

Do European bison bulls in Białowieża Forest differ in their rutting behaviour depending on age?

Katarzyna Daleszczyk¹, Elżbieta Czykier²

¹ Mammal Research Institute, Polish Academy of Sciences, Białowieża, currently Białowieża National Park

² Department of Histology and Embryology, Medical University in Białystok

Abstract: In species with highly competitive typical pattern of male mating behaviour, some males may adopt different and non-competitive behavioural patterns which allow them to increase their chances of participating in reproduction. The behavioural pattern adopted may depend on the male's size; however, the status of individuals of similar sizes varies with population parameters. In European bison *Bison bonasus* (L.), males aged 4–6 years are sexually mature, but do not participate in breeding when older bulls are present. The free-living bison population in the Polish part of the Białowieża Forest was studied between 1972–2001. The number of adult females per adult male had increased in the last decade of this period but the level of reproduction remained stable. This might result from lengthening of the rutting season and the occurrence of different behavioural patterns among younger bulls, enabling them to participate in reproduction. During a radiotelemetry study between 1999–2002, in the rutting season the peaks of spatial activity of younger (5–6 years old) and older (≥ 7 years old) bulls were asynchronous and younger bulls visited more groups with females and spent more time in them than did older males. The stable level of population reproduction may confirm that as the cows: bull ratio is increasing; some younger bulls do participate in breeding, presumably because of different behavioural patterns during the rutting season.

Key words: *Bison bonasus*, reproduction, rutting season, male, behaviour

Introduction

European bison *Bison bonasus* (L.) belong to polygamous species; therefore males have to compete for females. Home ranges of female bison groups are too large to be defended, so males are not territorial. Because European bison are grazers, the distribution of females is wide and unpredictable and is not affected by the distribution of scarce food resources. As a result, the mating system adopted by bison bulls is “roving males” (Clutton-Brock 1989) with adult males roaming during the rutting season from one group containing females to another. European bison males reach sexual maturity at the age of 4 years (Czykier *et al.* 1999) but they still develop over the next 2–3 years. Because of this, males aged 4–6 years are sexually mature, but do not participate in reproduction when older and larger bulls are present (Kraśniński,

Raczyński 1967; Caboń-Raczyńska *et al.* 1987; Krasieńska, Krasieński 1995). The bison population consists of mixed groups and bull groups. Mixed groups include cows, juveniles of both sexes, calves and adult males, seasonally. Bulls (=adult males) are solitary or live in small bull groups most of the year, and usually join mixed groups only during the rutting season (Krasieńska *et al.* 1987; Krasieńska, Krasieński 1995). At this time, dominance hierarchy among bulls present in a mixed group is established and only the most dominant male mates with cows in oestrus (Caboń-Raczyńska *et al.* 1987).

In species in which the typical pattern of male mating behaviour is highly competitive, some males may adopt different and non-competitive behavioural patterns to increase their chances of participating in reproduction. Those behavioural patterns are called alternative mating tactics (Dominey 1984). Such alternative mating tactics were recorded in invertebrates and vertebrates (e.g. review in Dominey 1984), including various ungulates (Hogg 1984; Wolff 1998; Thirgood *et al.* 1999). It was found that individuals chose mating tactics according to their status so as to improve their reproductive success. Fighting for access to a female or sneak copulation are alternative mating tactics depending on male's size. However, the status of individuals of similar sizes may vary because of external factors like population density, age structure or the proportion of adult males to adult females (Gross 1996).

The Polish part of the Białowieża Forest supports the largest European bison population in the world (456 individuals at the end of 2008, European Bison Pedigree Book 2008). Since 1980, a urogenital disease of males (balanoposthitis) has been recorded there. Balanoposthitis is found in all age classes of males – bulls, juveniles, and calves. Every year 6.5%, on average of all males die or are culled because of this disease (Krasieńska, Krasieński 2007), which has undoubtedly influenced the age-sex structure of the bison population. It seemed important to study the consequences of such modification. Changes in the age-sex structure could create an opportunity to participate in breeding for younger, sexually mature bulls, especially if during the rutting season they adopted behavioural patterns different from those of older bulls.

In the presented study we examined (1) the reproduction level of the free-living bison population from the Polish part of the Białowieża Forest compared to the age-sex structure of the population in the long term, and (2) the differences between younger bulls (5–6 years old) and older bulls (≥ 7 years old) in their spatial activity, frequency of visiting mixed groups and periods spent within mixed groups during the rutting season.

Materials and Methods

Long-term data from years 1972–2001 concerning the age-sex structure and reproduction level of the free-living bison population from the Polish part of the Białowieża Forest (Krasieńska, Krasieński 2007) was analysed. Age-sex

Table 1. Observations of radio-collared European bison in years 1999–2002. Younger bulls (5–6 years) : Nos 574, 670, 720. Older bulls (≥ 7 years): Nos 832, 851, 892, 526. Cows (≥ 4 years) : Nos 681, 812. A-pre-rut period, B-rutting season.

European bison (No.)	Year							
	1999		2000		2001		2002	
	A	B	A	B	A	B	A	B
574			X	X	X	X		
670					X	X	X	
720					X	X	X	
832	X	X	X	X				
851	X	X	X	X				
892	X	X						
526	X							
681	X	X						
812	X	X	X	X				

classes were divided as follows: calves (of both sexes, up to one year old), juveniles (of both sexes, aged 2–3 years), cows (adult females ≥ 4 years old) and bulls (adult males ≥ 4 years old). During winter, the majority of bison gather around winter feeding sites. Surveys of these sites were conducted in 1992–2001 in order to collect information on the number of calves born outside the typical calving season (Z.A. Krasiński unpublished data).

Between 1999–2002, data on the activity of adult males during the rutting season was collected, based on observations of nine radio-collared bison (seven bulls and two cows) from the free-living herd in the Polish part of the Białowieża Forest (Table 1). Information concerning immobilization and marking of bison was published elsewhere (Krasińska *et al.* 2000). Estimates of the age of radio-collared bison were based on the replacement and wear of teeth (Węgrzyn, Serwatka 1984), body size, and the size and shape of horns. Observations included the pre-rut period (1 April – 15 July, for comparison with the rutting season) and the rutting season (16 July – 31 October). Data from radio-collared bulls came from a total of 12 pre-rut periods and 9 rutting periods and from radio-collared cows from 3 pre-rut periods and 3 rutting periods (Table 1). Bulls were located and observed three times a week and cows twice a week. After a radio-collared bison was located, the size and composition of a group and all records of rutting behaviour were noted. Rutting behaviour includes sexual activity (anogenital controls, tending cows, copulations) and agonistic behaviour (all types of threats up to fights). Oestrus in female European bison is only recognizable from the behaviour of a bull

(Kraśiński, Raczyński 1967). Results of other studies on European bison and American bison *Bison bison* confirm that the rutting behaviours observed in this study are good indicator of the duration and intensity of the rutting season in free-living European bison (Jaczewski 1958 ; Komers *et al.* 1992; 1994a). To find out the differences in activity balance of bulls within and outside mixed groups, the activity of all bulls encountered in the forest was recorded (foraging, lying, standing, and walking without foraging). Komers *et al.* (1992) grouped lying and foraging as comfort behaviour (aimed at condition improvement) and standing and walking as activity behaviour (aimed at searching for females).

To check whether the age of bulls influences their behavioural patterns during the rutting season, we compared behaviour of two groups of adult males: (1) younger bulls (5–6 year old) which are already sexually mature but have no access to females in oestrus while in the presence of older males, and (2) older bulls (≥ 7 years old) normally participating in breeding (Kraśiński, Raczyński 1967; Coboń-Raczyńska *et al.* 1987; Kraśińska, Kraśiński 1995).

Size of home ranges (100% Minimum Convex Polygon) and average distances walked between the localizations taken every second day were calculated with the use of Tracker software (A. Angerbjörn, Radio Location System, Huddinge Sweden). The number of locations for one bull in one year of the study ranged from 85–118. In statistical analyses we used both parametric tests (t test) and nonparametric tests (χ^2 , Mann-Whitney test, Spearman's correlation rank) depending on the distribution of data.

Results

The age-sex structure of the Polish bison population in the Białowieża Forest has changed during the analysed period of 30 years. The number of cows increased while the proportion of bulls decreased, especially during the last decade. As a result, the ratio of adult females to adult males, that is the number of cows per bull, grew from the mean of 1.43 in the years 1972–1981 and 1.42 in 1982–1991 to 1.71 in the years 1992–2001. However, the fecundity ratio, i.e. the percentage of cows that calved the following year, remained constant at 42.8%, 41.1% and 42.1%, respectively.

Based on the records of the presence of bulls in mixed groups and occurrence of rutting behaviours, the rutting season was assumed to begin in the second half of July and cease in the second half of October, with the period from August through the first half of October constituting the strict rutting season (Fig. 1). In the years 1992–2001, 7% of calves were born after the typical calving season, which falls within May through July. This means that some cows had mated in November or even later.

Activity of bison bulls in the rutting season is reflected, among other factors, in their spatial activity, i.e. in the size of home ranges and the length

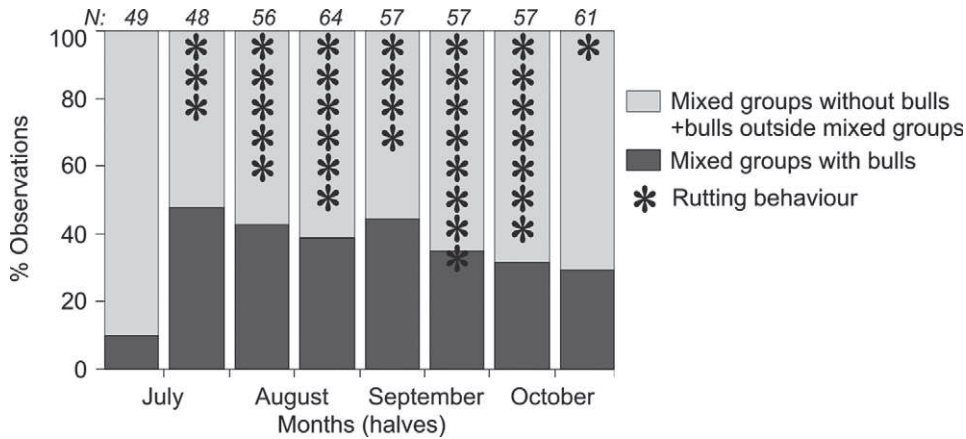


Figure 1. Duration and intensity of the rutting season in European bison population from the Polish part of the Białowieża Forest in 1999–2002, based on the records of presence of bulls in mixed groups and occurrence of rutting behaviours (sexual and agonistic). Sample size is given above each column representing a half of a month.

of distances walked. The size of bull home ranges during the rutting season was significantly greater than in the pre-rut season (52 sq.km and 24.2 sq.km, respectively, $Z = -3.34$, $n_1 = 9$, $n_2 = 12$, $P < 0.001$). During the rutting

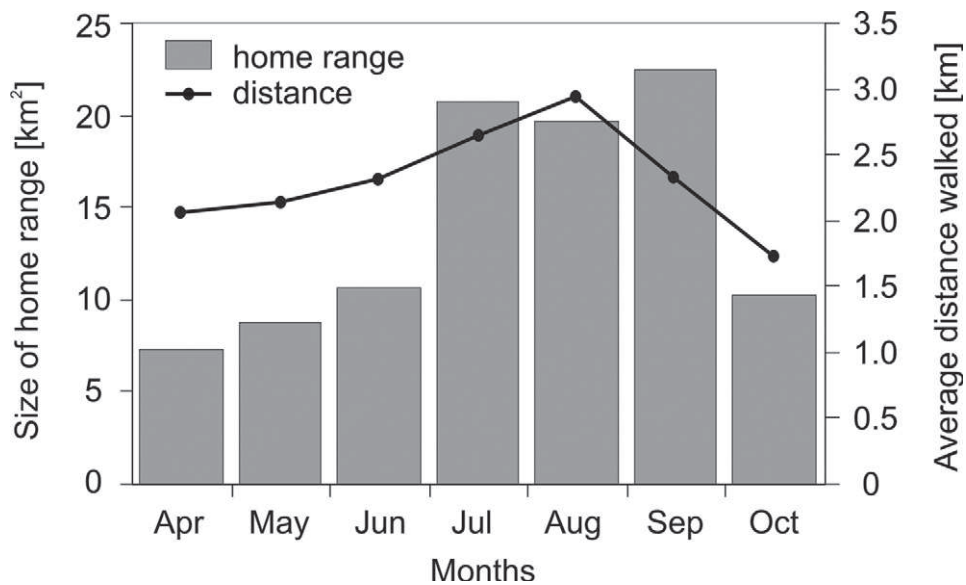


Figure 2. Size of monthly home ranges and length of average distances walked between localizations taken every second day of radio-collared European bison bulls. Sample sizes were as follows: for average distance length: 51, 44, 55, 42, 48, 41, 51; for home range size: 12, 12, 12, 12, 9, 9, 9.

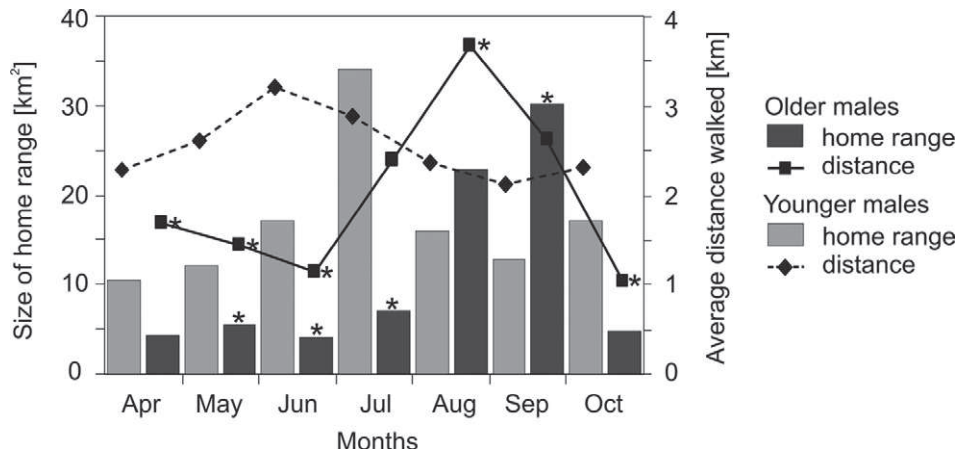


Figure 3. Size of monthly home ranges and length of average distances walked between localizations taken every second day of younger (5–6 years old) and older (≥ 7 years old) radio-collared European bison bulls. * indicates a significant difference ($p < 0.05$) between younger and older bulls in a given parameter in a given month. Sample sizes were as follows: for younger bulls – average distance length: 32, 26, 31, 22, 27, 25, 28; home range size: 6, 6, 6, 6, 4, 4, 4; for older bulls – average distance length: 19, 18, 24, 20, 21, 16, 23; home range size: 6, 6, 6, 6, 5, 5, 5.

season, the size of home ranges did not differ between younger and older bulls (58.2 sq.km and 47.1 sq.km, respectively, $Z = 0.98$, $n_1 = 4$, $n_2 = 5$, $P > 0.05$). Distances walked by adult males did not differ between the pre-rut and rutting periods (2260 m and 2335 m, respectively, $t = -0.37$, $df = 330$, $P > 0.05$) or between younger and older bulls during the rutting season (2325 m and 2347 m, respectively, $t = -0.07$, $df = 158$, $P > 0.05$). Rut home ranges of bulls overlapped with their pre-rut home ranges from 21.3% to 100%. There was a positive correlation between the age of a male and the degree of home range overlapping ($r_s = 0.75$, $n = 9$, $P < 0.02$). Comparison of monthly home ranges and average distances walked between two locations gave a more precise picture of spatial activity of males and revealed a distinct increase from July through September (Fig. 2). However, the peaks of spatial activity of younger and older bulls did not occur simultaneously (Fig. 3). Activity of older males was the highest during the strict rutting season in August – September, while younger bulls had the largest home ranges in July.

During the rutting season, the social structure of bison population was transformed. The occurrence of bulls in bull groups decreased from the average of 51.6% in the pre-rut season to 13.9% in the rutting season (Fig. 4; younger bulls: Chi-square = 28.47, $df = 1$, $P < 0.0001$; older bulls: Chi-square = 44.24, $df = 1$, $P < 0.0001$). Radio-collared males were observed in mixed groups almost exclusively during the rutting season (Fig. 4, Chi-square = 82.90, $df = 1$, $P < 0.0001$). In the pre-rut period, 22.2% of mixed groups

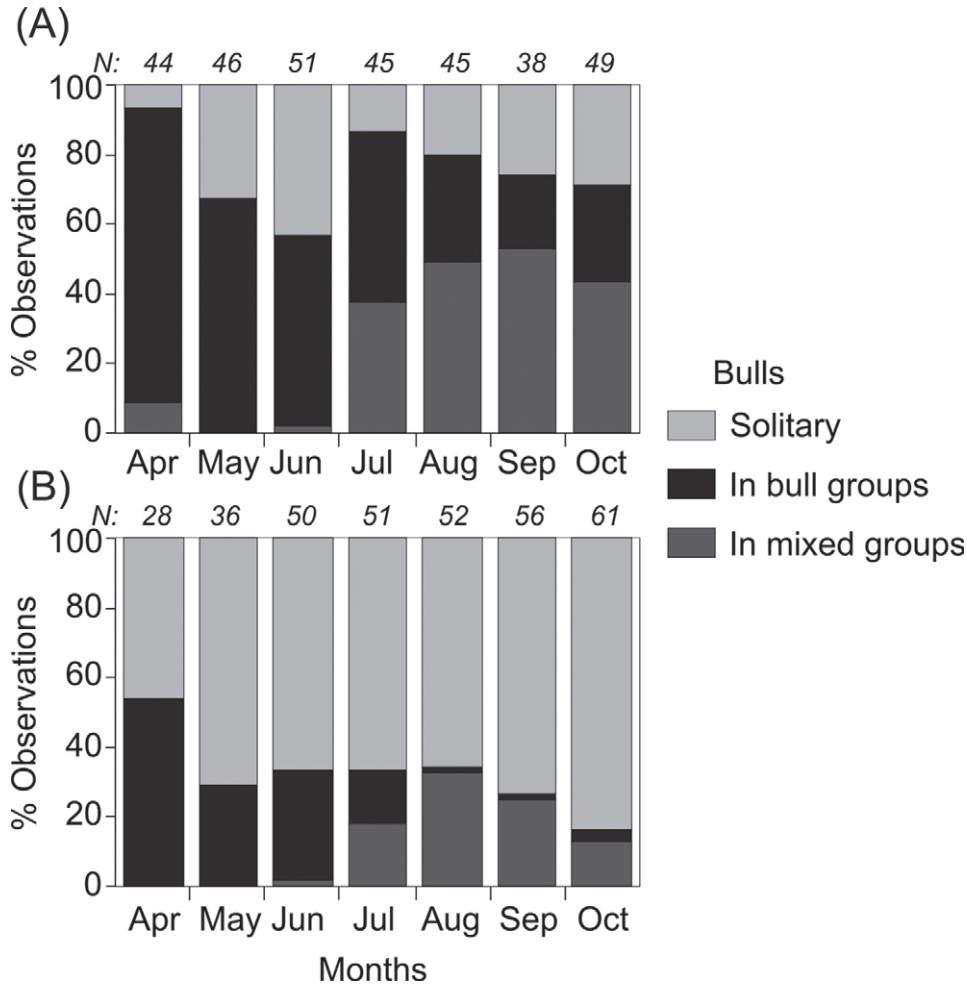


Figure 4. Percentage of records of (A) younger (5–6 years old) and (B) older (≥ 7 years old) bulls while solitary, in bull groups and in mixed groups in various months. Sample size is given above each column representing a month.

with radio-collared cows contained bulls while during the rutting season the estimated value rose to 91.3% ($\chi^2 = 11.03$, $df = 1$, $P < 0.001$). Also the mean number of adult males in a mixed group was significantly higher in the rutting season than in the pre-rut period (1.79 and 0.67, respectively, $t = 6.09$, $df = 157$, $P < 0.0001$). During the rutting season, younger bulls were observed in mixed groups twice as often as older ones (Fig. 4, Chi-square = 15.66, $df = 1$, $P < 0.0001$). Nevertheless, younger bulls were the only adult males in mixed groups in only 25% of such observations compared to 50% of records in older bulls. On average, each bull visited 5–6 mixed groups during one rutting season; however, the number of mixed groups visited by a bull was

negatively correlated with his age ($r_s = 0.72$, $n = 9$, $P < 0.03$). Moreover, younger bulls spent more time in each mixed group than did older males (5 and 2.4 days, respectively, $Z = -2.41$, $n_1 = n_2 = 21$, $P = 0.013$).

In analysis of activity balance of bulls within or outside mixed groups, data from direct observations of both radio-collared and unmarked bulls was used ($n = 456$). Bulls outside mixed groups were more often engaged in activity behaviour than bulls within mixed groups (47.9% and 34.6% of observations, respectively, Chi-square = 4.44, $df = 1$, $P < 0.036$) whereas there was no difference regarding comfort behaviour (52.1 % and 65.4%, Chi-square = 3.31, $df = 1$, $P > 0.05$).

Discussion

In the free-living European bison population of the Polish part of the Białowieża Forest, the age-sex structure changed to the detriment of adult males; however, the level of reproduction remained stable. Among possible reasons for this were lengthening of the rutting season and occurrence of different behavioural patterns enabling younger bulls to take part in breeding. The rutting season may be distinguished quite clearly based on the changes in the composition of bison groups and occurrence of typical behaviours for this period. According to the earlier studies, the rutting season in the bison population from the Białowieża Forest took place in August-September and tended to lengthen to October (Wróblewski 1927; Jaczewski 1958; Krasiński 1978; Krasiński *et al.* 1994). In this study the rutting season lasted from mid-July through October. Parturitions after the typical calving season formed another indicator of lengthening of the rutting season. The heightened activity of younger males early in the rutting season may also contribute to the extended calving season. In captive breeding centres some parturitions take place before the typical calving season (for example in 2008 about 5% of captive calves were born in April, European Bison Pedigree Book 2008), but in the wild, because of great caution and alertness of bison mothers, calves are usually observed only when several months old and it is difficult then to assess whether they were born in April or in May. The tendency of European bison to extend the rutting season was noted previously and linked to a lack of a natural period of limited food availability because of supplementary winter feeding of bison (Kulagin 1919; Wróblewski 1927; Jaczewski 1958).

Within a species variety of mating systems may occur (Clutton-Brock 1989). In our study on the European bison younger bulls showed behavioural patterns related to the rutting season which were different from those of older males. An increase in home range size of bulls during the rutting season as compared to the pre-rut period was recorded by some authors (Krasińska, Krasiński 1995; Krasińska *et al.* 2000) but the activity peaks of males in various ages have not been determined before. As the rut home ranges of older and younger bulls did not vary in size (Krasińska *et al.* 2000, this study), it

can be assumed that their spatial activity was similar in extent but did not take place in the same time. The temporal shift in spatial activity of younger males might have helped them to avoid competition with more dominant bulls, which limited their activity to the strict rutting season. In both bull age classes the peak in the length of distances walked was one month prior to the peak in the sizes of monthly home ranges, so that searching for females started with more intense coverage of already known areas and was then extended to other areas. Overlapping of pre-rut and rut home ranges occurred less in younger bulls than in older males implying that during the rutting season younger, less-experienced bulls mostly explored new areas while older bulls still used their pre-rut home ranges and extended their activity to neighbouring area. Observations from other species may also suggest that less competitive males could participate in breeding at a slightly different time than dominant ones. For example in red deer *Cervus elaphus*, during the rutting season the highest quality of semen in younger males was observed later than in alpha males which could probably form a chance of becoming pregnant for hinds not successfully mated by alpha males (Giżejowski 2002, 2004).

Komers *et al.* (1992) examined two hypotheses on why male wood bison *Bison bison athabasca* left cow groups during the rutting season – in order to regain body condition or to find another group with receptive cows and fewer potential rivals. Their results supported the condition improvement hypothesis contrary to our present findings on European bison, which seemed to leave mixed groups in order to search for other ones. Changes in the composition of wood bison groups allows bulls to encounter new females without leaving a group and that explains the difference (Komers *et al.* 1992). Whitehead (1990) proposed the rule as to when males of “roving males” species should rove during the rutting season and when they should not. If there is a population with many mature males and dominance hierarchy, males of a lower social rank should stay in a group (if they can find a group without a more dominant resident male) while those of a higher rank should rove (they are able to gain access to receptive females even if there are other males in a new group). If groups with females vary in size, males should rove more in the beginning of the rutting season (allowing more opportunity to find a bigger group with a greater number of females) and increase residency towards the end of the rut. In the present study, older and so probably higher-ranking European bison bulls spent more time outside mixed groups than younger, lower-ranking males and walked longer distances during the strict rut. Younger bulls roved more in the beginning of the rutting season and became more resident later in the rut; they also stayed longer in mixed groups.

One of the factors considerably reducing the time spent by a bull in cow groups was greater success in agonistic interactions (Forchhammer, Boomsma 1998). In this study, older bulls were more frequently the only adult males in mixed groups than younger bulls; this suggests the discrepancy in social status

of two classes of adult males. Older bulls of a higher social rank gained access to cows by chasing other males away. Younger bulls lower in the dominance hierarchy, had little chance in direct competition with older males so presumably they spent more time in mixed groups simply waiting for a chance to mate. The results of this and other studies (Maher, Byers 1987; Komers *et al.* 1992) indicate that mating chances of sexually mature males are not equal and this may modify behaviour of males. Moore (1991) suggested hormonal control of alternative male phenotypes connected with different behavioural patterns related to reproduction. A change in hormone level may influence social status. In male European bison, the mean level of free testosterone is the highest in bulls aged 6–12 years (Czykier, Krasińska 2006), so the status of sexually mature males may be affected by their hormone level.

Unfortunately, there is little information on age differences in male behaviour during the rutting season before the sex ratio in the bison population became skewed in favour of females. Krasińska and Krasiński (1995) analysed data from 1976–1990 and found no significant difference in the number of days spent in a mixed group between bulls over 6 years old and younger males. Marked bison bulls (aged from 3 years old up to 15 years old) visited on average 2.4 mixed groups during one rutting season (Krasińska, Krasiński 1995), that is much less than in the present study. In our study, during the rutting season younger European bison bulls visited more mixed groups than older males and stayed within them much longer. The differences in the results mentioned above could suggest a change in male behaviour related to a shift in the sex ratio.

Changes in density and age structure of ungulate males affect their breeding activity and reproductive tactics (Komers *et al.* 1994b; Coltman *et al.* 1999; review in Thirgood *et al.* 1999). Komers *et al.* (1994b; c) suggest that males can adjust their behaviour to the current level of competition in a herd. The present study showed that in the European bison population in Białowieża Forest, younger bulls intensified their spatial activity outside the strict rutting season, visited more groups with females and spent more time in them. Asynchronous peaks of spatial activity and more intense visiting of mixed groups might increase breeding chances of younger bulls. The presented study was based on a relatively small sample size and so the question of occurrence of alternative mating tactics in the European bison needs further investigation. However, the stable level of reproduction in the studied population may confirm that when cows: bulls ratio is growing, at least some younger European bison bulls participate in breeding, presumably thanks to different behavioural patterns during the rutting season.

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Czy zachowania rujowe samców żubra w Puszczy Białowieskiej zależą od ich wieku?

Streszczenie Wśród gatunków, u których typowy wzorzec zachowań samców w sezonie godowym jest wysoce konkurencyjny, niektóre samce mogą przyjmować odmienne, niekonkurencyjne wzorce zachowań, które pozwalają im zwiększyć szanse na udział w rozrodzie. Przyjęty wzorzec zachowania może zależeć od rozmiarów samca, jednakże status osobników podobnej wielkości zmienia się w zależności od parametrów populacji (zagęszczenie, stosunek liczby dorosłych samic do dorosłych samców, itd.). U żubra *Bison bonasus* (L.) samce w wieku 4–6 lat są dojrzałe płciowo, ale nie uczestniczą w rozrodzie w obecności starszych samców. Przeanalizowano dane dotyczące wolno żyjącej populacji żubrów z polskiej części Puszczy Białowieskiej z lat 1972–2001. Liczba dorosłych samic przypadająca na jednego dorosłego samca wzrosła w ostatniej dekadzie badanego okresu, jednakże poziom rozrodu nie uległ zmianie. Mogło to być wynikiem wydłużenia sezonu godowego oraz pojawienia się u młodszych byków odmiennych wzorców zachowań, które umożliwiałyby im udział w rozrodzie. W czasie badań radiotelemetrycznych prowadzonych w latach 1999–2002, w sezonie godowym szczyty aktywności młodszych (5–6 letnich) i starszych (7 lat i więcej) byków były asynchroniczne, a ponadto młodsze byki odwiedzały więcej grup z samicami i spędzały w nich więcej czasu niż starsze byki. Stabilny poziom rozrodu może świadczyć o tym, iż kiedy stosunek liczby krów do liczby byków wzrasta, niektóre młodsze byki biorą udział w rozrodzie, przpuszczalnie dzięki odmiennym wzorcom zachowań w czasie sezonu godowego.
