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EVALUATION OF THE INFLUENCE OF DEMOGRAPHIC FACTORS ON THE SUCCESS OF REINTRODUCTION OF SMALL HERDS OF EUROPEAN BISON

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Abstract. The aim of the study was to determine the optimal size and composition of founding groups to create new herds of European bison. The computer simulations of the development of new herds in a period of 20 years was conducted with VORTEX software. The initial size of the founding groups N_0, sex ratio (M:F) and carrying capacity (K) impact on the new population development was estimated. The expected level of preserved heterozygosity (EH) and the risk of extinction of these populations were also analyzed. It was proved that the most favorable founding group considering the growth rate, the highest level of expected heterozygosity and the lowest level of extinction probability are those with small prevalence of females. The influence of carrying capacity on population growth rate was observed only in the most numerous founding groups.

Key words: European bison, population viability analysis, reintroduction, small populations, VORTEX

INTRODUCTION

Currently, the number of endangered animal species is continuously increasing and many of them has already gone extinct. Although the extinction of species is a natural process, it is now caused mainly by the human activities and expansion, which leads to habitats destruction and fragmentation, populations overexploitation and introduction of alien species. The endangered animal

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populations can be characterised by small size, which is equal to low genetic diversity, which in turn leads to an increase in the extinction probability [Mackenzie et al. 2005]. It is therefore necessary to develop conservation programs and manage populations in a way so they preserve their biodiversity as well as to recreate natural/free living populations of such kind. When approaching the restitution of a free living population usually the biggest problem is small number of the animals that could create a new herd. Because of the small initial number such herds are especially vulnerable to extinction as a result of demographic factors (age, male to female ratio, reproduction level, size of the population), genetic factors (inbreeding and limited genetic diversity) and random events (natural disasters, catastrophes, poaching etc.). Considering this, before establishing a new herd and the attempt to introduce it into a natural habitat it is necessary to determine its most favourable composition (animals age, male to female ratio, initial population size) in order to ensure high population growth rates and at the same time maintaining the highest genetic diversity level possible. Therefore it is necessary to quantitatively assess the impact of the used population establishing strategy and its management on its survival.

The PVA computer programmes (Population Viability Analysis) are useful tools in forecasting the fate of a population. They use various mathematical models in order to estimate the development of population dynamics and allow to precisely assess its viability. The priority in the protecting measures is usually to minimise the risk of the extinction of an endangered species, whilst the PVA programmes allow the attribution of a particular extinction risk value (%) to a chosen scenario – a way of establishing of a population with various assumptions for the starting group (age, male to female ratio, population size, inbreeding level). The mean prognosis of a population growth (SD $\pm$) is obtained by multiple repetitions of the simulation (10,000 times). The choice of a particular data set in PVA programme depends on the species, its condition, detailed project requirements as well as quantity and quality of the data concerning the species. In order to create a population prognosis it is necessary to collect long-term demographical data for the particular species, preferably in its natural conditions, or for similar species. The present study used the data set VORTEX [Lacy et al. 2005] with a stochastic model in order to create prognoses concerning the development of small herds of European bison (*Bison bonasus*). The European bison is an example of a species which experienced a bottleneck in its history, was extinct in the wild and reintroduced after years. Currently living population originates from 12 founding animals and is divided into two genetic lines: a lowland and a lowland–caucasian lines [Olech 2003]. According to the data in the European Bison Pedigree Book for the year 2012 [Raczyński 2013] there were 4987 bison in the world, of which 3102 in the wild. The analyses carried out in the study aimed at establishment of the optimal size (N_0) and composition (M:F) of the founding group in such a way that the chances of the population survival and the rate of its development were highest in a particular carrying capacity (K) and the loss of heterozygosity (EH) was possibly lowest.

MATERIAL AND METHODS

The simulations of the population development were carried out using the demographic parameters defining a free living European bison lowland line population in Białowieża. The data was taken from PHVA for European bison [Pucek et al. 1996] and the parameters were calculated according to the data collected since the beginning of the herd existence. The analysis of the data revealed that on average 47.2% (SD = 9.7%) of the females participate in reproduction in a particular year, which was included in the simulations. It was assumed that 100% of the males participated in reproduction. It was also assumed that the sex ratio at birth equals 1:1 [Krasiński and Raczyński 1967]. The mortality applied in the simulations in the sex/age classes are presented in Table 1.

Table 1. Mortality rates (%) in the free-ranging Białowieża population in 1984–1993 [Pucek et al. 1996]

Tabela 1. Wskaźniki śmiertelności (%) w wolnej populacji żubrów w Puszczy Białowieskiej w latach 1984–1993 [Pucek i in. 1996]

Age class – Klasa wieku	Females (SD) – Samice (SD)	Males (SD) – Samce (SD)
0–1	10.32 (5.98)	9.40 (6.70)
1–2	3.53 (3.00)	7.04 (6.84)
2–3	6.55 (5.53)	3.29 (3.72)
3–4	3.87 (2.68)	3.66 (5.42)
4–5	–	5.85 (5.87)
Adults – Dorosłe	3.74 (1.68)	5.19 (2.03)

Each scenario was repeated 10.000 times, there was no critical population size defined and a population was considered extinct in case of individuals of only one sex remaining in the herd. All of the scenarios assumed that the close relatedness had a negative influence on the population development. The inbreeding was taken into account as a lethality equivalent LE as it most commonly causes lower fertility and decreases survival of the offspring in the first year of life and its mean value for the lowland line animals born between 1996–2002 was equal 0.48 [Olech 2003]. The value of 3.14 was applied, as it was calculated for 40 isolated mammal herds by Ralls et al. [1988].

The simulations were carried out for the founding groups with the initial size N_0 between 3 and 8 mature five–year old individuals with various male to female ratios. The development of the herds took place in the conditions of various carrying capacity (K = 30, 50, 100, 200, 500; SD = 10%). The comparison criteria for the scenarios were the three basic indices of a population viability: expected heterozygosity – EH [%], population extinction risk – PE [%] and population size – N reached in the period of 20 years. There was also the effective population size N_e calculated for all of the founding groups according to the formula:

$$N_e = \frac{4 \cdot N_m \cdot N_f}{N_m + N_f}$$

where N_m is the male number and N_f is the female number.

According to the definition the effective population size is the one which in an ideal population would cause the same sample variability or the same inbreeding increase as observed in the studied population [Falconer 1974]. The founding groups with the same effective size N_e were compared in order to check whether the populations with inverted sex ratios and identical initial size N_0 ensure the same herd development with special regard to the level of maintained heterozygosity.

RESULTS AND DISCUSSION

Small populations are especially vulnerable to the loss of genetic diversity, which is a result of parents generation passing onto their offspring only a portion of the gene pool. The more numerous the offspring the bigger part of the parental genetic material is passed onto the progeny and preserved in the herd gene pool. Therefore it is important that the newly-established herd could have the highest possible growth rate in its first generations, until it reaches the carrying capacity (K). Because each individual possess only a portion of the genetic diversity characteristic for the species the founding herd should be created with the possibly highest number of animals [Ralls and Ballou 1992, Ballou and Foose 1995, Lacy 1995].

Table 2 shows the influence of the population size N_0 and the male to female ratio of the founding group as well as the carrying capacity K on the expected heterozygosity level (EH) in the population after 20 years and on the initial heterozygosity (H_0) depending on the founding groups sizes. The presented values show that the populations created from only 3 or 4 animals in the studied period preserve the lowest part of the variability, wherein having less than 90% of heterozygosity at the beginning. The percent of the retained variability was dependent on the polygamy ratio in the founding herd, the female prevalence had a positive influence on its value whilst the carrying capacity did not show a significant impact.

In the populations with $N_0 = 5$ and $N_0 = 6$, similarly to the smaller populations, the level of preserved diversity was mainly dependent on the male to female ratio in the founding herd whilst the differences between particular scenarios resulting from the carrying capacity limitation were no larger than 1%.

Table 2. The expected levels of populations heterozygosity E H (SD) [%] preserved after 20 years from establishment, depending on the size N_0 and sex ratio in the founding groups and carrying capacity K

Tabela 2. Oczekiwany poziom heterozygotyczności EH (SD) [%] zachowanej w populacji żubra w ciągu 20 lat od jej utworzenia, w zależności od liczebności początkowej N_0 i stosunku poligamii w stadzie założycielskim oraz pojemności środowiska K

N_0(M:F)	H_0	EH (SD) for K = 30	EH (SD) for K = 50	EH (SD) for K = 100	EH (SD) for K = 200	EH (SD) for K = 500
3 (1:2)	83.3	72.3 (7.3)	72.3 (7.5)	72.3 (7.4)	72.2 (7.4)	72.4 (7.2)
3 (2:1)		69.5 (8.9)	69.5 (8.9)	69.6 (9.0)	69.7 (8.9)	69.4 (9.0)
4 (1:3)		76.9 (6.0)	77.2 (5.9)	77.4 (5.8)	77.4 (5.8)	77.4 (5.6)
4 (2:2)	87.5	77.2 (6.9)	77.2 (6.8)	77.1 (7.1)	77.3 (7.0)	77.2 (6.8)
4 (3:1)		72.9 (8.2)	72.9 (8.3)	72.9 (8.3)	72.9 (8.1)	73.0 (8.2)
5 (1:4)		79.7 (5.0)	80.5 (4.7)	80.5 (4.7)	80.5 (4.7)	80.5 (4.7)
5 (2:3)	90.0	81.3 (5.2)	81.7 (5.1)	81.8 (5.1)	81.7 (5.2)	81.7 (5.3)
5 (3:2)		79.8 (6.2)	80.0 (6.4)	80.0 (6.3)	80.0 (6.4)	80.0 (6.4)
5 (4:1)		75.0 (7.8)	75.1 (7.9)	75.1 (8.0)	75.0 (7.9)	75.1 (7.8)
6 (1:5)		81.6 (4.4)	82.4 (4.2)	82.6 (4.1)	82.6 (3.9)	82.6 (4.0)
6 (2:4)		83.7 (4.0)	84.4 (3.9)	84.6 (4.0)	84.5 (4.1)	84.6 (4.0)
6 (3:3)	91.7	83.6 (4.5)	84.1 (4.6)	84.2 (4,7)	84.2 (4.6)	84.1 (4.7)
6 (4:2)		81.6 (5.9)	81.9 (5.8)	81,9 (5,9)	81.8 (6.0)	81.9 (5.9)
6 (5:1)		76.5 (7.7)	76.7 (7.6)	76,6 (7,5)	76.8 (7.6)	76.7 (7.5)
7 (2:5)		85.1 (3.6)	86.1 (3.4)	86.4 (3.3)	86.4 (3.4)	86.5 (3.3)
7 (3:4)		85.7 (3.5)	86.5 (3.5)	86.8 (3.4)	86.7 (3.5)	86.8 (3.6)
7 (4:3)	92.9	85.0 (4.2)	85.6 (4.3)	85.7 (4.2)	85.7 (4.3)	85.7 (4.3)
7 (5:2)		82.8 (5.6)	83.1 (5.6)	83.1 (5.5)	83.1 (5.6)	83.2 (5.6)
7 (6:1)		77.7 (7.4)	78.0 (7.1)	77.9 (7.1)	77.9 (7.2)	77.7 (7.3)
8 (1:7)		83.5 (3.9)	84.8 (3.3)	85.3 (3.1)	85.3 (3.1)	85.3 (3.1)
8 (2:6)		86.0 (3.2)	87.3 (2.8)	87.8 (2.8)	87.8 (2.8)	87.8 (2.8)
8 (3:5)		86.9 (2.9)	88.0 (2.8)	88.4 (2.7)	88.4 (2.7)	88.4 (2.9)
8 (4:4)	93.8	86.9 (3.2)	87.9 (3.0)	88.1 (3.2)	88.1 (3.1)	88.0 (3.2)
8 (5:3)		86.1 (3.9)	86.6 (4.0)	86.7 (4.1)	86.7 (4.1)	86.7 (4.0)
8 (6:2)		83.8 (5,2)	84.0 (5.5)	84.0 (5.6)	84.0 (5.5)	84.0 (5.4)
8 (7:1)		78.9 (6.9)	78.7 (7.2)	78.7 (7.1)	78.7 (7.1)	78.6 (7.2)

In the groups with the biggest initial size $N_0 = 7$ and $N_0 = 8$ the maximum differences in the variability preserved at the end of the 20 years period varied according to the initial male to female ratio and the carrying capacity K and were equal 9.1 and 9.8%, respectively. The increasing difference between the extreme EH values indicates that with the increase of the initial group size its composition becomes more important as it influences the level of variability preserved in the herd. The obtained results also show that the carrying capacity does not influence significantly the preserved heterozygosity in the studied period. In case of the largest studied founding groups ($N_0 = 8$) the differences between the scenarios resulting from a habitat capacity limitation ranged from 0.3 to 1.8%. For each N_0 value the influence of the target population size on the level of the preserved genetic diversity decreases with the increase of the male participation. Its highest impact was observed in the herds with only one male.

Figure 1 shows the influence of the population size and the polygamy ratio in the founding group on the expected heterozygosity level preserved at the end of the 20 years studied period in the habitat with the capacity K = 100. The EH value depends of the initial herd size, the lower the N_0 the lower the variability level potentially preserved in the population. In the founding groups with equal N_0 the observed significant differences in EH values are due to the sex ratios, whilst the herds with only one female always preserved the smallest part of the initial gene pool. The highest values of the analysed parameter were observed in case of the herds with the sex ratio equal or close to 1:1 and those with the females prevalence. The groups with the identical effective size (N_e) but reversed sex ratios do not guarantee the preservation of the same H_0 part. The tendency is clear even in the smallest initial herds ($N_0 = 3$) where with the same $N_e = 2\frac{2}{3}$ the differences in the EH values between the scenarios reached 3%. In the groups with a higher initial size the differences are even larger, like in the population with $N_0 = 8$ with the male to female ratio 1:7 where the preserved heterozygosity equals 83% and in case of a reversed ratio about 7% less.

Many endangered species breeding programs aim at preserving 90% of the genetic diversity of the existing initial population through a period of 200 years [Soulé et al. 1986, Ralls and Ballou 1992], but sometimes this objective can be adapted to be less demanding, i.e. preserving the 90% of variability through a period of 100 years. None of the analysed scenarios of creating new European bison populations guarantees fulfilling this requirement. The compared founding groups are small and even at the start some of them have less than 90% of the genetic diversity of the population from which they originate. None of the groups with H_0 >90% preserved the required parameter value even for 20 years. The retained genetic diversity could be raised by increasing the founding groups size, however, it is not always possible to obtain an appropriate number of animals at once. In such cases it may be useful to apply the rule commonly used in endangered populations management: 'one immigrant per generation' (OMPG) [Mills and

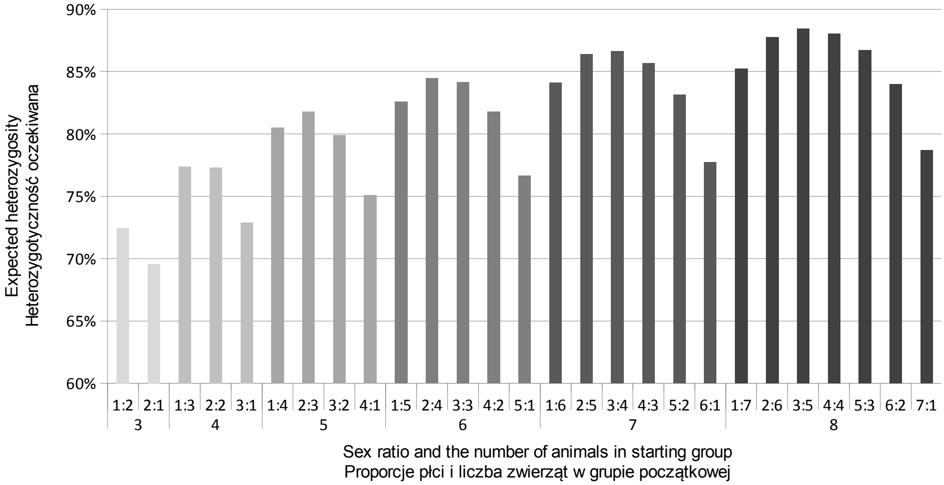

Fig. 1. Founding group size and sex ratio influence on the expected heterozygosity retained in the population after 20 years (carrying capacity K = 100)

Rys. 1. Wpływ liczebności i stosunku poligamii w grupie założycielskiej na poziom zmienności genetycznej (heterozygotyczności) zachowanej w populacji w okresie 20 lat (K = 100)

Allendorf 1996], which enriches the population by introducing additional individuals [Wang 2004 for Wright 1931]. In case of lack of the immigration channels or too large distances between the populations the natural migration is impossible, therefore only human-caused individual exchange between populations can guarantee the movement of the animals as well as preservation of the genetic diversity.

In case of European bison, which is a polygamous species, the growth rate depends mainly on the females of reproductive age, and they must be at the core of the founding group. The European bison females can have one offspring a year, however, even in the free herds in Białowieża, which has high reproduction indices, usually the females have one offspring every second year (fertility 47.2%). The groups of the same N_e value but reversed sex ratios do not exhibit the same potential to create new populations despite the identical effective size. An exemplary group with a 2:6 male to female ratio after 20 years of development will reach the size of 60 individuals whilst a group with the reversed sex ratio has a lot lower growth potential. The male prevalence leads to the population reaching the size of only 24 individuals in the same period of time and carrying capacity.

The expected size reached by the European bison populations in the period of 20 years is presented in Figure 2. The new European bison populations created from the smallest starting groups did not reach the size equal to the smallest ana-

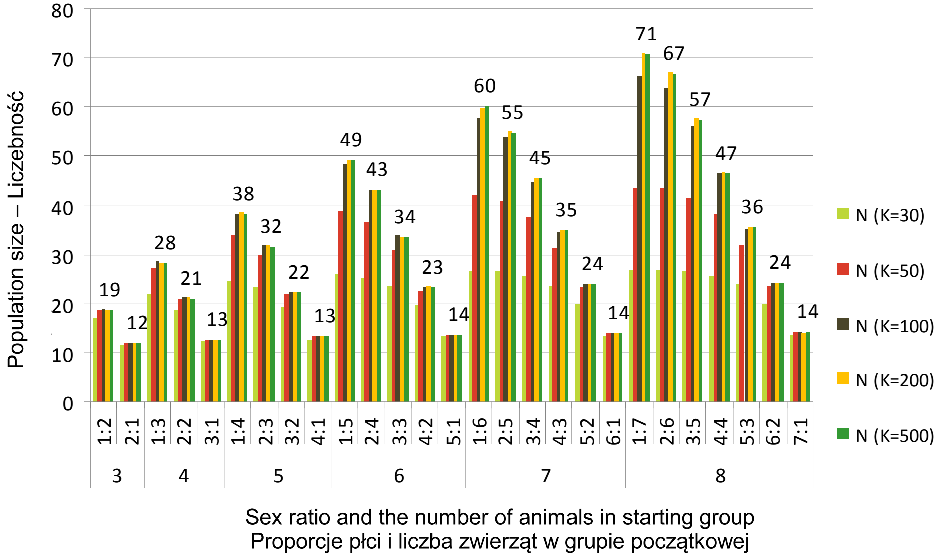

Fig. 2. The average population size after 20 years, depending on the initial size N_0 and sex ratio in the founding group and carrying capacity K

Rys. 2. Przewidywana liczebność osiągana przez populacje żubra w ciągu 20 lat, w zależności od liczebności N_0 i stosunku poligamii w stadzie początkowym oraz dostępnej pojemności środowiska K

lysed carrying capacity of 30 individuals, regardless of the polygamy ratio or the habitat capacity. When $N_0 = 5$ and 1:4 and 2:3 polygamy ratios the populations developing in the habitats of capacity higher than K = 30 did reach or exceeded the size of 30 animals. Regardless of the N_0 and K, the herds that initially only had one or two females did not increase in size in the examined period of time. None of the populations increased in size to the point that would fulfil the capacity K = 100 of the habitat. The size of 50 individuals when $K \geq 100$ was only exceeded by the populations created according to the five most favourable scenarios for the populations of $N_0 = 7$ (1:6, 2:5) and $N_0 = 8$ (1:7, 2:6, 3:5).

In order to visualise the influence of the possible target population size, there were two different herd creation scenarios chosen (Fig. 3). The first one with $N_0 = 3$ and 2:1 sex ratio seems to be the least favourable for the predicted herd survival, quick increase in size as well as the level of the heterozygosity preserved in the population. The curves showing the population growth at all carrying capacities during the first 20 years overlap, which is a result of a very low growth potential of such a population. Regardless of the K value none of the populations created this way in the analysed period reached the minimum target size and finally they consisted of 13 to 14 individuals. The second scenario, with $N_0 = 8$

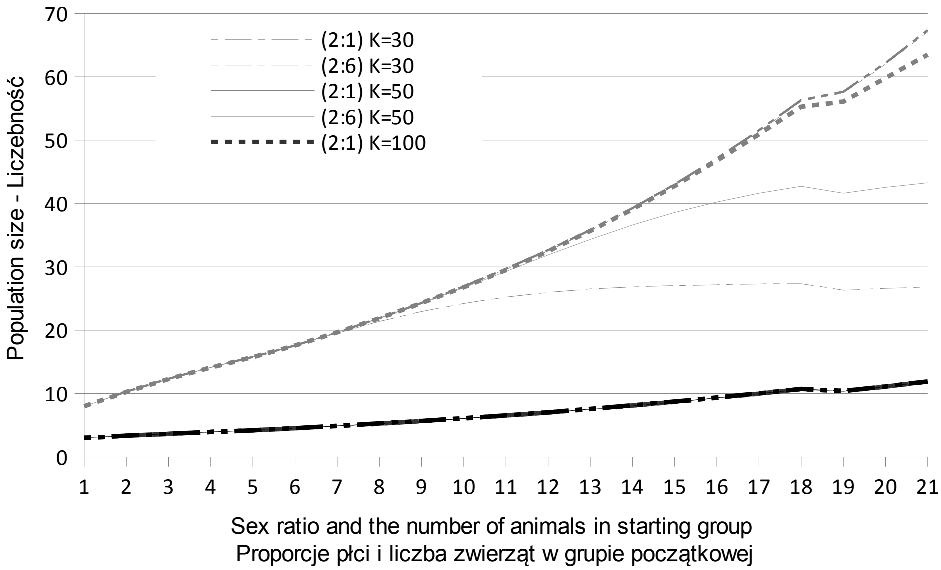

Fig. 3. Growth of a population started with 3 (2:1) and with 8 (2:6) animals, in 20 years period, at different carrying capacities (K)

Rys. 3. Wzrost liczebności populacji utworzonej z 3 (2:1) oraz z 8 (2:6) zwierząt w okresie dwudziestu lat w zależności od pojemności środowiska (K)

and 2:6 guarantees high survival chances and quick increase in size as well as preservation of a large portion of the original gene pool. In this scenario the herds growth is almost identical at any K value for the first 7 years, when they reach size of 21–22 individuals. It is caused by a high growth potential of the group resulting from large initial size N_0 and female prevalence. At the end of the studied period the herds reached size of 27 to 67 individuals and only K = 30 and K = 50 capacities significantly limited their increase in size.

The results of the simulations show that in the 20 years period the carrying capacity of a habitat is not a factor determining the risk of extinction of a new population. As the Figure 4 shows the probability of a population extinction differed significantly between the scenarios and ranged between 0.06 and 26%, however, it remained at a similar level within the same scenario and the differences resulting from the habitat capacity limitation were no higher than 2%. More significant differences were observed between the scenarios within the groups with similar N_0. In the herd with $N_0 = 8$ the differences reached even 20% as 3:5, 4:4 as well as 2:6 sex ratios guaranteed the survival success at a level of 99% and higher, whilst 7:1 ratio lead to less than 80% survival success. For the smaller founding groups the risk of extinction is very high. An extremely high extinction risk of 30% concerns the smallest group, with $N_0 = 3$ and 2:1 polygamy ratio.

Figure 4 shows that the most favourable composition of the group for each initial size is the one with a slight females prevalence. The more males participate in the reproduction the higher the risk of extinction of the population. High extinction risk is also observed in cases in which the founding group contains only one individual of either sex. It is the highest if there is only one female participating, regardless of the group size.

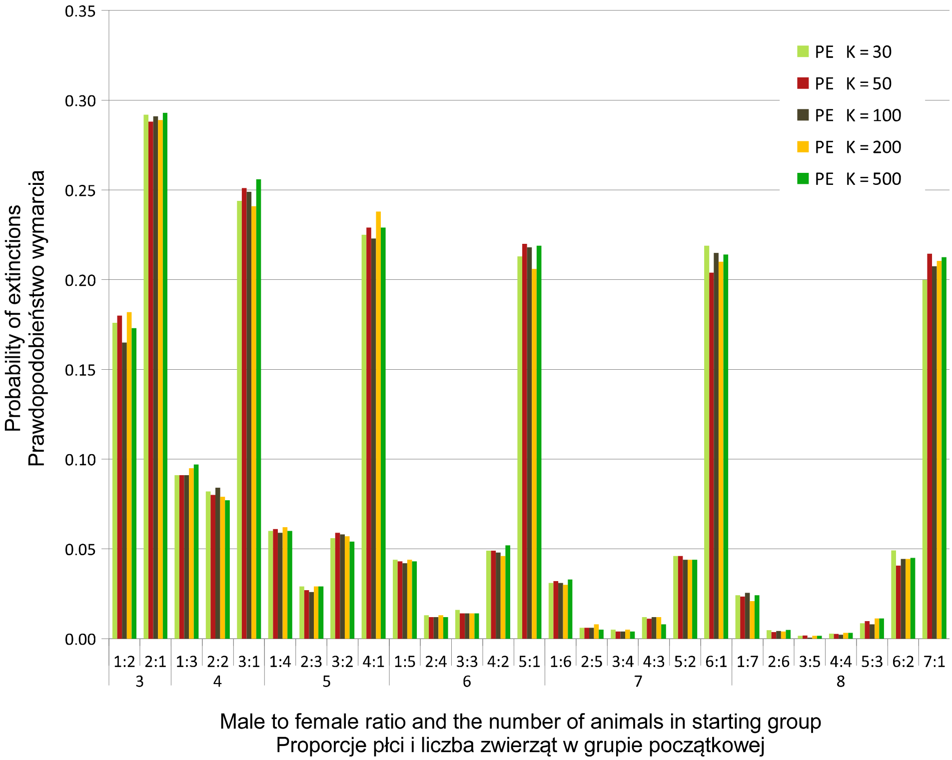

Fig. 4. New populations extinction probability over the 20 year period depending on the initial size N_0 and sex ratio of the founding group and carrying capacity K

Rys. 4. Prawdopodobieństwo wymarcia (PE) tworzonych populacji w ciągu 20 lat od ich utworzenia w zależności od wielkości i stosunku poligamii w grupie początkowej oraz pojemności środowiska (K)

On the basis of the conducted analyses it can be concluded that in a short period of time the carrying capacity K of a habitat does not influence the studied population vitality rates or that the influence is minimal. The increase in impact is proportional to the founding group size and the changes in the sex ratio (female prevalence). In long periods of time the carrying capacity gains importance; if low, it causes the loss of genetic diversity and does not allow a free population growth, but even in case of the smallest capacity (K = 30) it does not negatively influence the population probability of survival.

Many authors emphasise that apart from the habitat capacity it is also its quality that is essential for a population survival. Studies of the causes of slow growth of mountain zebra (*Equus zebra zebra* L.) population in the Gamka Mountain reserve showed that no more than 30% of the reserve area fulfils zebra's dietary requirements [Watson et al. 2005]. The results of Fahring's simulations [2001] show that the most important factors for survival of divided or dispersed populations are the reproduction level and the level of migration, which have to be supported by a diverse habitat with variety of plants and with little factors directly affecting migrant mortality (traffic, poaching). The author also claims that in particular circumstances a habitat smaller even by 58% can ensure a population survival if only its quality was significantly improved, therefore the preservation and habitat reconstruction should be one of the priorities in species protection.

The growth rate of the newly created populations is particularly important in case of small populations, which are the most vulnerable to extinction. The studies of the initial population size and the age and sex structures on the growth rate of newly reintroduced ungulates populations (European bison, forest bison, mouflon) show that the population growth rate increases with the number of released animals and when the group consists of more mature individuals with female prevalence [Komers and Curman 2000]. According to this, in order to increase the reintroduction success it is recommended to create herds of minimum 20 individuals, with a larger share of mature animals and a sex ratio close to 1:1. The chances of success are also increased in case of releasing 40 animals divided into two groups. However, in the mentioned study the authors assumed the habitat capacity was unlimited which is very difficult to obtain in case of European bison. Daleszczyk [2009] on the other hand claims that it is most advantageous to reintroduce European bison herds with 1:2 sex ratio. Saltz [1996] conducted research on minimizing the risk of extinction of reintroduced Mesopotamian fallow deer (*Dama dama mesopotamica*) herds as a result of demographic stochasticity and concluded that in the polygamous species the population growth depends mainly on females, whose maximum number in an initial herd is very significant.

CONCLUSIONS

The founding group size and its composition have an impact on all of the analysed indices: the herd growth rate, the chances of the population survival in a particular time and the level of the preserved genetic diversity. Because the stage of the individuals selection for the reintroduction is the first one in which the future faith of the herd can be influenced, the number of the released animals should be as high as possible. The initial herd should count at least 6–8 animals and have a slightly oblique sex proportion with female prevalence (62–75% female participation is the most advantageous), because their number and condition determine the herd growth rate, the level of preserved variability as well as the herd survival in the studied period. In case of a founding herd consisting of 6 European bison females should constitute $\frac{2}{3}$ of the number, in case of a founding herd consisting of 8 animals either 6 or 4 females guarantees a high herd growth rate.

On the basis of the obtained results recommendations can be developed regarding the choice of a habitat for new European bison populations. An ideal habitat should allow high population growth rates in the first years of its development, therefore it is beneficial for the habitat to be of a capacity K = 100. Because of obvious problems with finding many such places the habitats of K = 50 can also be considered sufficient, however, even the smallest habitat capacity K = 30 gives high chances of the reintroduction success. Where possible, the carrying capacity should be increased, which could be obtained through creation of metapopulations. It should be emphasised that through appropriate monitoring it is possible to support a small herd by adding new animals, therefore the herd can be sustained in a long period of time even if it was of a small initial size.

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OCENA WPŁYWU CZYNNIKÓW DEMOGRAFICZNYCH NA SZANSE PRZETRWANIA REINTRODUKOWANYCH MAŁYCH STAD ŻUBRA

Streszczenie. Celem pracy było znalezienie optymalnej grupy założycielskiej do tworzenia nowych stad żubra. Symulacje rozwoju stad obejmujące okres 20 lat przeprowadzono przy pomocy programu VORTEX. Oceniano wpływ wielkości i proporcji płci w stadzie początkowym N_0 (M:F) oraz pojemności środowiska (K) na tempo wzrostu nowopowstałych populacji. Analizowano również poziom zachowanej zmienności genetycznej (EH) i ryzyko wymarcia (PE) nowopowstałej populacji. Dowiedziono, że najkorzystniejsze z punktu widzenia zarówno tempa rozwoju, poziomu zachowanej heterozygotyczności, jak i najmniejszego ryzyka wymarcia populacji są grupy założycielskie z niewielką przewagą samic. Wpływ pojemności środowiska na tempo wzrostu nowej populacji był widoczny tylko w najliczniejszych grupach założycielskich.

Słowa kluczowe: analizy trwałości populacji, małe populacje, reintrodukcja, VORTEX, żubr

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