were transported to other unoccupied territories (Bunevich 1989, 1994). Recent distributions in Białowieża Forest cover practically the whole forest complex (Fig. 11.1).

Deciduous forests types are the most suitable habitats for European bison. In BPF they mainly forage in fresh and moist deciduous forests and then in mixed coniferous forests (Krasińska *et al.* 1987, Krasiński and Krasińska 1994). Forest complexes with a mosaic-like forest type arrangement (Białowieża and Borecka Forests, Poland) are most favourable. In fresh deciduous forest, European bison find food throughout the vegetative season. In the Caucasus region, European bison prefer foothill forests; in summer, they feed on alpine meadows (Kazmin and Smirnov 1992, Kazmin *et al.* 1992). However, considerable plasticity of European bison with regard to food means they forage in environments where coniferous forests predominate (e.g. the Belarusian part of the BPF) (Krasiński *et al.* 1994a, 1999).

All European bison populations inhabit ranges that include open areas (mown meadows, deforested feeding glades covered with grass, clear cuts and young plantations up to 10 years old) penetrating forest and open areas to the same extent (Dzięciołowski 1991, Krasińska and Krasiński 1994, Krasiński *et al.* 1994a, 1999). The attraction of open areas results from the fact that exploited meadows and glades provide ungulates with much more food than the same area of the forest herb layer and food is more easily available there (Korochkina and Bunevich 1980, Kazmin *et al.*, 1992). In Lithuania, free-ranging European bison spend most of their time in open, half-open areas, fragments of forest grooved, agrocenoses and meadows (Balčiauskas 1999). Bearing in mind the historical distribution, this species may survive not only in a zone of deciduous forests. Little information is available on the populations inhabiting the Caucasus Mountains (Russia) or the Carpathians (Poland, Ukraine). Therefore, it is necessary to conduct systematic studies on the ecology of free-ranging populations on other regions, and particularly of animals of the Lowland-Caucasian line.

The forest herb layer also provides food for other ungulates, constituting approximately 30% of roe-deer diet and 40% of red-deer diet (Dzięciołowski *et al.* 1975). However, among the ungulates inhabiting the BPF, only red deer are viewed as a potential food competitor with the European bison. Therefore, the management plan for European bison should also incorporate the feeding needs of other ungulates living in the same forest complex.

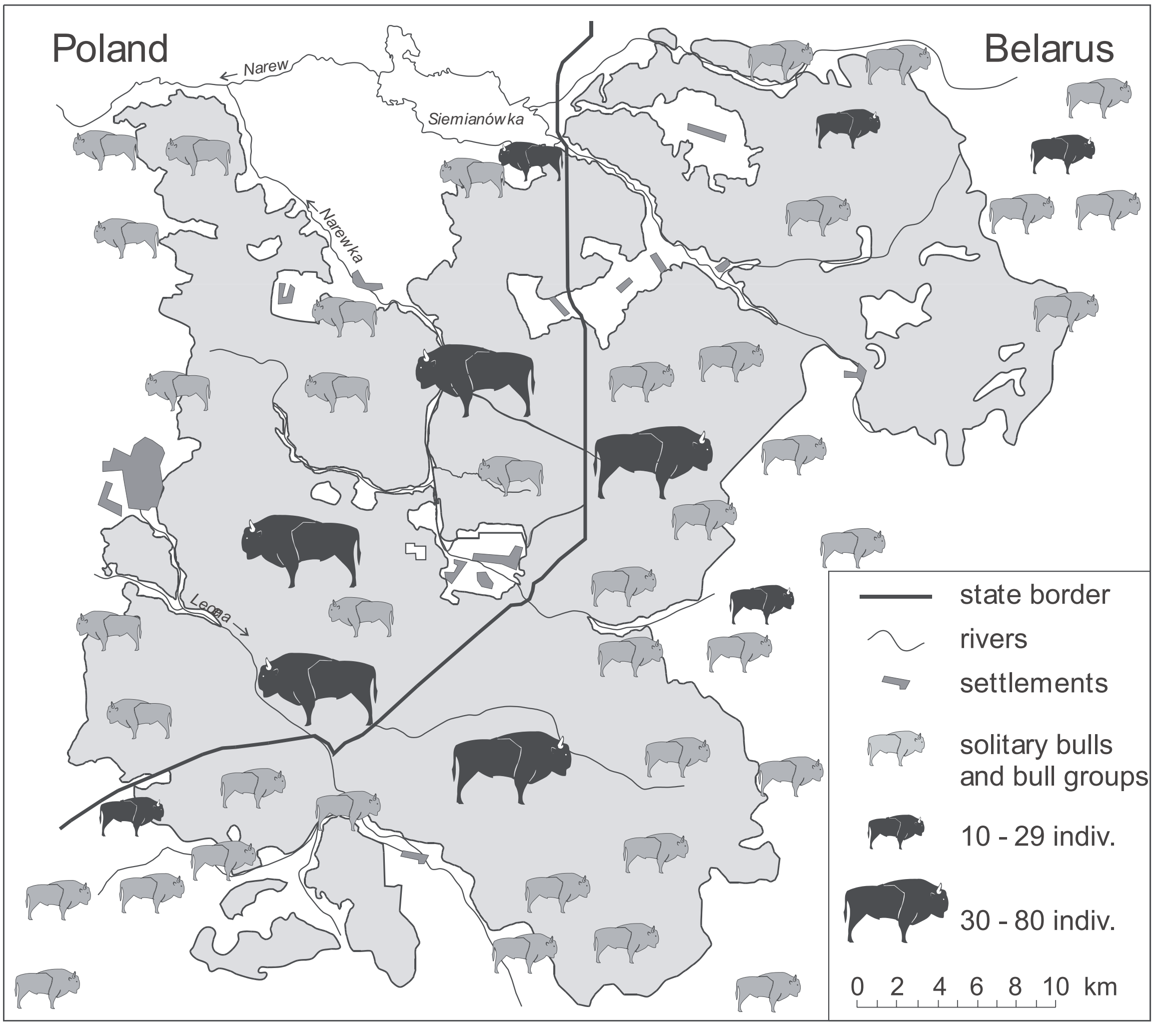


Figure 11.1.
Distribution of European bison herds in Białowieża Primeval Forest in 1998. (acc. to: Krasiński *et al*. 1999.)

European bison habitat should be properly managed, with the formation of watering places, cultivated meadows or feeding glades for the use of other ungulates. European bison pressure on the forest could be decreased considerably by creating properly managed feeding glades and forest meadows of an adequate size.

11.2. Food and feeding

Studies on the European bison's feeding habits were conducted mainly in Białowieża Forest, Prioksko-Terrasnyjj reserve and Cejjskijj zakaznik. Borowski and Kossak (1972) have shown that the European bison's diet in the Polish part of Białowieża Forest includes 131 plant species, with 27 species of trees and shrubs, 14 species of grasses and sedges and 96 species of dicotyledonous forbs – they did not recognize many of the grasses. In the total diet, trees and shrubs constitute 33%, while grasses, sedges and herbs 67%. Among trees and shrubs *Carpinus betulus*, *Salix caprea*, *Fraxinus excelsior* and *Betula pubescens* are preferred. Favourite grasses and sedges include *Calamagrostis arundinaceae, Carex sylvatica* and *Carex hirta*; Dicotyledonous forbs – *Aegopodium podagraria, Urtica dioica, Ranunculus lanuginosus* and *Cirsium oleraceum*. The trees most barked are *Quercus robur, Carpinus betulus*, *Fraxinus excelsior* and *Picea abies*.

A favourite food of European bison is acorn; however, its yield only occurs in the forest every few years. Analysis of the rumen contents has confirmed that the European bison's basic diet contains grasses, sedges and herbs, constituting 90% of rumen capacity, while trees and shrubs only 7–13% (Gębczyńska *et al.* 1991). Other investigators note that the basic part of the European bison's rations include more than 50 species of grasses and about 10 species of trees and shrubs; species preference can be dissimilar depending on the regions (Zablotskaya 1957, Korochkina 1969, 1972; Kazmin and Smirnov 1992, Kazmin *et al.* 1992).

European bison living in anthropogenic landscapes (as in Lithuania) feed mostly on grass and agricultural crops. Browse usage is restricted mainly to the non-vegetative period of the year (Balčiauskas 1999). In the North Caucasus Mountains, bison are living in the forest but during the summer period forage on sub-alpine meadows (Kazmin *et al.* 1992).

As ruminants, European bison have adapted to use a variety of vegetable food. High food demand means that European bison roam the forest continuously. It has been established experimentally that calves up to 1 year of age eat 8.5 kg of fresh food every day, the young (2–3 years old) 19.5–28.5 kg and adults 23–32 kg. This food contains a considerable amount of leaves and browse (40%) (Gębczyńska and Krasińska 1972). According to other authors, a hybrid adult bull of the North American and European bison in the Caucasus eats 30–60 kg of fresh food daily (Kalugin 1968, Aleksandrov and Golgovskaya 1965). Daily food consumption in European bison, living in enclosures in the Prioksko-Terrasnyjj Reserve, was between 25 to 50kg of fresh matter (grass, hay and willow branches) daily, depending on the age of animals and the kind of food (Kholodova and Belousova 1989). A food requirement, defined as dry matter of food eaten, was from 15 to 22 g per one kg of animal body mass (Kholodova and Belousova 1993).

In Białowieża Forest, it was calculated that a herd of European bison is able to consume 0.9% of herb layer biomass from coniferous and deciduous forests during one vegetative season. This value can slightly decrease in the spring and particularly autumn consumption of herb layer plants in alder woods. Basic herbage food is seasonally supplemented with a small amount (up to 10% of diet) of woody plants (Aleksandrov and Golgovskaya 1965, Borowski and Kossak 1972, Dzięciołowski *et al.* 1975, Gębczyńska *et al.* 1991). . In winter, the portion of woody plants can increase to 70–90 % of the diet (Korochkina 1969, Kazmin and Smirnov 1992).

Natural food is well utilised by European bison, this is confirmed by the high digestibility of its components: 51–61 % of dry matter (Kowalczyk *et al.* 1976, Kholodova and Belousova 1989). The ability to digest lignin in a higher rate than cattle indicates a specific adaptation of European bison to forest conditions (Gębczyńska *et al.* 1974).

In Poland and Belarus, all free-ranging herds, large, medium-sized and small, have been traditionally fed with hay in winter since their formation (Korochkina 1974, Krasiński 1978a, 1983, Krasiński and Krasińska 1994). Winter supplemental feeding limits natural mortality of European bison, but at the same time leads to a few-months concentration around the feeding places, which may affect European bison health. We believe that winter feeding of European bison in BPF should be continued. However in other sites of bison re-introduction, with larger areas of meadows or agrocenoses (like in Lithuania, Balačiauskas 1999), it may not be necessary. Constant observation of animals' condition and forest damage is recommended to ensure an immediate response to an unfavourable situation.

11.3. Seasonal and daily activity rhythms

European bison's daily activity rhythm is polyphase and thus typical of other ruminants; phases of foraging alternate with resting spent mostly on rumination. In the summer period, the main phases of European bison daily activity rhythms are highly synchronised in the group, thus confirming the consolidation of herd as a structural unit of the population. Common feeding in the group allows utilisation of the European bison's food strategy based on active feeding during movement. In the vegetative season, European bison spend approximately 60% of their daily activity on feeding, 30% on resting, and the remaining 10% on roaming without feeding. A reverse situation can be observed in winter, when European bison are additionally fed with hay and spend about 30% of their daily activity feeding and 60% resting, the roaming time being the same (Caboń-Raczyńska *et al.* 1983, 1987). It has been found that European bison from mixed groups share their feeding activity in the vegetative season feeding on herb layer plants (95%), browsing (3%) and debarking (2%) (Caboń-Raczyńska *et al.* 1987). Debarking is seasonal, being most intensive at the turn of winter and spring, in BPF conditions in April (18% of feeding activity).

Drinking in the snow-free period is not regular in the daily activity rhythm of European bison. Those living in mixed groups normally use permanent water reservoirs or watercourses (small rivers and streams). Solitary bulls frequently drink water from road pools. During winter, European bison also use snow-water, crumble ice on streams, or tread frozen soil in alder woods to get to water.

11.4. Reproduction and development

According to European Bison Pedigree Book data , bulls living in reserves begin to mature sexually in the second year of life (Zablotsky 1949, Jaczewski 1958). However, histological studies of the testes and epididymes have revealed that European bison from free-ranging populations and reserves begin to mature sexually at the 3rd year of life. Bulls aged 4–12 are characterised by fully developed spermatogenesis and are able to produce mature spermatozoa (Czykier *et al.* 1999). Young bulls from free-ranging populations, aged 4–6 years, are sexually mature, but do not take part in reproduction for behavioural reasons; they are not allowed to cover cows by older bulls (Krasiński 1967, Krasiński and Raczyński 1967, Krasińska and Krasiński 1995). The breeding period in males in a free-ranging population is short, lasting from the 6th to 12th year of life and later it is limited due to attenuated spermatogenic process (Czykier *et al.* 1999).

Cows usually reach sexual maturity in the third year of life, giving birth to their first calf in the fourth year. In a free-ranging population, approximately 20% of females give birth to the first calf in the third year of life, but frequently (36.5%) at the age of 5 or 6 (Krasiński and Raczyński 1967). Females can give birth until the end of life, although the upper limit accepted for cows from free-ranging populations is about (15) 18– 20 years of age (Krasiński 1978b, Balčiauskas 1999).

The rutting season in free-ranging populations continues from August to October. The gestation period of a cow lasts for 264 days on average (254–277) (Krasiński and Raczyński 1967) or 265.7 days (256–279) (Jaczewski 1958) and 267.4 days (259–279, *n*=21) (Kiseleva 1969). A female European bison usually gives birth to one calf at a time; twins are sporadically observed in captive breeding. Parturition, lasting from 1h 30min to 2h 11min, has only been observed in reserves. Cows calve lying and immediately after giving birth, begin to lick neonates intensively. The first standing of a calf takes place 22–45 min following birth, and the first suckling occurs within the first hour of the calf's life (Daleszczyk and Krasiński 2001). In a free-ranging population for the period of parturition, the cow leaves the herd to return with a calf after a few days. The calving period in a free-ranging herd lasts from May to July; however, late parturitions can happen (August-October) (Krasiński and Raczyński 1967, Krasiński 1978a, 1978b, Balčiauskas 1999).

Long-lasting observations of European bison in Białowieża Primeval Forest and from Cejjskijj zakaznik revealed that the sex ratio at birth did not differ significantly from 1:1. However, in the some years deviations are observed.

The reproductive potential of the population is expressed by the coefficient of births (the ratio of the number of calves born to the population size) and the coefficient of fecundity (the ratio of the number of calves born to the number of cows capable of reproduction). In large and medium-sized European bison populations, the mean coefficient of births ranges between 14 and 17% in multi-year cycles (the minimum 5%, the maximum 35%) (Krasiński and Raczyński 1967, Krasiński 1978a, Krasiński *et al.* 1994a, 1999, Krasiński and Krasińska 1992, 1994). The coefficient of fecundity has been estimated only for the Białowieża Forest population, being on average at the level of 50% in the Polish population and 40% in the Belarusian population in a multi-year cycle. This indicates that almost half of the females capable of reproduction in free-ranging herds give birth to calves every year (Krasiński 1978a, Krasiński *et al.* 1994a, 1999). The highest value mean coefficient of births (22.4%) and coefficient of fecundity (70.3%) was in first years of population's rapid increase (1958–1966) (Krasiński and Raczyński 1967, Krasiński 1978a). In populations living in Caucasus Mountains coefficient of fecundity varied from 22 to 62% (Kazmin 1989). Both means of coefficients of reproduction were higher in European bison living in enclosures, as compared with those in free-ranging populations (Raczyński 1975, Pucek 1984).

Bulls from captive breeding reach the age of 20, while those from free-ranging populations do not live longer than 14–16 years. Cows bred in captivity live up to the age of 28, while the oldest marked cow from a free-ranging herd in the Białowieża Forest lived for 24 years (Krasiński 1978a).

The mean body mass of European bison males at birth is 27.6 kg, being higher than in females (24.4 kg), but the difference is insignificant. In males, body size (mass and measurements) increases proportionally to age up to 6 years. In females, the highest increase in body mass is observed in the first year of life, at the age of 3–5 the growth rate become slower than in males, declining at the age of 5. The mean body mass of European bison males from Białowieża reserves aged 6 years and older is 747.1 kg (*n*=25), females 460.2 kg (*n*=19), while in European bison living in a free-ranging population it is 634.1 kg (*n*=79) and 423.7 kg (*n*=76) respectively (Krasińska and Krasiński 2002).

The highest increase in the rate of body measurements occurs in the first year of life. Later the increase is slower and declines at the age of 5–6. The rate of increase in body measurements is higher with age in males than in females. Body measurements are correlated significantly with body mass. The maximum body measurements of 6-year-old bulls and older living in reserves and in free-ranging herds in BPF are: withers heigh – 188 cm, body length – 300 cm, oblique body length – 270 cm, heart girth – 280 cm, in adult cows being 167 cm, 270 cm, 172 cm and 246 cm respectively. The hump formed by spinal processes of the thoracic vertebrae surrounded by powerful muscles gives adult European bison an impressive appearance. The hump of cows is less developed.

Sexual dimorphism expressed by body mass and measurements develops gradually during the postnatal period, becomes pronounced at the age of 3 and is maintained until the end of life. The physical development of European bison ends at the age of 5 years in females and at the age of 6 years in males (Krasińska and Krasiński 2002).

11.5. Population structure and organisation

In the first 10–20 years after re-introduction to Białowieża Forest, the size and structure of large and medium-sized European bison populations developed without human interference.. The established population structure formed is believed to ensure normal development. Bulls (4 years old and older) constitute 25% of the population, cows (4 years old and older) 35%, the young of both sexes (2–3 years old) 25% and calves 15% on average (Krasiński *et al.* 1994a, 1999).

The European bison is a gregarious animal. Mixed groups and bull groups are the basic units of European bison population. Mixed groups contain cows, the young aged 2–3, calves and temporarily adult bulls. The average size of mixed groups is environment-dependent. As a rule, groups consist on average of 8–13 animals in different populations (Krasiński and Krasińska 1992, 1994, Krasiński *et al.* 1994b, 1999). In BPF the mixed group, size ranges between 2 and 92, with groups of 20 being the most common (65–85%). Sometimes, European bison foraging in open areas (mown or mountain meadows and deforested grassland glades) form larger groups, amounting to 23 individuals on average (2–140) (Bunevich and Kochko 1988, Krasińska *et al.* 1997, Kazmin and Smirnov 1992). Groups of bulls in all populations are small and contain 2 animals on average (1–11). More than half of the males lead a solitary life (Krasiński and Krasińska 1994, Krasiński *et al.* 1994a).

Groups of European bison are not family units. The size and structure of mixed groups change, some of the changes being seasonal (calving, joining of bulls in the rutting period), others for behavioural reasons. Groups meet frequently, combine and then quickly split exchanging some of the individuals. The bonds between the young are the least permanent; young bulls exchange most frequently (Krasińska *et al.* 1987).

European bison movements within ranges are connected mainly with feeding activity and ensure optimum utilisation of food supply. European bison strategy of habitat utilisation is a joint effect of group size and structure, habitat preferences, and its rotational exploitation of the environment, which prevents an overgrazing (Krasińska *et al.* 1987).

In winter, the majority of European bison gather around feeding sites and form large mixed aggregations and smaller bull groups. Depending on the population size, there are one or more winter aggregations of different sizes. The largest mixed aggregations of 100 European bison are observed in BPF (Krasiński *et al.* 1999). In all populations, some bulls take advantage of extra winter-feeding in a limited way.

The size of home ranges of bulls is correlated with their age. In BPF the average home range of younger bulls (5–6 years old) is 44 km2, being significantly smaller than that of older, over six-year old bulls (84.3 km2). Bulls inhabiting the forest periphery occupy the largest home ranges (136.5 and 151.6 km2). The maximum home ranges of cows cover approximately 100 km2. Winter home ranges of bulls in BPF are larger than of cows (10.7 km2 and 7.9 km2 respectively), and are correlated with duration of permanent snow cover and mean winter temperature. Low temperature and long-lasting snow cover delimit European bison mobility in winter. In the snow-free period the mean size of home ranges of bulls is 69.5 km2 and does not differ significantly from that of cows (68.8 km2) (Krasińska *et al.* 2000).

European bison home ranges are not defended and greatly overlap. European bison most intensively penetrate the centre of their ranges. Small core areas are sited around watering places and meadows (Krasiński *et al.* 1999). The core areas of Lithuanian populations is about 20 km2; however, animals frequently visited territory of between 100–200 km2 (Balčiauskas 1999). This data should be taken into consideration when planning European bison re-introductions. An area of 200 km2 seems to be sufficient for a population of 50–70; in smaller forest complexes, conflicts with agriculture may arise.

11.6. Regulation of European bison number in the population

11.6.1. Mortality

In large and medium-sized free-ranging European bison populations, natural mortality is low and does not contribute significantly to the regulation of population numbers. The coefficient of mortality (the ratio of dead animals to the number of individuals in a population) is 2.8% – 3.9% on average (range from 0 – 12.5%) in different populations. Mortality among males is significantly higher than in females, but the data available refers only to the Białowieża Forest. The ratio is 63%:37% in the Polish part and 57%:43% in the Belarussian part (Korochkina and Kochko 1982, Krasiński and Krasińska 1994, Bunevich 1999a, Krasiński *et al.* 1999). European bison has no natural predators in BPF. Causes of natural mortality are known only from Białowieża Forest. In the western part, during 1952–2000 death included traumas of different origins (10.0%), injuries caused by other bison (7.6%), parasitic diseases (9.6%), posthitis/balanoposthitis of males (diseases of prepuce and penis) (8.0%), poaching (6.0%), senility (6.4%), and other causes (17.1% altogether). In the Belarussian part (1981–1998), the major cause of mortality is poaching (16.9%), balanoposthitis of males (12.7%), diseases of the alimentary tract (10.6%), injuries caused by other bison (9.2%), drowning (6.3%), pneumonia (4.9%) and others (10.5% altogether). (Bunevich 1999b). In both populations more than 20% of death causes are unknown (Krasiński *et al.* 1994a, 1999).

11.6.2. Culling

No free-ranging European bison populations have the possibility of unlimited growth; excess animals are caught, and transported to other breeding centres or culled. Culling is the practical way of maintiaining European bison populations at a desired level. For example, in the Polish part of Białowieża Forest, in the years 1971–1999, the mean annual reduction in European bison numbers was 11%, thus ensuring stability at approximately 250 individuals (Krasiński *et al.* 1994a). A similar reduction in the number of European bison is conducted in other populations (Krasińska and Krasiński 1994, Krasiński *et.al.* 1999).

The choice of sites for newly created free-ranging European bison populations should involve an estimation of habitat capacity with regard to other ungulates living there. In this way, the target number of European bison and other ungulates can be established; when the optimal number is exceeded, regulation is necessary. Reduction in the number of adult males should be treated with great caution to maintain population stability (Pucek *et al.* 1996b).

A number of biological parameters have been used for simulation modelling of population extinction using the VORTEX package (Lacy 1993, Lacy *et al.* 1995) in Białowieża Forest's free-ranging bison herd. It appears that this bison population has the potential for rapid population growth with a low risk of extinction. Isolated populations should, be at least 100 to reduce the effect of demographic and environmental stochasticity. It also appears that such bison populations are most sensitive to the elimination of adult females. No such effect is seen in the case of males or young animals. It means that careful attention needs to be directed at the precise amount of elimination that is carried out in European bison herds if stable numbers are to be maintained (cf. Pucek *et al.* 1996b).

The regulation of local bison populations, as a protected species, may be viewed negatively by some, yet it is a necessary action in particular cases, for the sake of both European bison and its habitat. An uncontrolled increase in populations in human-transformed ecosystems could lead to their degradation and to a subsequent decrease of the protected species itself. On the other hand, in most of free-living populations, the European bison has no natural predators. The regulation of European bison by selling hunting licenses for the shooting of a protected species is legally and ethically ambiguous, and has little in common with sport. We may conclude that while the European bison is a protected species, its number should be locally controlled by elimination. Another view suggests that controlled sport hunting could stimulate an increase in the number of animals affording it better protection by interested landowners and hunters.

12. Actual and potential threats

The effects of restitution generally show a positive picture of the species' rescue from extinction. However, stating that the European bison is completely safe would be rather premature. A thorough and more critical analysis of the current state of the species reveals serious threats stemming mainly from its genetic structure and from its management.

The risk of extinction to the species, both in captivity and in the wild, is still very high. We see many reasons for this:

There is **little space** for a large herbivore such as the European bison in Europe's contemporary ecosystems, especially in the west. The most significant limit for the enlargement of European bison populations is human population density; forestry and agricultural activity is not a limiting factor. Bog areas could also naturally limit bison distribution.

Fragmentation and **isolation** of free-ranging (and captive) herds with little or no, exchange of genetic material. Isolated populations, small in size, quickly lose their genetic heterogeneity and are doomed to extinction (Franklin 1980).

As yet, there is still no opportunity for the **reconstruction** of at least a fragment of a more compact **geographic range** to facilitate migration of bison between herds. Reconstructed ranges have recently declined in some parts of the previous range (e.g. Caucasus Mountains).

Genetic structure of the species, a consequence of passing a dramatic bottleneck, the gene pool is limited and animals are highly inbred. The average value of inbreeding coefficient is very high, as compared to other large mammals, and is equal to 44% in Lowland line and 26% in Lowland-Caucasian line for individuals with a pure pedigree (Olech 1998). It is interesting that the negative effects of inbreeding, manifested in the decline in reproduction rate, are more strongly pronounced in the Lowland-Caucasian Line than in the Lowland line (Olech 1987, 1989, 1998). Inbreeding exerts a harmful effect on the skeleton growth, particularly in females (Kobryńczuk 1985), and possibly lowers the resistance of bison to disease and pathologies.

Genetic **contribution of founders** is uneven, highly dominated by one pair (see Chapter 6), and changing very little in the species' entire gene pool throughout the decades of its restitution (Olech 1989). In the last few years, a decrease in the founders specific for the Lowland-Caucasian line has been observed (Bielousova 1999, Olech 1999). The retention of founders' genes also decreased, this means continuing loss of genetic variability in the species. There are very serious worries about the reduction in genetic variability through losses represented by very rare founder's genes.

Because of the 'second' bottleneck between 1940 and 1945, the founder's **Y-chromosomes** are not equally spread throughout the recent world population of European bison. Lowland line animals have copies of the same Y-chromosome from the founder No 45. The Y-chromosome of founder No 100 can be found in Bieszczady and in some captive groups. The Y-chromosome of the founder No 15 and No 147 were lost in the breeding process in 1945–1997 (Sipko *et al.* 1999).

At the beginning of restitution (1924) the contribution of the Lowland Line to the world population approximated 70%, today only 42% due to mixing of L and LC lines. In enclosed breeding centres, the Lowland-Caucasian line predominates, constituting 75%. On the other hand, in free-ranging herds the proportion of Lowland line to Lowland-Caucasian line is almost equal, 57%:43% (cf. EBPB 2001 and Tables 10.1 and 10.2). The further mixing of both lines leads to **losses of genes of founders** specific for Lowland-Caucasian line.

The impetus for **re-introduction** into the wild seems to have slowed down recently due to a lack of suitable habitat or limited economic possibilities within particular countries. As a result, numbers and other demographic characteristics of the global European bison population are increasing rather slowly (see for example Sipko *et al.* 1999).

Inappropriate (traditional) forms of **management**, based on zootechnical practices, rather than on forest ecosystems ecology, as well as supplementary feeding during winter, slow down the process of adaptation of the European bison into contemporary woodlands. Artificial woodlands are not appropriate for European bison. Such practices do not lead to the naturalization of bison within communities of large herbivores and in modern European forest ecosystems.

Possibilities of **mixing** free European bison populations in some regions of reconstructed range **with hybrids** of European and American bison (See Appendix I), as well as with pure prairie bison, introduced for farming/ranching in several European countries.

Diseases appearing in European bison populations can bring serious threats to the whole species. It is not certain whether the species has always shown a weak resistance to disease or if immunity has declined, due to limited genetic heterogeneity. In the previous century, cases of epizooty were noted among bison in Białowieża Forest. It is known that European bison exhibit a particular sensitivity to foot-and mouth disease (*Aphte epizooticae*), appearing in the Forest nearly each year at the beginning of XX century and causing about 5% mortality (Wróblewski 1927). Half a century ago, foot-and-mouth disease caused the deaths of 35 bison in reserves in the south of Poland in the years 1953/54 (Jaczewski 1960, Podgurniak 1967). Cases of tuberculosis were registered recently (1996) in Bieszczady Mountains (Poland) (Żórawski and Lipiec 1997).

The most important disease, however, affects the male reproductive organs and is manifested in the inflammation of the penis and prepuce, leading to diphtheroid-necrotic lesions, diagnosed as **balanoposthitis**. This disease was discovered at the beginning of the 1980s in Białowieża Forest (Kita *et al.* 1995, Piusiński *et al.* 1997, Jakob *et al.* 2000); although similar symptoms had been reported earlier (Korochkina and Kochko 1982) in Russia and Ukraine (Shabailo and Pererva 1989, Krasochko *et al.* 1997). This disease was also sporadically observed in other regions of Poland (Gołuchów, Puszcza Borecka, Bieszczady). At the end of the 1990's, similar symptoms were observed in five young European bison from Bayerisher Wald National Park, Germany (Wolf *et al.* 2000). Despite many years of study, its pathogenesis has not yet been elucidated.

Bulls with those symptoms do not exhibit changes in the general **physiological mechanism** as indicated in the long term studies of 30 physiological indices in nearly 300 (Gill 1989, 1992a 1992b, 1999, Wołk and Józefczak 1988). Generally, however, the non-specific immunity of the species is very low (Gill 1995). From the other hand, in Białowieża Primeval Forest it was recently found that several biochemical indices of blood signifantly differed from those observed some 20 years ago. This is believed to be related to an increased intensity of pathological changes observed in this population (Wołk and Krasińska, in prep.). Some authors believe that genetic factors may predispose bison to the disease, due to reduced resistance. Winter concentration and associated environmental pollution are a likely source of bacteria which is transmitted from soil to the organism and are then found in the affected tissues.

Parasitic diseases are a serious threat to bison health in the present population. Besides parasites which are specific to this species, 11 additional species have been found in recent years, all being characteristic parasites of Cervidae (Dróżdż 1961, Dróżdż *et al.* 1989, 1994). New parasites may still be found (Dróżdż *et al*. 2000).

Poaching as a result of administrative disorders and a failure to enforce nature conservancy law threatens free-living herds of European bison in many countries. World population numbers have decreased, with some populations seriously decimated and others becoming extinct in recent years (cf. Table 10.2).

Several administrative bodies responsible for managing the same population may create serious threats for bison populations. Different owners observe different aims (e.g. forest administration unit, national park /or reserve, and agricultural land). Therefore, the **management** of European bison populations should be the responsibility of one administrative body.

The legal status of the species is not clearly established, particularing with regard to its position as a protected species, management, and conservation procedures, such as international animal transfers, monitoring and the controversial issue of elimination and hunting.

13. Research needs

The most important European bison problems in need of further study were formulated some 25 years ago (Pucek 1967) and later supplemented in many other articles (among other, Pucek *et al.* 1996a). These papers serve as guidelines for numerous studies on bison biology and ecology during the last decades, predominantly in Białowieża Forest and elsewhere. At present, research is focusing on the problems concerning European bison genetics and health. This chapter lists the problems that remain important for furthering our knowledge of this protected species, its recovery and management, as well as to encourage bison specialists to solve them. Some problems are divided into groups, indicating in which areas further scientific research is essential for European bison conservation.

Undoubtedly, studies on the **genetic variability** of the world population take precedence. As previously stressed, the fundamental problem for *Bison bonasus* is the very low level of original genetic variability. There is a serious need to assess the present genetic variability for the whole world population. Until now, the main method for such studies was by genealogical analysis, which is not sufficient for the whole population because of the lack of pedigree data. A genetic study must be completed with analysis of genetic markers (molecular or/and biochemical) for the whole population to supplement the genealogical analysis. The results of these genetic studies should be included in breeding programmes aimed toward saving the genetic variability of the contemporary species. Such a co-ordinated programme already exists for some zoos (EEP) but should be extended to all captive herds.. There is also a need for genetic studies to help plan re-introduction and re-stocking programmes.

The need for programmes to save genetic variability is also very important because of the probability of increasing homozygosity in European bison, which seems to be correlated with a lowered resistance in the species. Therefore, there need to continue and intensify studies on recent European bison **diseases and parasites** to find the pathogens responsible. Application of these studies should lead to elaboration of a programme for health protection and prophylactic.

Studies on European bison **ecology** are of particular importance. At present, there are no sufficient scientific grounds for establishing the principles of rational planning of new re-introductions, re-stocking, and enlargement of the geographical range. Investigations on ecology, genetics, behaviour and management of bison populations are therefore required. Great progress has been made in this field during the last decade, concerning forest habitats and bison populations in Białowieża Forest; however, little information is available on populations inhabiting other environments such as the Caucasus Mountains (Russia) or the Carpathians (Poland, Slovakia, Ukraine). Therefore it seems necessary to conduct systematic studies on the ecology of free-ranging populations in other regions (mountains, forest-steppe zone, northern ranges of Europe) and in particular of animals from the Lowland-Caucasian line. Special attention should also be paid to those habitats where no supplementary winter-feeding is provided.

Standard **demographic and population characteristics** for the European bison are needed for habitats not yet studied, particularly in mountains. These should also include studies of daily and seasonal activity rhythms, seasonal migration and habitat preferences. Special attention should be paid to the behaviour of European bison towards people and forestry and agricultural activity, particularly in densely populated areas.

An important problem for the future concerns the **enlargement of the bison's range** in Europe, as well as its acclimatisation in new areas, both within and beyond the historical range of this species. Studies are required on determining the most suitable habitats for this species within and outside the limits of its contemporary geographical range. In particular, observations of reproduction**,** condition parameters, and the **behaviour** of free-living populations are important for future extension of the species range.

The **place and role of European bison as a component of the ungulate community** in forest ecosystems of the temperate zone should be determined based on extensive studies of their habitat preferences, foraging behaviour, food and energy requirements, *etc*, in age, seasonal and geographic aspects. Habitat evaluation and utilisation by European bison in different ecosystems is needed. The effect of European bison feeding on tree stands or agricultural systems has also to be determined and damages estimated/evaluated.

Details of the numerical progress of European bison populations should be continuously monitored both in captive and free-ranging populations. Models for the regulation of European bison numbers in different ecosystems are necessary for forecasting the effects of culling on world and local population dynamics.

Problems of **reproduction biology** are well understood in enclosed breeding centres (reserves), but less so in free-ranging herds. Variation in the reproduction potential in different parts of the species reconstructed range and different habitats, are required for estimating an increase in bison population numbers and their optimal density. For the future of any conservation programme, the study of reproduction is very important.

Due to the fragmentation of captive and free-ranging herds, there is a serious need for the application of modern technologies in the reproduction process; in particular, **sperm collection and freezing**, artificial insemination, and *in vitro* fertilisation. The establishment of a European bison Gene Resource Bank could be very important for the future of the species.

Research on the rational diet for European bison in captive and free-living herds and the role of supplements in different conditions is important; in particular, studies to determine if **supplementary winter-feeding** is necessary, and in which regions, habitat conditions or season. What kind of forage is most appropriate, if necessary, for the European bison in winter?

Studies on the **zoological characteristics of this protected species** should continue. Much has already been done in morphology (especially anatomy) for the species, and in some respects it is better known than the anatomy of cattle. However, we are still waiting for a monographic description of European bison morphology and development, as well as its variability in the contemporary range. These studies should be continued and material collected.

The recent "Outline of European bison physiology" (Gill 1999) indicates how much has been achieved during the long-term study of this species in Poland. More studies are necessary, to understand the bison's adaptations to different habitats; however, this would require access to representative data for the entire contemporary range of the species.

14. The Conservation Strategy and Recommended Action Plan

The objective of the conservation strategy is to create the conditions conducive for the long-term survival of viable wild (or naturalized) populations of European bison (Lowland and Lowland-Caucasian lines). European bison can only be saved from extinction as a wild species and a natural element of the forest and steppe-forest ecosystems of Central and East Europe. This could be achieved by creating large (1000 animals, or more) viable populations of the species. A target number of 3000 free-ranging animals as a single genetic population is recommended as a management goal for self-sustaining populations for each genetic line [recommendations of joint meeting of Bison Specialist Group (SSC/IUCN, Conservation Breeding Specialist Group SSC/IUCN and European Endangered Species Programme (EEP), 1996]. At present, we are far from reaching such a satisfactory conclusion.

Two basic directions in European bison recovery should be maintained and continued, namely:

(1) Captive breeding in zoological gardens and reserves, and the
(2) Development of free-ranging (or semi-free) populations.

Consequently, it is necessary to create the following foundations for the action plan for European bison:

(1) **To continue captive breeding** of the species.The captive population constitutes an extremely valuable reserve of the species gene pool. According to data presented in tables 7.1–7.4, the gene pool of the captive population is unique for every line. The pedigree of animals in captivity is well known, and can be traced to the founders of the species. This portion of the European bison world population primarily serves as a reserve gene pool and aids protection against any catastrophic genetic losses; and secondly, as a source of animals for further re-introduction, or possible supplementation of under-represented genetic material in free-ranging populations. Special attention should be given to the long-term conservation of the whole gene pool and genetic variability, including the part of the genome not represented in the free-ranging population. This part of the world population should be subject to a programme of genetic variability conservation treating European bison as one world population. The programme should ensure:

(a) Separation between the existing breeding lines, i.e. between the pure Lowland bison and the Lowland-Caucasian line, which is particularly important for preserving the genetic variability of LC line.

(b) Avoidance of the possibility of contact and breeding with any European and North American bison hybrids or cattle, or pure American bison introduced for farming/ranching in several European countries. Europe is the range of European bison so any imports of American bison should be avoided [!]

(c) Application of a coordinated programme aimed at maintaining genetic variability. This requires professional methods focusing on the conservation of unique genes, maximization of effective population size, increasing the tendency towards equalization of the founders genotypes contribution, and minimization of inbreeding or kinship coefficient,

(d) Successful co-operation between herds in the genetic programme and improved management conditions,

(e) An increase in the number of herds and animals, i.e. the contribution of the Lowland line to the world herd [?]

To realize the above goals, genetic material must be exchanged between enclosed herds, which should be treated jointly, as one population, within the respective lines.

The genetic programme of bison breeding ought to be based on genealogical analysis of EBPB data (Ballou *et al.* 1995) and simulation analysis of demographic characteristics and reintroduction results in the respective populations, or herds (Soule 1987, Seal 1991). The EEP (European Endangered Species Programme) should be extended to encompass the whole captive population.

A **Gene Resource Bank** (Semen collection in the first phase) should be created to serve as a security against the loss of important genetic variation, to decrease the number of animals required for maintaining optimal genetic variability, and to facilitate the exchange of genes between herds. Studies in this direction have already been undertaken in Russia. Methods for the collection of sperm its conservation and use have already been worked out (Sipko *et al.* 1993, 1997). Much more must be done for obtaining sperm from the most important animals for the protection of the species and its heterogeneity. Adequate resources for its continuous collection, supplementation and preservation are very important for obtaining satisfactory results.

(2) **To continue the process of re-introduction** of the European bison into forests or other ecosystems, including vast areas where human activities are abandoned (former farmland or military training grounds). According to IUCN position statement – *“Translocation of living organisms: Introductions, re-introductions and re-stocking”,* Gland, 1987), this process should be based on adequate scientific knowledge and requires identification of new re-introduction or introduction sites, particularly within the historical range of the species, but also outside it.

A target number of 3000 free-ranging animals is recommended as a management goal for a self-sustaining population for each genetic line (Pucek *et al*. 1996b). If this is to be achieved it would mean that the total world population of European bison would increase (at least be doubled) in the near future. Additional sites are therefore required in order to establish such a high number of bison. The separation of the Lowland Line and the Lowland-Caucasian Line should be maintained in free-ranging populations for as long as possible, or at least up until they make contact naturally. European bison from both lines have been released on different occasions with little regard to their separation (cf. Chapter 9.2). More genetic studies are required to determine the differences between lines and the future consequences if they are merged.

It is necessary to link isolated populations, one with another, to form a common meta-population for exchange of animals in a natural way (e.g. ‘building’ ecological corridors) or stimulated transfers of individuals from one herd to another. These practices should incorporate knowledge of the genetic structure of respective populations and the history of their development. This is particularly important, since many populations originate directly or indirectly from material obtained from Poland or from larger enclosed breeding centers, which did not have descendants from all the founders. Recent re-introductions in Belarus are a good example of this (see below).

Establishing sufficiently large populations or a network of meta-populations is necessary for minimizing the effects of stochastic gene loss in small isolated populations. The reproducing size (75–100 individuals) of these populations should exceed at least 50 effective individuals – the bigger the better. Simulations conducted using the Białowieża population has indicated that free-ranging populations need a carrying capacity of at least 100 to be demographically safe. If small groups (15–20 individuals, selected according pedigree, age and sex) are chosen, they should be allowed to grow quickly, at least, up to 100 to found new population. Theoretical population models that guarantee steady long-term development indicate that only effective populations of approximately 500 unrelated and intensively reproducing animals can fulfill these conditions (Franklin 1980, Soule 1987, Nunney and Campbell 1993). Analysis of the size and genetics of the European bison population show that there is still a long way to go until this goal is achieved.

It is also very important to **include all the founder’s genes into free-ranging population** as represented in the captive world population. In practice, the process of releasing captive animals into free-ranging conditions needs some form of adaptation centres. There are some special centres in Poland and Russia for adaptation and breeding of European bison for release, but more are required. During the last few years, only a few transfers of European bison from zoos into such breeding centers took place. The process has to be more intensive. The future of the species lies in managing free-ranging populations of various sizes. Successful co-operation between captive breeders, adaptation centres, and free-ranging herds needs special attention and financial support, greater international and regional funds should be provided for scientific research.

The creation of a **more compact geographic range** for the species should be initiated. Certain possibilities seem to exist in the Carpathians (Lowland-Caucasian line), on the border between Poland, Slovakia and Ukraine, and even more probably, between Ukraine and Romania, because of the existing large Bukovynska population. The Polish-Ukrainian agreement signed for the protection of border territories and free-ranging populations of European bison inhabiting that part of the Carpathians creates a solid base for the reconstruction of the bison’s geographic range there (Flint *et al*. 1986, Pucek 1994, Perzanowski and Kozak 1999, Perzanowski and Paszkiewicz 2000).

The Russian Federation has begun to create large populations in the Orel – Bransk region and the neighboring areas of northeast Ukraine (Desnjansko-Starohutski National Park, Sumy region), as well as, in the Vologda region.

Similar initiatives could be suggested for the Lowland line in the region of Belarus, if northern Poland and Lithuania sub-populations are included (see under Belarus).

European bison re-introductions are most frequently located in forest ecosystems, which are far from natural and affected by anthropogenic alterations. Such populations require constant control by man. This refers particularly to the regulation of bison numbers and its adaptation to current environmental resources available for the large herbivore community. Locally, regulation is necessary and intended for the good of the species whose unlimited increase could exceed the carrying capacity of the habitat. Despite the status of the European bison as an endangered species, the regulation of its number becomes a necessary practice for the sake of the species and its further restitution. However, **models of bison population management** should be elaborated to ensure effective actions.

European bison habitat should be properly managed, with the formation of watering places, cultivated meadows or feeding glades for use by other ungulates. European bison feeding pressure on the forest can considerably decrease by creating properly managed large glades and forest meadows.

Poaching is a serious threat to the European bison in several countries. Regulations that are more restrictive are necessary to preserve free-ranging bison. Financial support and a system for compensation should be developed in particular countries. Including the European bison in the Habitat Directive of the European Union, especially in Appendix II (which lists animals in need of specially protected areas) and Appendix IV (listing endangered species in need of special protection), may guarantee **better protection for the species**. It has also been suggested that the European bison – an endangered species of the IUCN List (2000) – should be placed in Annex 2 (strictly protected fauna species) of the Bern convention.

There are also some general problems, which should be addressed, and included in an Action Plan for European bison. These are:

The **European Bison Pedigree Book** (EBPB) has been published for 70 years nearly unchanged in terms of basic format and the scope of data presented. Poland is responsible for this task, sometimes with differing success rates in the regularity of publication. All European bison owners take, however, responsibility for the accuracy of the actual data published.

The role of EBPB cannot be overestimated (cf. Chapter 2). It is the only source of information about European bison registered in the world and the basic source of data about number, location, and the genealogy of the species. Breeders use the EBPB editorial office to make contacts and find information about the species.

The tasks preformed by the EBPB should increase in the near future according to the recent state of the species. These should include:

(1) Evaluation of the global European bison population, based on knowledge of pedigree, calculation of some coefficients, for example inbreeding, genetic uniqueness or contribution of founders to the gene pool of the species. It should be based on an official register for the European bison (individual registration in captivity and group registration for free-ranging and semi-free herds).

(2) The information provided by EBPB should be extended to include results from the genetic evaluation of animals in captive herds and of free herds as a tool helpful in the conservation of genetic variability.

(3) The EBPB office should serve as an advisory and information centre for breeders and for re-introduction purposes, in order to obtain the best results of the species restitution.

(4) The EBPB should be located in an established institution, (currently Białowieża National Park, Poland), but not in *ad hoc* specialist groups, societies, ministries, *etc*). The main products of EBPB are archives and databases of great importance for the restituted species. All this information should be based on accurate genealogies supplied to the studbook keeper.

(5) EBPB should develop other databases, for example with species bibliography, photos, *etc*.

(6) Federal or governmental authorities for nature protection should supervise the activity of European bison breeding centres.

Establishing an **International European Bison Breeding Centre** (IEBBC) is proposed for the coordination of restitution, re-introductions, monitoring of captive and free-ranging herds, and most of all – gene pool preservation and genetic management of particular herds. EBPB database – as the main source for information on European bison worldwide - should have its role extended and should cooperate very closely with the proposed IEBBC, or be a part of it. This Centre must provide all kinds of information and be available to all interested users (free of charge?). A mutual agreement should be achieved in cases of data publication, and appropriate acknowledgements given.

Detailed **methods of transportation** of European bison should be worked out to minimize eventual losses during international transfer.

The creation of a **web site** at the Centre and an official European bison Newsletter (EBNL) available on the Internet is essential for the quick exchange of ideas, recommendations and instructions for breeders and those seeking information on European bison.

Details concerning an Action Plan for European bison developed in particular countries

Belarus

The forest ecosystem of Białowieża Primeval Forest (now Belarus and Poland) was the last sanctuary for wild Lowland European bison in the beginning of XX century. (It does not mean, however, that it was the most adequate habitat). The first free-living herds of the species (Lowland subspecies, *Bison bonasus bonasus*) were re-established in the 1950s. Today, the forest complex is divided by a state border and a frontier fence (see Chapter 9.2.2). The territory of Belarus part of Białowieża Forest is sufficient for 200–250 European bison only, and that is not enough for long-time survival of the species. There are no other sufficiently large ranges for free-living populations of European bison in Belarus.

The main purpose of the regional Belarus State Programme on Resettlement, Conservation and Use of the European Bison (1998) is to establish 10–12 small (50–100 animals) free-living populations ("satellite micro-populations") of the Lowland line, connected with ecological corridors and treated as one population. Before 1994, 3 micro-populations of European bison had been established, in 2000 there were already 7, the process of enlarging their size and number continues today (see Fig. 14.1). In 2001, there were 520 European bison living free in Belarus. There has been some artificial exchange of Lowland line animals between all bison populations in Belarus and other herds situated elsewhere (Poland, Lithuania). Herds inhabiting national parks and reserves have the status of an insured species. Herds formed in managed forests were given the status of a reserve species; once their numbers sufficiently increase, there may be regulated hunting (Kozlo 1999, and pers. information).

Priorities of this project, running until 2005, include the formation of further micro-populations in this scheme, arranging contacts with other population of this genetic line (outside of Belarus), monitoring and scientific investigation of the process of re-introduction.

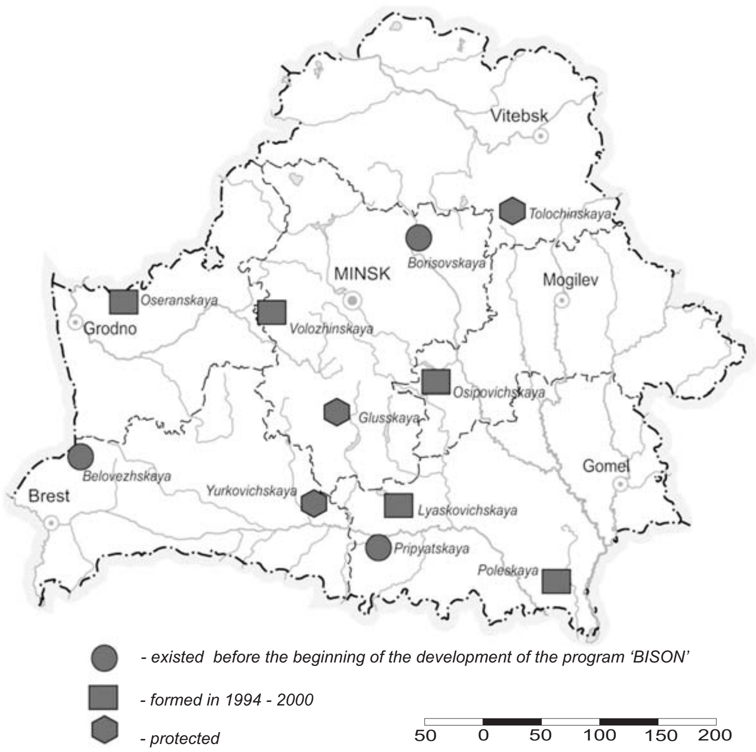


Figure 14.1.
Distribution of free-ranging populations of European bison in Byelorussia (acc. to P. Kozlo, pers. communication).

Lithuania

There is no official conservation strategy for European bison in Lithuania. The status of free-ranging animals is under discussion at the Red Data Commission of Ministry of Environment. It is worth noting that Lithuania is an exclusive example of the European bison's existence in a highly anthropogenic agricultural landscape, with different ecology and human dimension aspects.

Details on the status of the European bison, and the potential for the extension of its range in Lithuania, have recently been published (Balčiauskas 1999). European bison from Panevezys-Pasiliu migrate widely throughout Lithuania, and animals from Belarus or Poland (?) are spreading northwards into southern regions of the country (Fig. 14.2). This natural process is worthy of support and the new free-ranging herd in the region of the Bukta or Kalniškės forest is thought to be established. Together with Belarus and the herds in northern Poland, it could be a fragment of more compact range of the Lowland European bison. When Lithuanian bison herds increase in size their regulation by means of hunting and a change in the status of bison to a game animal is proposed (Balčiauskas 1999, but see also Chapter 10). There is also a project in Latvia aimed at restoring the large herbivore community, including re-introduction of European bison from NW Lithuania.

There is a need for a management plan for Lithuanian bison, which should include, among other tasks, new re-introductions, exchange of animals, scientific research, and monitoring.

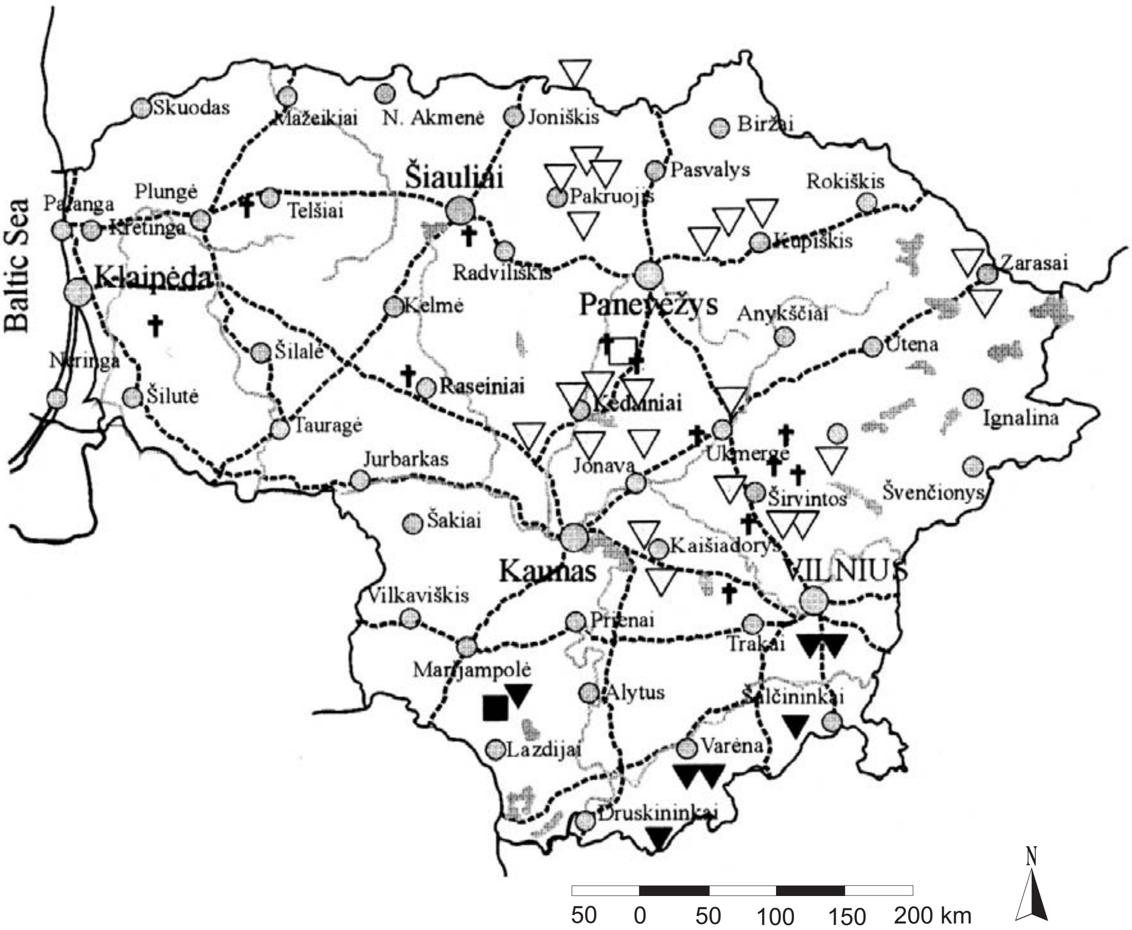
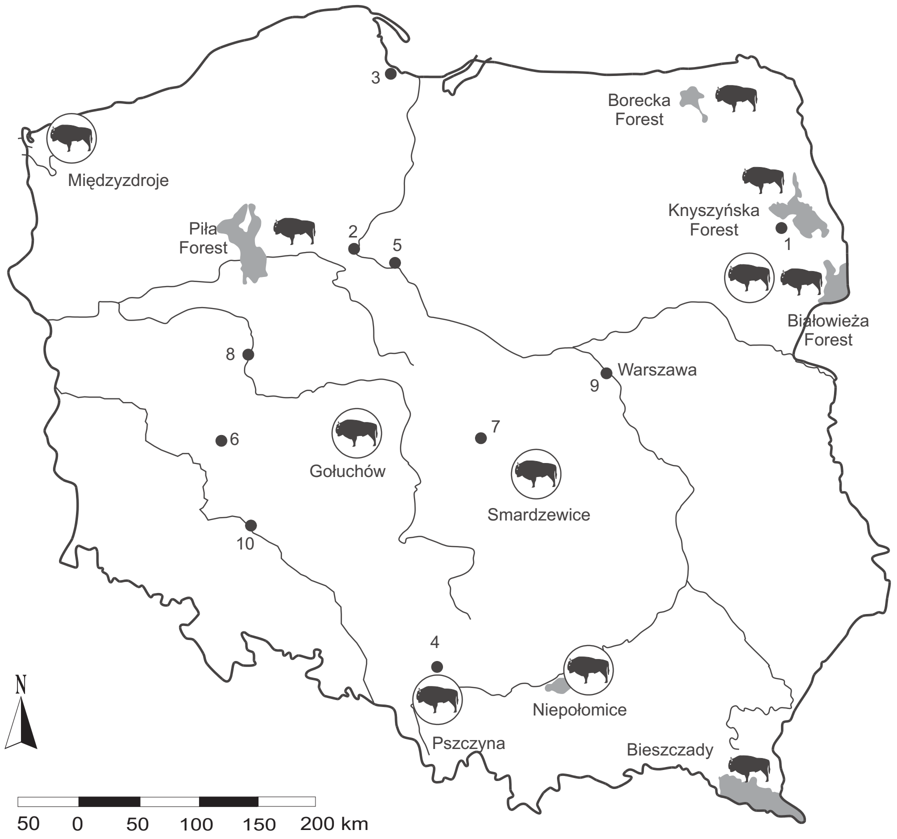


Figure 14.2.
Movements of free-ranging European bison outside the Pašiliari area and the proposed site for the new bison herd. † – places where bison were poached, shot or killed in accidents; (white) – places where bison of Lithuanian origin were seen alive; ▼(black) – visits by bison of Byelorussian (or Polish?) origin; □ – Enclosed Breeding Centre Pašiliali; ■ – the proposed centre of a new bison herd. (acc. to Balčiauskas 1999, and in litt.).

Poland

There is no official strategy for European bison conservation in Poland; although some ideas were previously presented (Pucek 1994). Below are the main points concerning how to better preserve bison in Poland.

The total number of European bison maintained in Poland at the end of 2000 was equal to 717, and for many years, it has been stable at this level (of 600–700 animals). There are five free-ranging herds (Fig. 14.3) containing 75–80% of all bison, six enclosed breeding centers (EBC) (17%) and 10 zoological gardens with approximately 5% of all bison. It has been suggested that all bison kept in enclosed centers and zoological gardens should constitute one breeding herd of known pedigrees, regulated according to a uniform conservative breeding programme (Olech 1997). The programme assumes the existence of a total effective population of approximately 100 bison in all EBC's with not less than 10 effective individuals in each centre. The mating system should be optimized by the exchange of bulls between centres and avoid the introduction of animals



Enclosed breeding centers

Reserve	Year of foundation
Białowieża	1929
Pszczyna	1865
Smardzewice	1934
Niepołomice	1938
Międzyzdroje	1976
Gołuchów	1977

Free ranging herds

Region	Year of foundation
Puszcza Białowieska	1952
Puszcza Borecka	1962
Bieszczady	1964
Puszcza Knyszyńska	1973
Lasy Pilskie	1983

• ZOO's

1. Białystok
2. Bydgoszcz
3. Gdańsk - Oliwa
4. Katowice
5. Toruń
6. Leszno
7. Łódź
8. Poznań
9. Warszawa
10. Wrocław

Figure 14.3.
Distribution of Enclosed Breeding Centres, free-ranging populations, and Zoos possessing European bison in Poland (acc. to Krasiński 1994, changed).

from free-ranging herds (i.e. animals of unknown pedigree). More than 60% of captive Lowland European bison are kept in Polish reserves and zoos. In consequence, Poland plays a special role in the breeding of this line. Unfortunately, the exchange of animals between countries is very limited, therefore, in the future, some attention should be focused on developing a coordinated, international network for the captive Lowland line.

Free-ranging populations are found mainly in the large forest complexes of Eastern Poland (the Borecka, Knyszyn, Białowieża and Bieszczady Forests) (Fig. 14.3). Limited contact may exist between Białowieża and Knyszyn Forest, while the distance to Borecka Forest is too great for bison migration. Contact of these herds with the population in Bieszczady is not recommended since only bison of the Lowland-Caucasian Line live there. Eastern Poland was recently suggested for prairie bison breeding but the governmental nature protection authorities did not allow it.

The enlargement of small groups of bison in Knyszyn Forest (up to 30–50) and Borecka Forest (up to 70 heads) has been suggested (Krasiński and Krasińska, 1992). The same concerns apply to the Wałcz herd (26 individuals in 2000). All these herds should increase in size and be incorporated into a meta-population if the genetic principles of long-term survival in viable populations of threatened species are accepted (see: Chapter 10)

Białowieża Primeval Forest plays a special role in European bison restitution in Poland. Both the historical aspects and the present size of the population contribute significantly to the whole forest complex – a future trans-border biosphere reserve. This population is also of great significance in the expansion of the Lowland bison population throughout the world. [In the post-war period until 2000, 434 bison were transported from the Białowieża to 11 countries, Z. A. Krasiński in litt.].

Białowieża Primeval Forest (now Poland and Belarus) is undoubtedly the last backwoods of the European bison, which deserves a special attention and priority there (Pucek 1993, 1994). The structure of the deer community and other models of game management and preservation in this forest complex should offer the best chances for the European bison to thrive.

Territory for further European bison re-introductions is limited to Northeastern Poland (Lowland bison) and to the Bieszczady (Lowland-Caucasian line). Extension of this range and attempts to form more free-ranging bison herds, which would facilitate contact between the already existing ones, is necessary for the progress of bison naturalization, but faced objections till now from those involved in the forest economy.

Lowland line bison in Polish EBC's have the same founder contributions and other characteristics as the rest of the world captive herd. Animals of the Lowland line are however strongly inbred. The inbreeding coefficient ranges mainly between 0.3 and 0.5 (Olech 1987, 1998). Therefore, cooperative action for the exchange of males in other countries has already started.

There is a necessity for a definite breeding policy within one European bison herd, covering all bison in Poland, centrally controlled with a supervised breeding system. Therefore, a European bison breeding and management centre should be established. The centre could be located in Białowieża National Park, which is the home of the international bison database and editorial board of the European Bison Pedigree Book.

Serious threats to the future of the European bison in Poland (and elsewhere) lie in its state of health. In the previous century, cases of epizooty were noted among bison in Białowieża Forest (Wróblewski 1927). Foot-and-mouth disease liquidated whole herds in Polish reserves in the 1950s (Jaczewski 1960, Podgurniak 1967). The disease affecting the male reproductive organs, manifested in the inflammation of the penis and prepuce leading to diphtheroid-necrotic lesions, is a new phenomenon revealed at the beginning of the 1980's in Białowieża Primeval Forest and in Nadworniański Forest (Ukraine) (Piusiński *et al*. 1997); its etiology has not yet been elucidated. Cases of tuberculosis were recently recorded in Bieszczady Mountains (Żórawski and Lipiec 1997). A decision has been made to eliminate the infected herd in the Brzegi Dolne Forest District (about 15 animals). Additionally, all dead bison found in the area of the Bieszczady Mountains are examined to determine the presence of TB.

The elimination of diseased animals can seriously affect a population's structure. To ensure that care is taken during such procedures, a system of elimination based upon sex and age groups/classes is recommended (Pucek *et al*. 1996b).

European bison breeding in Poland is lacking investment with regard to the equipment found in enclosures, means and methods of bison transportation, prophylactics and veterinary supervision. They currently receive food traditionally given to domestic animals, which is very different from the bison's natural diet composition. New methods for feeding captive animals and prophylactics should be developed, and the necessity of supplementary feeding of free-ranging herds during winter re-considered.

Russia Federation

The strategy for European bison conservation in Russia was prepared in 2000 and published in 2002, after acceptance by the Ministry of Environment (Strategy… 2002).

The Russia Federation (as a part of the former USSR) began the programme to re-establish European bison to the forest ecosystems of Europe about 50 years ago. Two large breeding centres worked to produce a stock of young animals annually, adapted for free-living conditions. These animals were used for establishing free-living herds in Carpathians, lowland Ukraine, Caucasus region (North Osetia, Chechnya). There has been a very rapid decline of free-living populations in the Caucasus region during the last few years (Table 10.2), and it appears the process cannot be stopped in this politically unstable region.

The main purpose of the regional Russian Action Plan for the European Bison is to preserve the species as a natural component of the European forest ecosystem, with maximum possible genetic diversity. This is intended to be reached through preserving existing populations and the foundation of at least two large (500 - 1000 or more animals) free-living populations. The populations should be designed to contain all the preserved genetic diversity and to have possibilities for a long-term viability and survival. Some areas have been already suggested for the foundation of new large free-living populations of the species in the European part of Russia. One of them is the territories of Brjansk, Smolensk, Kaluga, Novgorod and west part of Orel regions, in eastern part of the historical range of the species. Another possibility is the Vologda region (59°N). The broad-leafed forest of the Ural and Siberia could also be considered. (More detailed suggestions to be seen in Strategy…2002). The possibilities for the successful development of large free-ranging populations of European bison in Russia must be examined carefully. Some priority projects for 2002–2005 are indicated below:

Projects of the highest priority:

1. Population of European bison in Orel-Brjansk region:
   (a) Project of restoration of a large complex population on an ecological and genetic foundation (2000–2003);
   (b) Re-introduction and development of new free-living herds (2001–2005, and future years);
   (c) Continuous monitoring and scientific monitoring of the European bison population (years 2001–2005);
   (d) Extending this population into the north-east regions of Ukraine (for details, see under Ukraine).
2. The development of an experimental free-living population of European bison in the northern region of the European part of the Russia Federation (Vologda region):
   (a) Projects for establishing a large complex population based on ecological, behavioural and genetic backgrounds;
   (b) The reinforcement of the current experimental population with new animals and its development into a larger population;
   (c) Monitoring and scientific investigations of the bison population (years 2000–2005);
3. The reconstruction of European bison Central Breeding Centres in State Prioksko-Terrasny Biosphere Reserve and in Oka Reserve include:
   (a) The reconstruction of the reserve's territory;
   (b) The re-stocking of most breeding groups with animals of high genetic diversity or with rare genomes;
4. Monitoring and scientific investigation in all current Russian populations of European bison.

Romania

Four 'free-living' [!] European bison populations are located in Romania in *"The Atlas of European mammals"* (edited by Mitchell-Jones *et al.* 1999), according to information of D. Murariu and I. Coroiu. Neither of these 'populations' has been registered in the EBPB 2001. As far as we know, there is one European bison captive herd (162 ha enclosure) in Neagra-Bucşani Reserve, counting 45 animals (2000). Four animals are living in 4 ha enclosure in "Dragoş Voda" Vanatori-Neamt Reserve and four in Hateg-Slivut Reserve. Except those in Dragoş-Voda all Romanian bison are of unknown pedigree (R. Deju, in litt.). The National Strategy for Romania is under preparation and further aims are to enrich and create a larger herd in "Dragoş-Voda" Reserve to support general plan of reintroductions in Eastern Carpathians.

Slovakia

L. Brtek (in litt.) prepared a detailed conservation strategy for European bison in Slovakia. It includes active protection of animals migrating in a natural way from Poland (from Bieszczady Mountains), new re-introductions of animals from other countries and from EBC Topolčanki. This should lead to the formation of new free-living herds, in the eastern Carpathians on the Slovakian side of this mountain's chain and in National Park Poloniny, where European bison year round occurrence has been observed since 1997. Acclimatization enclosures are under construction there (near artificial Lake Starina). The programme also includes modernization of EBC Topolčanki (Brtek in litt.), which was unfortunately removed from EBPB in 2000 because of the lack of any official information.

Ukraine

The Carpathians and north-west Ukraine were selected for the re-introduction of European bison in 1965. Some free-living herds were established there, the others in the forest complexes of Polesie and one in the forest-steppe zone. All exist in areas containing hunting farms and exploited woods. The populations were successful in most cases, and were used for so-called "experimental/selective hunting". There are nine sub-populations of European bison in Ukraine, counting 9 to 138 individuals (in year 2000). Two of them account for more than 100 individuals and the other 2 for over 50 individuals (Tables 10.1 and 10.2). At the beginning of the restitution, the total number of bison doubled in 10 years (1971–1980), and later during 6 and 5 years (1980–1986 and 1986–1990, respectively. The maximum number of free-living European bison (664 animals) was registered in 1994; however, declined to 426 in the year 2000, due to social and economical instability, insufficient protection, and poaching.

There is a strategy for the protection and rebuilding of the European bison population in Ukraine, worked out by Specialist Group at the Ministry of Ecology and Natural Resources. It proposes the creation of new free-ranging and regulated populations in nature reserves of different landscape zones – one containing over 500 individuals in the Chernobyl Exclusion Zone, which is believed by Ukrainian aythorities as unique territory for such herd. This programme has not yet occurred, however, because of the many frequent changes in the authorities responsible for nature conservancy and little interest in bison restitution in this country. Even the European Bison Specialist Group has no information about research or management programmes for the species in Ukraine or about any regional Action Plan.

A special initiative and re-introduction programme was developed, covering the eastern Carpathians, including Polish Bieszczady Mountains, Slovakia, Ukrainian Carpathians and even Romania (Fig. 14.4). The suggestion to found a more continuous range for the species was expressed earlier (Pucek 1994, 1996) and is now in progress (Perzanowski and Kozak 1999, Akimov *at al.* 2001). However, such an approach is recommended only for bison herds in the Carpathians. Other Ukrainian herds are effectively isolated either due to considerable distances, or because of impenetrable barriers such as large rivers, highways, railroads or dense settlements (Perzanowski, Olech and Kozak, in prep.). In those cases, active management of the gene pool, including the controlled exchange of individuals, should be applied (Olech and Perzanowski 2002).

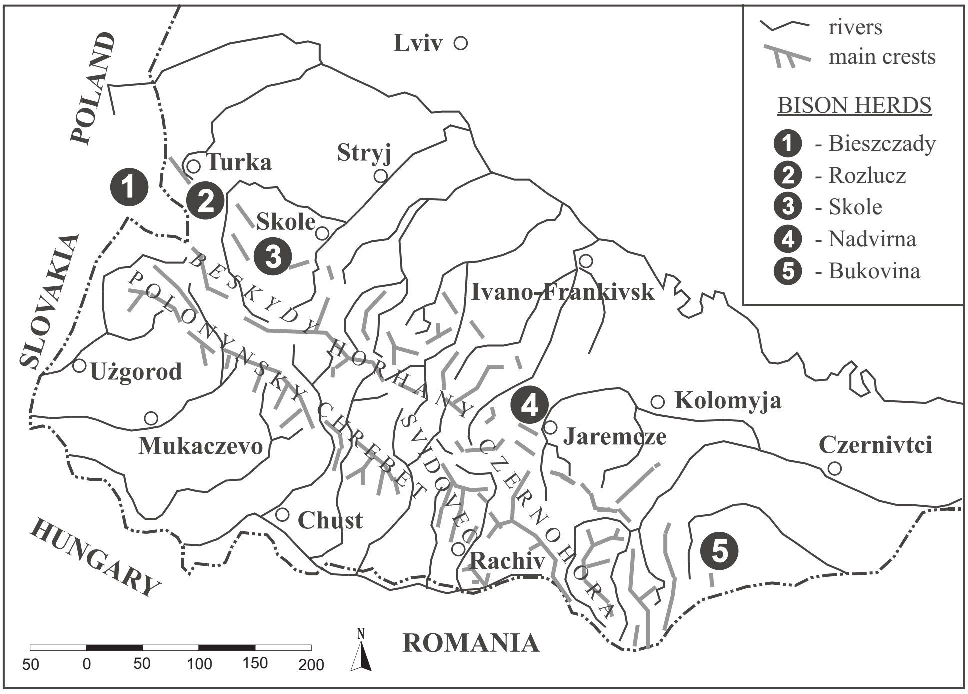


Figure 14.4.
Distribution of free-ranging herds of European bison in the Ukrainian Carpathians. Herds 2 and 3 are treated as one population in Fig. 9.4 and Table 10.2 (Majdanska). (acc. to Perzanowski and Kozak 1999, modified).

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Appendix I

Origin of the hybrids of North American and European bison in the Caucasus Mountains*

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and Marina M. Zablotskaya

Abstract. The last Caucasian European bison (*Bison bonasus caucasicus* Turkin *et* Satunin, 1904) was killed in 1927. In 1940 5 inter-specific hybrids of the European bison (*Bison bonasus* Linneus, 1758) and the North American prairie bison (*Bison bison bison* Linnaeus, 1758) were imported into the Caucasian Reserve. It was planned to conduct continuous absorptive crossing of these hybrids with European bison. This implied removal of hybrid males of each generation from the herd, to obtain animals close in exterior appearance to the European bison, and their subsequent release into the wild. This project failed to be implemented. In-breeding involved inter-specific hybrid males remaining in the herd. Only 43 hybrid males were eliminated from the herd. In 1948–1957 15 European bison males (Lowland-Caucasian line) were imported, but only two of them became significantly involved in the breeding programme. Consolidated breeding of inter-specific hybrids was initiated in 1964, although in this period there was divergence in the exterior appearance of animals either towards the European bison or towards the North American prairie bison. Thus, recent Caucasian animals are of hybrid origins and were bred by mating amongst them. They inherited a number of ethological and ecological features of the North American prairie bison. The hybrids cause negative changes in the Caucasian Biosphere Reserve's ecosystems. In 1959 a group of hybrids was imported from the Caucasian Biosphere Reserve to the Nalchik Forestry Game Management Unit. These hybrid animals (numbering over 1000 animals) endangered the genetic purity on the Caucasus populations of pure-blood European bison (totalling over 300). Complete elimination of the hybrids in the North Caucasus and replacement by pure-blood European bison is suggested.

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The mountain (Caucasian) subspecies of the European bison, *Bison bonasus caucasicus* Turkin *et* Satunin, 1904 populated a considerable area of the North Caucasus as far back as 17th century, from the Pshish River in the west to the Terek River in the east, and from the Inguri River in the south to Kuban River in the north (Ruzskij 1898, Satunin 1898, Dinnik 1910,). With clear-cutting of the forests, and increased population of these areas by Russian settlers, the range of this subspecies in the Caucasus region was sharply reduced in the northern and eastern parts of this range. By the end of the 19th century, due to more intensive human settlement in the mountains, the range of the Caucasian European bison (= Caucasian bison – for short) was reduced to roughly one tenth of its original range (Bashkirov 1939a). The eastern edge of its range became the Bolshaya Laba River and numbers also dropped sharply during this period. Although the numbers of Caucasian bison was 2000 – in the 1860s (Bashkirov, 1939a), it had dropped to 500–600 in 1917 (Silantyev 1919). It means nearly a fourfold decrease over a 50 yr period. In 1919 the herds of B. b. *caucasicus* suffered from epizootics of foot-and-mouth disease and anthrax introduced with domestic cattle brought into the mountains. Mortality of Caucasian bison from these diseases, and from poaching, reduced the population to 50 by 1921. Since it was difficult to organise conservation in 1922–1926, local poaching continued and in 1927, the three last Caucasian bison were killed (Bashkirov, 1939a). In 1924, when the Caucasian Reserve was established in the upper reaches of the Belaya and Malaya Laba Rivers for the conservation of the Caucasian bison, it was too late to save the mountain subspecies. Numerous expeditions over a 10-year period revealed that the Caucasian subspecies of the European bison had become extinct.

In the 1930s, the Caucasian Reserve launched a project to restore the European bison on its territory.

* Text presented in Russian at 2nd Conference of Bison Specialist Group, SSC/IUCN in Sochi, on 26–30 September 1988, and translated into English in 1990, but never published.

There were no pureblood European bison in the whole USSR at that time and no possibility of buying them abroad. On the suggestion of I. S. Bashkirov (1930b) females of inter-specific hybrids of European bison *Bison bonasus* and North American prairie bison *Bison bison bison* were used for this project. A herd of 60 hybrids, tended by stockbreeders, was maintained in the steppe reserve 'Askania Nova' in Ukraine, and used as initial stock. It was intended to obtain animals close in exterior appearance to the European bison, by consecutive absorptive crossing. This would involve using pureblood European bison as sires and then completely removing hybrid males from reproduction in each generation, in the fourth-fifth generation of consecutive back-crossing for the European bison according to the methodology of B. K. Fortunatov (1929). The term 'pure-bred' European bison (Zablotsky 1948) was proposed for the denomination of such animals. It was proposed to select among such, 'pure-bred' animals those that were close by type to the Caucasian subspecies (*Bison bonasus caucasicus*) in order to create a group of animals for release into the wild. During this period, at the stages of absorptive crossing and selection, the animals were to be maintained in semi-free conditions: herded by stockbreeders in summer and kept in an enclosure in winter.

However, the programme of absorptive crossing, selection and maintenance of the European bison was not fulfilled. The reasons were: (1) the impossibility of obtaining a pureblood European bison sires, (2) wartime difficulties.

In 1940 from the steppe reserve 'Askania Nova' 5 inter-specific hybrids of North American European bison were imported into the Caucasian Reserve: one male and three females of the second generation and one female of the first generation of absorptive crossing for the European bison. The share of European bison blood in these animals was equal from 48/64 to 54/64. Two females and one male from them had a small admixture of the blood of the Caucasian bison (Zablotsky 1939, 1948; Krainova 1947). Ancestors of all these hybrids, as well as of the bulk of the hybrids in Askania Nova were the North American prairie bison female called 'Staraya' [Old one] born in 1903 and the European bison 'Białystok' (EBPB no. 50) born ca 1899. Among subsequent ancestors there were both pure-blood European bison and pure-blood North American prairie bison, which were represented among ancestors of animals imported into the Caucasian Reserve in the ratio of 3.5:2 and 2:1. So, in fact, absorptive crossing have occurred for both the North American bison and for the European bison.

Such hybrids were brought into the Caucasian Reserve, and were maintained in an enclosure with a natural rangeland and supplemental feeding using concentrated feeds, mangle and hay in winter. In 1941 animals from the Moscow Zoo were evacuated into the Caucasian Reserve but during the journey they were infected by haemorrhagic septicaemia. This resulted in the death both of the evacuated bulls and of the hybrid male imported from 'Askania Nova'. The sire of the herd of hybrid females of the Caucasian Reserve became the young (1.5 years old) son of the hybrid male, which was imported from 'Askania Nova'. The blood for the European bison was lower in this young male born in the Caucasian Reserve (51/64) than that of his father (54/64).

Since the spring of 1942, a free keeping of the entire herd of hybrids in the forest out of the enclosure had been started (Krainova 1947). Supplemental feeding of this herd was completely discontinued in 1961 (Kalugin 1969). During the first 10 years, i.e. from 1940 to 1949, hybrids bred between themselves. The sire had a low share of European bison blood, equal to 51/64, and as a result the share of European bison blood in the herd as a whole decreased in comparison with imported group of animals (Krainova 1947; Kalugin 1965). From 1948 to 1959, 15 males of pure-blood European bison (Lowland-Caucasian line) were imported into the Caucasian Reserve (Kalugin 1968), but only two of the bulls 'Puszczanin' (EBPB no. 695) and 'Byerkut' (EBPB no. 800), became significantly involved breeding. Simultaneously with the European bison males, hybrids also took part in reproduction in the Caucasian herd (Kalugin 1965). From 1947 to 1965, only 43 hybrid males had been excluded from reproduction through export to zoological gardens, castration or shooting. By 1965 the total number of the hybrid herd constituted 449 individuals (Kalugin 1969). Since the sex ratio of hybrids was close to 1 : 1, there were no less than 200 hybrid males in 1965 in the Caucasian Reserve herd. Among them there were many robust animals in their prime, which later formed the main body of sires. The shooting of hybrid males was insufficient. According to decisions of the Central Board of Game Management of the RSFSR ('Glavokhota RSFSR'), the Caucasian Reserve should have had to shoot from 50 to 80 hybrid males annually, however only from 4 to 5, (maximum 8), males were, actually shot.

In 1960, name-by-name registration of calves born in the Caucasian Reserve was discontinued, and beginning in 1964 consolidated breeding of hybrids by mating them between themselves was initiated (Kalugin 1965, 1968, 1969).

According to the data of Kalugin (1965, 1969) the divergence in the exterior of hybrid animals both towards the European bison and the North American prairie bison was still noted. However, the genetic structure of the herd was heterogeneous, and this continues to be at the present. Thus, animals, which nowadays populate the territory of the Caucasian Biosphere Reserve, are a closed herd of inter-specific hybrids *Bison bonasus*   *Bison bison bison*, one of whose parental form is a steppe animal of Nearctic origin, and the other represent the recent Palaearctic fauna.

From their steppe ancestor, the hybrids inherited a number of ethological and ecological features. These were a greater extent of gregariousness, a particular mode of grazing and use of forage, high environment-forming activity and poor adaptability to the snow-abundant winter conditions of the mountain-forest habitat.

Are there grounds to believe that the hybrids of the Caucasian Reserve have become adapted to mountain--forest conditions, have become acclimatised in the Caucasian mountains and that their ecology has become balanced with the environment? All these questions can only be answered in the negative, since: (1) The hybrids of North American and European bison constantly migrate from the Caucasian Reserve down to the piedmont; (2) They periodically perish on a mass scale during severe winters. Over the last 20 years four winter periods have been recorded when, according to the Caucasian Reserve censuses, 24 to 30% of wintering stock died (Nemtsev 1988a, b). This was not, however a case, observed in other mountain-forest ungulates of the Caucasian Biosphere Reserve or in pure-blood European bison populations in mountain-forest regions of the Northern Caucasus, i.e. Northern Ossetia, Checheno--Ingushetia and in the Teberda Reserve; (3) Hybrids modify the environment intensively, causing the transformation of forest ecosystems to meadow ecosystems on wintering grounds and the disappearance of a number of herbaceous plant species (Dyrenkov, Durov, Pridnya – personal communications), depression of thickets of wild fruit-trees and young growth of the Nordmann fir and other woody plants. This brings about irreversible changes to the Caucasian Reserve's ecosystems.

In 1959, a group of hybrids (2 males, 3 females) from the Caucasian Reserve were transferred into the Nalchik Forestry Game Management Unit (Kabardino-Balkariya). Subsequently, some pureblood European bison of the Lowland-Caucasian (LC) line were released there to form a single mixed herd together with the hybrids.

The presence of herds of hybrids in the Caucasian Biosphere Reserve and in the Nalchik Forestry Game Management Unit (total individuals being + 1000, ca 1990), and their fast dispersal is hazardous to the genetic purity and the very existence of the populations of pureblood Lowland-Caucasian European bison (*Bison bonasus*) (numbering over 300). Therefore, the recommendation of complete elimination of the hybrids from the Caucasian Reserve, from the adjacent territories and from the Nalchik Forestry-Game Management Unit, and their replacement by pure-blood European bison of the Lowland-Caucasian (LC) genetic line (Zablotsky 1981, 1983; Zablotsky and Zablotskaya 1986a, b, 1987) should be urgently fulfilled.

It should be taken into account that inter-specific hybrids of the European bison and the North American prairie bison could cause irreversible disturbance of the native fauna and introduce changes in the Reserve's ecosystems. This is in irreconcilable contradiction with the status and goals of the Caucasian Biosphere Reserve. It should also be noted that in the Khopersky Reserve, a herd of hybrid animals with a high degree of European bison blood has already been eliminated, although this Reserve is not a biosphere one.

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Appendix II

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GENERAL BIOLOGY

A New Subspecies of the European Bison, *Bison bonasus montanus* ssp. nov. (Bovidae, Artiodactyla)

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Early in the 20th century, the European bison was completely exterminated in nature, and only a small group was preserved in some European zoos. Subsequently, the European bisons were maintained in breeding centers and a number of free-ranging populations were formed for return to the wild. To date, only the Lowland subspecies (*Bison bonasus bonasus* L.) and Lowland–Caucasian and Highland breeding lines of European bisons are preserved. The Lowland–Caucasian breeding line originates from hybrids between European bisons of the Lowland subspecies and one male of the Caucasian subspecies (*B. bonasus caucasicus* Satunin). The Highland breeding line consists of descendants from the Lowland subspecies, male Caucasian European bison, and three American bisons. The latter breeding line was formed in order to establish bisons adapted to highland conditions, stably inheriting their characteristics, and possessing morphological and functional features of the completely exterminated Caucasian subspecies [1]. In 1940, five hybrids between European and American bisons of the second and third generations of backcrosses targeted at the European bison were brought to the Caucasian State Nature Reserve and mated between themselves up to 1950. Subsequently, females mated with purebred Lowland–Caucasian bulls, whereas the resulting males were not used for breeding. As a result, the American bison admixture in the gene pool of the population was reduced to several percents [2]. In 1960, the animals were introduced in the natural ecosystems of the Caucasian State Nature Reserve, and this was the onset of the stage of a free-ranging Caucasian population. The development of this population resulted in the formation of the modern Highland breeding line, which has substantially deviated from the animals originally introduced in nature in the course of adaptation to the environmental conditions of the forest belt of the northwestern Caucasus [3]. Rapid changes of the population in the natural environment were probably promoted by the destabilization of the adaptive norm in the founders, which was caused by hybridization and subsequent selection of pairs for backcrosses.

In the present study, we consider the distinctive features of the Highland breeding line of European bisons and substantiate the assignment of this line to a new subspecies of European bisons, *Bison bonasus montanus* ssp. nov.

We examined the skulls of adult animals from the natural populations stored at the Caucasian State Natural Biosphere Reserve, Maikop; National Museum of the Republic of Adygeya, Maikop; Zoological Institute of the Russian Academy of Sciences, St. Petersburg; Paleontological Institute of the Russian Academy of Sciences, Moscow; Zoological Museum of Moscow State University; and the Belovezhskaya Pushcha, Kamenyuki (Belarus): (1) 15 male and 19 female Highland European bisons collected in 1968–1994; (2) 57 male and 50 female Lowland European bisons (*Bison bonasus bonasus*) from Belovezhskaya Pushcha, 1832–1998; and (3) 32 males and 23 females of the Caucasian subspecies, *B. b. caucasicus* (before 1927). The data on the American plains bison (*Bison bison bison*) were used for comparison. The skulls of European bisons born and raised in breeding centers were excluded from the study, because preliminary analysis showed that they substantially differed from bisons of both modern and extinct natural populations. We analyzed data on 61 measurements, including those proposed by Gromova [4] and used in previous studies on European bisons [5, 6]. It was impossible to obtain a complete set of measurements for each skull because the material was not completely preserved; therefore, the sample sizes varied for different measurements. We calculated the mean of each measurement for either sex of each subspecies and estimated the significance of differences between the sample means using the t-test for independent samples. The measurements characterized by the highest significance ($p < 0.001$) of differences between the means for the Highland European bisons and other subspecies were included in the diag-

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nosis of the new subspecies. Discriminant analysis was used to create a graphic representation of differentiation among the European bison subspecies; data processing was performed with the use of the applied software package STADIA 5 [7].

Bison bonasus montanus Rautian, Kalabuschkin, et Nemtsev, ssp. nov.

Etymology. From Latin *montanus* (highland, mountain).

Holotype. NMRA (National Museum of the Republic of Adygeya), no. 12128/2, skull of adult male; Caucasian State Natural Biosphere Reserve, Taivan' Stow; December 14, 1988.

Diagnosis. Occipital crest elongated; on average, 216 ± 9 in males and 195 ± 6 in females (hereinafter, measurements are given in millimeters). Nasals and middle part of nasals long, 203 ± 11 and 125 ± 7 in males and 193 ± 9.0 and 117 ± 6 in females, respectively. Forehead between postorbital constriction and lateral edge of occipital crest short, 90 ± 3 in males and 71 ± 4 in females. Bases of male horn cores narrow, 209 ± 18 in circumference. Length of parietal small, 67 ± 8 in males and 59 ± 6 in females. Width of forehead between horn cores and minimum width and minimum height of occiput, on average, same as those of Lowland European bisons and substantially smaller than those of Caucasian subspecies, 295 ± 19, 161 ± 17, and 137 ± 7 in males; and 236 ± 20, 134 ± 7, and 121 ± 4 in females, respectively. Distance from nasal process of premaxilla to nasal bone shorter than that of Lowland European bisons and substantially longer than that of Caucasian subspecies; 30 ± 11 in males and 29 ± 9 in females.

Comparison. *Bison bonasus montanus* ssp. nov. is distinguished from both Lowland and Caucasian subspecies by a substantially longer occipital crest (Tables 1, 2, measurement A3), longer middle part of the nasals (A13), and a shorter distance between the postorbital constriction and the lateral edge of the occipital crest (A4). In addition, males of the new subspecies are characterized by narrower horn cores (G21); females are characterized by a shorter parietal (G16) and an intermediate morphological facial axis (G36). Besides the measurements listed, the Highland European bisons of either sex surpass the Caucasian subspecies in the diagonal length and width of forehead between horns (A1 and G14), minimum width and minimum height of the occiput (G17 and G19), and the distance from the nasal process of the premaxilla to the nasal (A16). The new subspecies differs from the Transylvanian–Carpathian subspecies (*B. bonasus hungarorum* Kretzoi, 1946) by its larger measurements [8].

Remarks. The major part of the gene pool of modern Highland European bisons originates from *B. bonasus bonasus*; however, the founders of this form included three American bisons, the genetic contribution of which to the population originally introduced was several percents [2]. Approximately the same genetic contribution was made by the founder named Caucasus belonging to the Caucasian subspecies (the genetic contribution of each founder was calculated on the basis of a complete pedigree of the population). At the same time, distinctive features of modern Highland European bisons cannot be explained by the admixture of American bisons. Actually, certain measurements of *B. b. montanus* differ from those of *B. b. bonasus* and *B. b. caucasicus* by smaller mean values (A4, G16, and G21), whereas the means of these measurements in American bisons are higher. Regarding the measurements in which *B. b. montanus* surpasses *B. b. bonasus* and *B. b. caucasicus* (i.e., A3, A13, and G38), the American bisons are characterized by higher mean values; however, skulls of the latter are also substantially larger [4, 9]. Therefore, relative values of these measurements in American bisons are smaller than those of

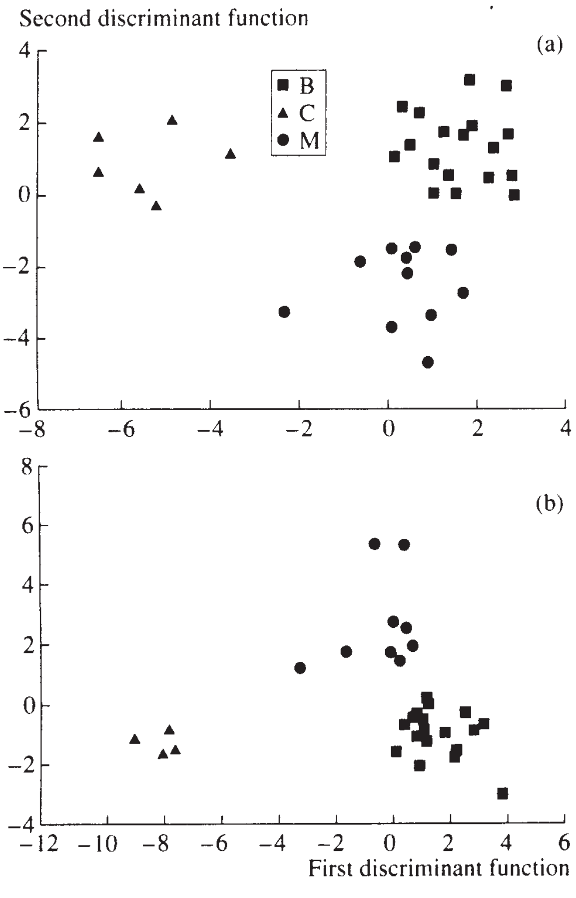

Fig. 1. Scatterplot of Highland, Caucasian, and Lowland European bisons obtained by means of discriminant analysis on the basis of a set of measurements: (a) males; (b) females; (B) Lowland, (C) Caucasian, and (M) Highland subspecies.

Table 1. Skull measurements in male (M) *Bison bonasus montanus* ssp. nov., (B) *B. b. bonasus*, and (C) *B. b. caucasicus*

Measurement, nos. after [4, 6]*	Subspecies of European bison						Significance of differences (*p*) between			American bison	
	M		B		C						
	n	*X*	*n*	*X*	*n*	*X*	B–C	M–B	M–C	*n*	*X*
G11	15	307.1	54	310.1	34	296.9	0.002	0.628	0.073	8	347.5
G14	15	295.9	27	283.2	20	256.7	0.000	0.028	0.000	3	351.5
G16	14	66.9	27	78.6	22	68.0	0.000	0.000	0.693	3	99.5
G17	15	161.1	52	166.7	27	137.2	0.000	0.224	0.000	9	182.5
G19	13	137.1	27	135.2	12	126.3	0.001	0.433	0.000	3	159
G36	13	306.1	25	293.8	9	302.9	0.046	0.008	0.593	3	343.5
G38	9	203.2	26	185.8	5	194.7	0.043	0.000	0.206	3	204.5
A1	15	168.3	53	166.9	21	151.5	0.000	0.595	0.000	8	173.9
A3	15	216.2	52	202.6	23	201.1	0.529	0.000	0.000	8	215.8
A4	15	90.5	51	98.8	23	97.8	0.535	0.000	0.000	8	107.8
A13	9	125.9	50	106.1	8	97.9	0.032	0.000	0.000	8	116.9
A16	14	29.7	39	34.0	16	12.1	0.000	0.177	0.000	3	38
B	15	73.0	53	72.9	19	66.7	0.000	0.964	0.000	8	80.6

* The measurements: G11, maximum width of forehead; G14, forehead width between horn cores; G16, parietal length; G17, minimum width of occiput; G19, minimum height of occiput; G36, morphological facial axis; and G38, nasal length (according to Gromova [4]; A1, oblique length of forehead; A3, length of the occipital crest; A4, length of forehead between the postorbital constriction and the lateral edge of the occipital crest; A13, lateral length of the middle part of the nasals; A16, distance from the nasal process of the premaxilla to the nasal; and B distance between the posterior incisure of the palatine (according to Puzachenko and Rautian [6]).

European bisons. The admixture of American bisons is not expressed in the exterior, fur, and coloration of *B. b. montanus* [3]; with respect to these parameters, they are similar to Lowland (for example, an uneven convex frontal surface of the skull bearing certain depressions and wavy or weakly twisted fur) or Caucasian (the hair of the beard no longer than 25 cm and some other characteristics) European bisons. Notwithstanding the fact that the population initially introduced into nature had approximately the same admixture of American bisons and Caucasian subspecies of European bisons, modern Highland European bisons undoubtedly show resemblance to the latter and lack almost any trace of contribution of American bisons. This indicates that the characteristics of Caucasian European bisons were not only inherited, but also developed in the course of adaptation to the natural environment typical of the latter subspecies. In addition, this gives indirect evidence for the conspecificity of Caucasian and Lowland subspecies of European bisons and their specific independence from the American bison. We used discriminant analysis to give integral characteristics of the relationships between Highland, Caucasian, and Lowland European bisons. The data on males and females were processed independently (Fig. 1) for the skulls for which all measurements considered were available (Tables 1, 2). In both males and females, the individuals belonging to each subspecies form a relatively compact group isolated from the groups of other subspecies. Thus, the set of parameters used in this study allows one to distinguish European bisons of different subspecies. Unfortunately, we could not compare *B. bonasus montanus* with *B. b. hungarorum* because of the absence of a complete set of data on the latter. However, *B. b. hungarorum* is similar to *B. bonasus caucasicus*, being distinguished from the latter by its smaller measurements [8]; this allows one to assume its substantial differences from the Highland European bison.

Materials. In addition to the holotype, 14 skulls of adult males and 19 females, stored in the collection of the Adygei Division of the Caucasian State Natural Biosphere Reserve (Maikop).

Distribution. Northwestern Caucasus, Caucasian State Natural Biosphere Reserve and adjacent territory with the total area of 250000 ha.

CONCLUSION

Thus, *B. bonasus montanus* is similar in morphological characteristics to the Caucasian and Lowland subspecies of European bisons and lacks specific features of American bisons; it presents an original form that can be confidently assigned to the species *Bison bonasus*. The close relationship with modern European bisons is corroborated by the data on genetic differentiation, i.e., the genetic distances between the European bison populations of the Lowland and Lowland–Caucasian breeding lines approximately equal to the distances between each of them and the populations of *B. b. montanus* [10–12].

Table 2. Skull measurements in female (M) *Bison bonasus montanus* ssp. nov., (B) *B. b. bonasus*, and (C) *B. b. caucasicus*

Measurement, nos. after [4, 6]*	Subspecies of European bison						Significance of differences (p) between			American bison	
	M		B		C						
	n	X	n	X	n	X	B–C	M–B	M–C	n	X
G11	19	257.9	47	263.7	21	243.2	0.000	0.083	0.001	3	281.3
G14	17	235.9	25	241.1	15	211.1	0.000	0.271	0.000	1	261
G16	18	59.4	24	69.5	13	66.7	0.156	0.000	0.003	1	72
G17	19	133.9	47	140.5	18	112.0	0.000	0.027	0.000	4	151
G19	16	121.6	25	123.1	4	110.0	0.000	0.408	0.000	1	136
G36	15	294.9	24	282.2	8	281.6	0.868	0.000	0.006	1	314
G38	10	193.6	23	181.0	4	181.0	0.991	0.001	0.047	1	202
A1	19	153.9	46	155.3	9	141.4	0.000	0.528	0.000	4	153.5
A3	19	195.3	47	182.1	10	177.3	0.083	0.000	0.000	4	192.0
A4	19	70.9	47	79.5	10	75.1	0.031	0.000	0.041	4	81.3
A13	10	117.6	44	102.9	4	91.1	0.040	0.000	0.000	4	113.5
A16	16	28.9	51	35.1	9	9.8	0.000	0.042	0.000	2	33
B	19	67.5	47	71.1	9	62.7	0.000	0.025	0.042	4	78.3

* For designations of the measurements, see Table 1.

The Highland subspecies of European bisons was distinguished on the basis of morphological differences (Fig. 1) and adaptation to specific environmental conditions of the highland forest belt of the Caucasus, where it has become a natural component of the ecosystems. The characteristic features of Highland European bisons can be interpreted as a result of adaptation of the plain-dwelling *Bison bonasus* to the conditions of highlands. The changes involve general skull lightening and elongation of the facial depart. In males, the braincase measurements (forehead and occiput) are almost the same as in the Lowland subspecies of European bisons; in females, some of them decreased and became intermediate between those of Lowland and Caucasian females. Apparently, this reflects the existence of certain barrier to a rapid (several generations) decrease in braincase measurements. The head of Highland European bisons lightened by decreasing the thickness and length of the horn cores and certain measurements associated with these parameters down to values unknown in the other forms of the genus *Bison*. The facial part of skull has become closer to that of the Caucasian subspecies, i.e., rapid changes of these measurements and horn cores are not forbidden. The extension of the occipital crest (in comparison with those of the ancestral forms) is attributable to the development of muscles raising the head, which is heavier than in *B. b. caucasicus*. We may assume that, in the course of further adaptation to the environmental conditions of the Caucasus, a similarity between the latter subspecies and *B. b. montanus* will increase. This conclusion is based on the fact that a number of features characteristic of the Caucasian European bison were observed in the extinct Transylvanian–Carpathian subspecies (*B. b. hungarorum*, Kretzoi, 1946); in the course of adaptation to highland environmental conditions, the latter independently acquired relatively small sizes, a slender constitution, a flat frontal skull surface, short and curly fur, a brush at the tail end, etc. [8].

The data considered in this study are noteworthy as a precedent of the taxonomic fixation of the products of an anthropogenic microevolutionary process. In the case considered, this was intentionally induced by humans [1]. Nevertheless, the key stage of the establishment of the new subspecies, i.e., the stabilization of effective reproduction of the species phenotype, occurred in natural conditions under the control of natural selection. In the future, increasingly more intense and often unintentional intervention of humans in the course of natural evolution (although anthropogenic in some cases) inevitably puts the problem of the inventory of new forms of biological diversity on the agenda.

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