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Some factors influencing reproductive parameters of European bison cows

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Abstract: Reproduction is one of features important for species survival that may be affected by various factors. In this study were analysed reproductive parameters of female European bison based on the long-term data from the captive breeding centre in Białowieża National Park. The study focused on looking for factors influencing fecundity and the sex of offspring and an attempt was made to estimate differences in costs of raising daughters versus sons. Age of bison females influenced significantly their fecundity, with cows 5–13 years old being most fecund. Age at first calving did not affect the fecundity coefficient based on the entire reproductive lifespan of a female. No correlation was found between the fecundity and inbreeding coefficients of a cow. There was no difference in the mean age of cows giving birth to male or female calves. Calving date influenced the reproductive status of a cow the next year. Cows calved on average 39 days later before barren than before parturient years. On the other hand, reproductive status of the cow influenced her calving date in the next year. Calves were born on average 38 days later after parturient than barren years, indicating the cost of reproduction borne by mothers of all calves. However, sex-biased maternal investment was not found. The sex of a calf did not influence the reproductive status of the female or the sex of the calf born next year. The length of interbirth intervals after birth seemed to be influenced more by individual variation of cows than by the sex of their offspring. No difference was proved in the length of interbirth intervals before the birth of calves of different sex, so the length of gestation and prenatal investment seem to be similar in both sexes. Analysis of birth sex ratio of offspring of various cows revealed that ratios were not homogenous among the progenies and data as a whole did not fit the expected sex ratio 1:1; however, factors influencing it were not found. There was no correlation between the inbreeding coefficient of a female and birth sex ratio of her offspring. Further research on factors affecting European bison reproduction is needed and should include a variety of external factors.

Key words: *Bison bonasus*, reproduction, fecundity, sex ratio of offspring, maternal investment

Introduction

Nowadays the world population of European bison *Bison bonasus* numbers about 4200 individuals (European Bison Pedigree Book, 2009); however, there are still many threats to the species' survival, among others, limited gene pool, distribution in small and isolated populations, and health problems (Pucek *et al.* 2004). Reproduction is one of features important for species survival that may be affected by various factors. Reproduction of European bison was extensively analysed by Jaczewski (1958) and Krasiński and Raczyński (1967). Results of those papers include, among other things, assessment of the length of pregnancy and oestrus cycle, age of sexual maturity for males and females, timing of the rutting season, distribution of parturitions during a year, fecundity level of cows of various ages, and description of sexual behaviour.

There is a variety of factors that may influence the pregnancy of a female and sex of her offspring. Clutton-Brock *et al*. (1983) found that in red deer hinds parturient last year showed substantially lower fecundity than barren hinds. The effect of successful reproduction on subsequent fecundity was most pronounced among young and old hinds; they were less likely to calve the following year than females 7–13 years old. Trivers and Willard (1973) suggest that females with small litter sizes, like bison, and in better body condition tend to produce more male than female offspring due to maternal energy investment. Maynard-Smith (1980) claims that if the fitness of sons and daughters depends differently on parental investment, it will be evolutionarily stable to invest differently in the two sexes. However, maternal quality may have greater influence on the future quality of daughters rather than sons (Hewison, Gaillard 1999) and growth rates in ungulates may be too high to allow mothers for extra investment in offspring (Byers, Moodie 1990). Regarding American bison, Green and Rothstein (1991a) found little support for the prediction based on Trivers-Willard hypothesis that maternal investment would be biased towards sons, because it appeared that mothers were able to influence the condition of daughters more than of sons. On the other hand, Rutberg (1986) suggests that male bison require more parental investment to be raised successfully because they are considerably larger than females by the age of 5 months and suffer higher mortality in their first year.

The European bison seems to fulfil the basic conditions for Trivers-Willard hypothesis to work. It is a dimorphic (Krasińska, Krasiński 2002), polygamy species, and the reproductive success of a male depends on his position in dominance hierarchy established temporarily in mixed groups during the rutting season (Caboń-Raczyńska *et al.* 1987).

Long-term data on reproductive parameters of female European bison from the captive breeding center of Białowieża National Park (BNP) could allow the analysis of some possible factors influencing fecundity, the sex of offspring and costs of raising daughters versus sons in this species.

Material and Methods

This study was mainly based on data from the European bison captive breeding center of BNP in 1986–2003. The breeding centre includes breeding reserves inaccessible to visitors as well as the show reserve open for tourists. The breeding reserves are divided into 8 enclosures of various sizes (from 3.64 to 54.7 ha, average 18,56 ha). The area is mostly covered with mixed coniferous forest, with glades serving as pastures. In the show reserve the section for European bison comprises 6.14 ha and is divided into 4 adjacent enclosures, partly covered with trees. During the vegetative season bison feed on natural vegetation, supplemented with crushed grain according to individual demands. In winter bison are fed on hay, beetroot and crushed grain.

The data comprised 30 cows; data for four youngest cows were used only in analysis of age of first calving. In analyses of inbreeding influence the database increased to 45 cows bred in the breeding centre of BNP in 1929–2010 (Tabl. 1). Age of all cows was exactly known. Reproductive lifespan was the number of years a cow lived after the age of two (Clutton-Brock et al. 1988). Barren years were defined as years in which females of reproductive age did not reproduce, and parturient years as years in which females calved (Green, Rothstein, 1991a). Fecundity coefficient of a female was calculated as the percentage of parturient years within her reproductive lifespan. In some analyses data for fecundity coefficient was limited to a shorter period (stated in the text) because of changes in fecundity with age. Interbirth interval was the number of days from the first day after one calving to the last day before the next calving. In our analysis only intervals between parturitions taking place in successive years were taken into consideration.

Tests used in statistical analysis are given together with the results. Before conducting parametric tests data were checked for normality and transformed appropriately when necessary. To compare frequencies, replicated goodness--of-fit test (G-statistic) and R x C test of independence using G-test were utilised (Sokal, Rohlf 1995). To allow calculation of G-test in analysis of birth sex ratio of bison offspring, in the case of 4 cows with no offspring of one sex one calf was added to each sex class. Coefficients of inbreeding were calculated with FSpeed Pro software (2003–2005).

Results

Females calved for the first time when they were 3–5 years old (mean = 4.04) so the reproductive part of a female bison's life was assumed to start potentially in her third year. Age of females influenced significantly their fecundity (Fig. 1), with cows 5–13 years old being most fecund. The percentage of females that calved two years in a row followed the same pattern and differed from 29% in females 3 years old to 88% in females 8–9 years old (G-test = 13,31, df = 6, $p < 0.05$). Age at first calving did not influence the fecundity coefficient of a female and for cows calving for the first time at the age of 3, 4, and 5 years mean fecundity coefficients were 62%, 66% and 53%, respectively (ANOVA $F_{2,21} = 1.22$, NS). No correlation was found between the fecundity and inbreeding coefficients of a female (Tabl. 1, $r = -0.2$, NS). Calving date influenced the reproductive status of a cow the next year. Cows calved on average 39 days later before barren than before parturient years (t-test = 3.27, df = 111, $p = 0.001$). On the other hand, reproductive status of the cow influenced her calving date in the next year and calves were born on average 38 days earlier after barren than after parturient years (t-test = 3.66, df = 132, $p < 0.0005$).

Table 1. Data on 45 cows bred in the European bison breeding center in Białowieża in 1929–2010, used in correlations between inbreeding coefficient of a female and her fecundity coefficient (based on the number of calves that survived the first week of life) or between inbreeding coefficient of a female and birth sex ratio of her offspring (given as percentage of males).

Pedigree number and name of a cow	inbreeding coefficient	fecundity coefficient	birth sex ratio of offspring [% of males]	number of years to determine fecundity coefficient and birth sex ratio of offspring
93 BISERTA	0	0.63	50.0	8
161 BISCAYA	0	0.9	22.2	10
519 POGANKA	0	0.6	57.1	10
520 POLANA	0	0.7	28.6	10
736 PODWIKA	0.312	0.8	50.0	10
737 PLAMKA II	0.484	0.7	57.1	10
740 POŚWIATA	0	0.9	33.3	10
770 POPIELICA	0	0.7	50.0	10
831 POZŁOTA	0.252	0.7	85.7	10
909 POCIECHA	0	0.4	60.0	10
912 KAMIONKA	0.406	0.75	33.3	8
939 POLANKA	0.453	0.4	50.0	10
975 POKUSA	0.195	0.43	80.0	7
1862 POWOLNA	0.283	0.7	28.6	10
1983 PODZWONNA	0.117	1	50.0	10
1984 POCIĄGŁA	0.123	0.5	60.0	10
2112 POLARNA	0.196	0.8	22.2	10
2248 POKRZYWA	0.289	0.6	33.3	10
2851 POPULARNA	0.308	0.57	50.0	7
3042 POMARAŃCZA	0.117	0.3	25.0	10
3278 PORADA	0.117	0.25	100.0	8
3751 POMONA	0.233	0.57	0.0	7
3963 PONTAWA	0.274	0.4	0.0	10
4954 POLONIKA	0.271	0.6	42.9	10
5155 POLENTA	0.264	0.8	55.6	10
5349 POMARA	0.312	0.6	28.6	10
5853 POGORIAII	0.318	0.6	71.4	10
5855 POLOPIRYNA	0.371	0.5	20.0	10
6125 PODNIEBNA	0.277	0.8	62.5	10
6127 POCZESNA	0.366	0.89	37.5	9

Table 1. (cd).

Pedigree number and name of a cow	inbreeding coefficient	fecundity coefficient	birth sex ratio of offspring [% of males]	number of years to determine fecundity coefficient and birth sex ratio of offspring
6128 POLICZNA	0.318	0.3	50.0	10
6603 POPRAWA	0.318	0.5	33.3	10
7380 PODANA	0.338	0.5	60.0	10
7381 POSTURA	0.338	0.4	25.0	10
7383 POGŁOSKA	0.277	0.57	20.0	7
7384 PODLEGŁA	0.344	0.5	33.3	10
7386 POSTAWA	0.344	0.5	40.0	10
8567 POLWITA	0.376	0.5	42.9	10
8568 PONTYJKA	0.382	0.3	50.0	10
8944 POKRYWKA	0.360	0.6	50.0	10
8945 POKUTNA	0.376	0.7	42.9	10
8946 PODPAŁKA	0.299	0.4	85.7	10
8951 POCHODNA	0.329	0.3	66.7	10
9170 POMYŁKAII	0.245	0.5	25.0	8
9172 PODLASIANKA	0.258	0.56	100.0	9

There was no difference in the mean age of cows giving birth to male or female calves (mean = 7.83, range 3–16, n = 59; mean = 7.78, range 3–16, n = 83; respectively). If offspring of one sex is more costly for bison cows than another, mothers would be expected to be barren more often after giving birth to the calves of the more costly sex. Bison cows were barren 37% of the time after male calves and 31% after female calves, and the difference was not significant (G-test = 0.36, df = 1, NS). Interbirth intervals after male calves were longer than after female calves when pooled data from all cows were analysed (ANOVA $F_{1,77} = 5.18$, $p = 0.03$), but the analysis within cows performed for females with offspring of both sexes did not confirm this result (Wilcoxon matched pairs test T = 23.00, Z = 1.26, N = 12, NS) and comparison of those cows revealed significant inter individual variation in their intervals (ANOVA $F_{11,49} = 2.06$, $p = 0.042$). If the length of pregnancy in bison cows differs between male and female calves, interbirth interval before their births could reflect it. However, interbirth interval did not differ before the birth of calves of various sex (data pooled: ANOVA $F_{1,77} = 1.12$, NS; analysis within cows: Wilcoxon matched pairs test T = 32.00, Z = 0.09, N = 11, NS).

Analysis of birth sex ratio of offspring included 275 (126, 149) calves from 45 cows (Tabl. 1) and revealed that ratios were not homogenous among the

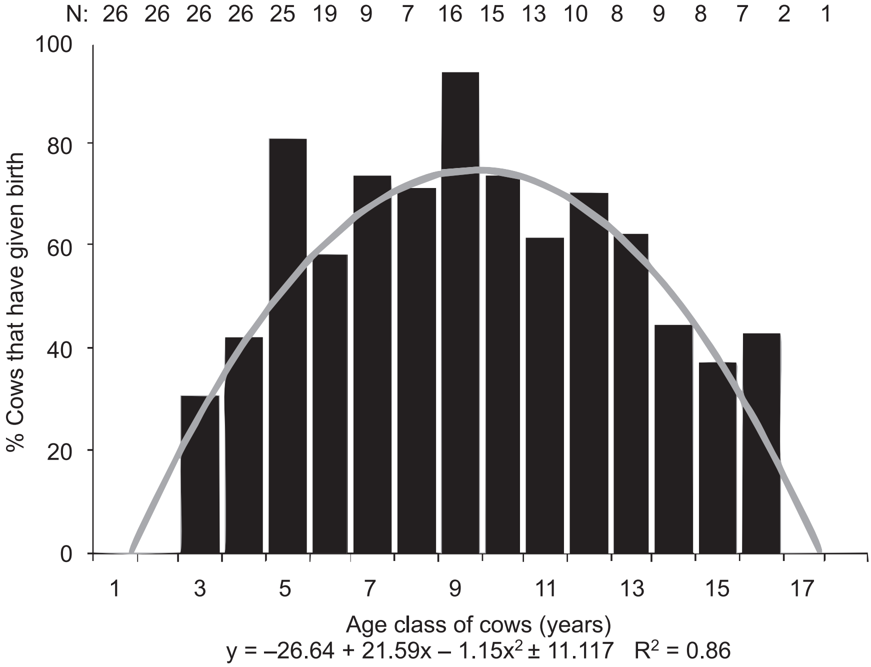

Figure 1. Percentage of female European bison of various ages that have given birth. Based on the data from the captive breeding center of Białowieża National Park from 1986–2003. Sample size is given above each bar.

progenies (G-test for heterogeneity = 63.85, df = 44, $p < 0.05$) and data as a whole did not fit the expected sex ratio 1:1 (total G-test = 65.72, df = 45, $p < 0.03$). There was no correlation between the inbreeding coefficient of a female and birth sex ratio of her offspring (Tabl. 1, r = -0.03, NS).

Discussion

In American bison, patterns of changes with age in fecundity and in tendency to reproduce in successive years are very similar to those of European bison presented in this paper, but female American bison start their reproductive lifespan one year earlier (Shaw, Carter 1989; Green, Rothstein 1991b). However, results of Krasiński and Raczyński (1967) for captive European bison living in 1954–66 were different; fecundity of 5–20 years old cows did not change with age and kept the level of 72–85%. Borgreen (2010) found out that calf production in American bison herd in National Bison Range was related to body weight of cows which is related to their body condition. Based on the historical trends, he suggested that the cause of anestrus during the breeding season might be the result of body condition of those cows, most probably connected with range resources or other environmental factors.

Sex ratio of mammal offspring may be related to various features of a mother, like maternal nutrition, age, age at first breeding, rank, or mother's previous reproductive status, and also to the sex of previous offspring, litter size, date of birth, weather, and timing of fertilisation (review in Clutton-Brock, Albon 1982; Kojola 1998). Results of presented study revealed that the sex ratio of offspring of various females differed significantly from 1:1 ratio, however, factors influencing it were not found. There was no relationship between the sex of a calf and the age or previous reproductive status of a mother or sex of previous offspring. In American bison data on the sex ratio of offspring of barren cows is contradictory (Rutberg 1986; Shaw, Carter 1989). An extensive discussion took place on the relationship between the age of a mother and the sex ratio of progeny (Saltz 2001; Hewison *et al.* 2002; Saltz, Kotler 2003). Proportion of female calves increased for elderly females in American bison (Green, Rothstein 1991a) and bighorn sheep (Berube *et al.* 1996), but not in European bison (see also Jaczewski 1958). Olech (2006) found out that increase of males in newborn calves was influenced by inbreeding level, however, the results presented here did not confirm this. Analysis of 66 captive mammal populations revealed that many species displayed long sequences of years with biased birth sex ratios, which might be caused by philopatry or stochasticity (Faust, Thompson 2000). According to Kruuk *et al.* (1999) there is more than one mechanism that affects the birth sex ratio and the action of these mechanisms depends on environmental conditions. In red deer the proportion of males born each year declined with increasing population density and with winter rainfall, both of which are environmental variables associated with nutritional stress during pregnancy.

Measures of maternal reproductive cost and differences in it regarding the sex of mammalian offspring include, among others, weight loss, subsequent survival and reproductive status of the female in the next year, length of interbirth interval, various estimates of milk intake, as well as sex differences in gestation length, birth weights or weights at weaning (Clutton-Brock, Albon 1982, Rutberg 1986, review in Byers, Moodie 1990, Green, Rothstein 1991a, review in Berube *et al.* 1996). Data from this study and others on European bison allow assessment and comparison of some of measures listed above. Bison calves were born considerably later after parturient than barren years, indicating the cost of reproduction borne by mothers of all calves. However, sex-biased investment was not found. The sex of a calf did not influence the reproductive status of the female or the sex of the calf born next year. The length of interbirth intervals after birth of male and female calves seemed to be influenced more by individual variation of cows than by the sex of their offspring. No difference was proved in the length of those intervals before the birth of calves of different sex, so the length of gestation and prenatal investment seem to be similar in both sexes (see also Jaczewski 1958). Weight of European bison does not differ between males and females from birth up to at least one year of age (Krasińska, Krasiński 2002) when the weaning takes place. Male calves suckle longer, but in rarer bouts than female calves and the suckling rates of calves of both sexes do not differ considerably (Daleszczyk 2004).

Clutton-Brock and Albon (1982) and Hewison and Gaillard (1999) surveyed the literature to check whether ungulate females of high rank and/or good condition produce more sons, but they did not found a consistent pattern to support the Trivers-Willard hypothesis. In our study cows from the breeding center should be in better than average condition, still the sex ratio of their newborns was female-biased, opposite to Trivers-Willard prediction. According to Kojola's review (1998), the sex ratio of ungulate offspring is usually coupled with the nutritional status of mothers in browsers but not in grazers, to which bison belong. Blanchard *et al.* (2005) claim that Trivers-Willard hypothesis may only apply to species where social rank of a female strongly affects her ability to provide maternal care.

According to Green and Rothstein (1991b), differences in individual quality determine reproductive patterns, and parameters related to breeding success of females show large individual variation (Lott, Galland 1985). They may be influenced by environmental factors (Krasiński, Raczyński 1967; Clutton-Brock *et al.* 1988; Grafen 1988), like climatic variations, local differences in habitat quality or in the sex ratio, changes in population density, size of the individual's group, and changes in group membership (Clutton-Brock 1988). Among factors limiting successful pregnancy in cattle were diet rich in proteins, mastitis, time of insemination with regard to follicle development, and heat stress (Hansen 2007). Reproductive physiology of an animal may also be affected by predation risk which was proved for wapiti *Cervus canadensis* (Creel *et al.* 2007). One of external factors that may influence the reproduction of bison cows is *Neospora caninum*, a parasite causing difficulties in fertilization, repeating miscarriages or stillbirths. *N. caninum* was found in various species, among them in both free-roaming and captive European bison (Cabaj *et al.* 2008; 2009; 2010). Further research on factors affecting European bison reproduction is needed and should include a variety of external factors.

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Czynniki wpływające na parametry reprodukcji krów żubra

Streszczenie: Rozród gatunku jest istotnym elementem jego przetrwania, podlegającym wpływom różnych czynników. W pracy przeanalizowano parametry reprodukcyjne żubrzyc w oparciu o wieloletnie dane z hodowli zamkniętej OHŻ Białowieskiego Parku Narodowego. Szukano czynników wpływających na płodność żubrzyc i płeć ich potomstwa oraz próbowano oszacować czy cielęta jednej płci są dla samicy bardziej kosztowne w odchowie niż płci przeciwnej. Wiek żubrzyc istotnie wpływał na ich płodność, samice w wieku 5–13 lat były najbardziej płodne. Wiek pierwszego wycielenia nie miał istotnego wpływu na współczynnik płodności odnoszący się do całego okresu reprodukcyjnego życia żubrzycy. Nie stwierdzono zależności pomiędzy płodnością krowy i jej wsobnością. Nie znaleziono też różnic w wieku matek cieląt różnej płci. Data porodu wpływała na status reprodukcyjny samicy w kolejnym roku; krowy cieliły się średnio 39 dni później przed latami jałowymi. Z drugiej strony status reprodukcyjny żubrzycy w danym roku miał wpływ na datę jej wycielenia w roku następnym. Cielęta rodziły się średnio 38 dni później po latach, w których ich matki się cieliły, niż po latach jałowych, co wskazuje na koszty reprodukcji ponoszone przez matki wszystkich cieląt. Nie znaleziono potwierdzenia zróżnicowanego inwestowania przez żubrzyce w cielęta różnej płci. Płeć urodzonego cielęcia nie wpływała na status reprodukcyjny samicy lub płeć potomstwa w następnym roku. Długość okresu międzywycieleniowego po porodzie wydawała się bardziej zależeć od zmienności indywidualnej krowy niż od płci cielęcia. Nie stwierdzono różnic w długości okresu międzywycieleniowego przed urodzeniem cieląt różnej płci, a więc długość ciąży oraz koszty matczynego inwestowania przed porodem wydają się być zbliżone w przypadku byczków i jałóweczek. Analiza stosunku płci przy urodzeniu u potomstwa różnych krów wykazała, że stosunek płci nie był jednorodny i analizowane dane jako całość odbiegały od przewidywanego stosunku płci 1:1, jednakże nie znaleziono czynników, które miałyby na to wpływ. Nie stwierdzono zależności pomiędzy współczynnikiem wsobności żubrzycy i udziałem samców w jej potomstwie. Istnieje potrzeba dalszych badań nad czynnikami mającymi wpływ na rozród żubrów, w tym czynnikami zewnętrznymi.