

Restoration and intensive management have no effect on evolutionary strategies

Matt W. Hayward^{1,2,5,*}, Rafał Kowalczyk¹, Zbigniew A. Kłosiński³,
Małgorzata Kłosińska¹, Jerzy Dackiewicz³, Thomas Cornulier^{1,4}

¹Mammal Research Institute, Polish Academy of Science, ul. Waszkiewicza 1, 17-230 Białowieża, Poland

²Centre for Wildlife Management, University of Pretoria, 0001 Pretoria, South Africa

³Białowieża National Park, 17-230 Białowieża, Poland

⁴Institute of Biological and Environmental Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

⁵Present address: Australian Wildlife Conservancy, Care P.O. Wentworth, New South Wales 2648, Australia

ABSTRACT: The European bison *Bison bonasus* is the largest extant terrestrial mammal on the European continent; however, the species went extinct in the wild in 1919. Restoration started in 1929 in Poland's Białowieża Primeval Forest using captive individuals sourced from zoological gardens and breeding centres. Of the 7 founders, 2 individuals contributed 85% to the genetic make-up of the lowland line of the species. The Białowieża bison population numbered 820 in 2008, but very low genetic diversity and a high level of management have raised questions as to whether it still conforms to evolutionary predictions. We tested whether the sex ratio of European bison calves conformed to the Trivers-Willard hypothesis at the population level, i.e. whether it became increasingly female-biased as bison condition deteriorated following increased population density. We found that increased population density and reduced female body mass led to increasing female-biased calf sex ratios, whereas mast years (abundant food resources) corresponded to male-biased sex ratios. Despite the high degree of inbreeding and management, European bison are still responding as expected to variations in female body condition; however, the precautionary principle cautions managers of small populations that artificial selection can alter the evolutionary strategy of wildlife even though we did not detect this in the Białowieża bison population.

KEY WORDS: Body condition · Local resource competition hypothesis · Maternal investment · Reproductive success · Sex ratio manipulation · Trivers-Willard hypothesis · European bison · Ungulates

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

Sex allocation has been an extensively studied area of evolutionary ecology for several decades (Charnov 1982, Frank 1990). There is strong evidence that invertebrate parents vary the sex ratio of their offspring to maximise their long-term fitness (Charnov

1982). However, there is a greater variation in the causes and effects in mammals, which has led to a greater number of explanations for the variation in the sex ratio of offspring in mammals (Clutton-Brock & Iason 1986, Cockburn et al. 2002). Theoretically, parents should bias their offspring sex ratio toward the sex whose cost of reproduction has the greatest

*Email: hayers111@gmail.com

benefit to their own fitness (Trivers & Willard 1973), and this can be driven by the condition of the mother (Cameron & Linklater 2002). Sex ratio variation should depend on the relative fitness of sons and daughters, the costs of the parents' future reproductive success in producing either sex, and sex differences in the extent of competition or cooperation with parents or kin (Clutton-Brock & Iason 1986). A common prediction for polygynous vertebrates is that parents in better condition than others in the population should invest more resources in reproduction and, therefore, invest in sons (Trivers & Willard 1973, Koskela et al. 2009). Parents may improve condition via processing food more efficiently or by being dominant over other individuals, which may reduce stress, provide subordinate assistants or allow access to high-quality food resources (Silk 1983, 1984).

The European bison *Bison bonasus* (Linnaeus 1758) is a polygynous mammal that would be predicted to exhibit optimal sex allocation with variation in offspring sex ratio because of the variation in population density, body mass, body condition and individual status to maximize lifetime reproductive success. However, overall analysis suggests that this is not the case for the calf sex ratio, which is at parity (Mysterud et al. 2007). This is surprising given that the closely related American bison *B. bison* does vary offspring sex ratio according to female body condition (Rutberg 1986). Here, we reanalyzed the data on European bison sex ratios and tested whether variation in female body condition drove any sex ratio variation we observed in the population.

There are several reasons why European bison may not follow the evolutionary predictions of sex allocation theory. Firstly, European bison have been under unnatural selection through selective human hunting for several centuries. Bison were first legally protected within the Białowieża Primeval Forest (among other forests of the Grand Duchy of Lithuania) in 1529 and, following that, only royalty were allowed to hunt them (Samojlik & Jędrzejewska 2005).

Secondly, management actions in and around the forest created and maintained suitable habitat for the bison that may have reduced natural selection on bison to use optimal natural habitats and to forage for wild foods (Kerley et al. 2011, Kowalczyk et al. 2011). For example, from the 15th century onwards people living near the forest were able to make hay by mowing riparian meadows (Samojlik & Jędrzejewska 2005). Hay was stored in haystacks that were raided by bison, which were under royal protection and thus could not be harmed by the populace while inside the forest; hay thereby provided supplementary win-

ter forage for the species. Whether this mowing replaced the ecological functions performed by bulk grazers (WalDRAM et al. 2008) that went extinct in the region around this time (aurochs *Bos taurus* or wild horse *Equus ferus*) is unknown. From 1700 onwards, permanent haystacks were created to feed the bison through the winter (Samojlik & Jędrzejewska 2005), and this practice continues today.

Thirdly, European bison are highly inbred. Only 2 populations (Białowieża Primeval Forest and Caucasus Mountains) survived into the 19th century. The 727 bison alive in the Białowieża Primeval Forest at the onset of World War I were extinct by its end (Pucek 2004, Krasińska & Krasiński 2007). The population in the Caucasus went extinct in 1927. The International Society for the Protection of the European Bison was established in 1923 and sourced 54 bison from captive breeding centres worldwide to use in the restoration of the species, which began in 1929 (Krasińska & Krasiński 2007). Only 7 of those individuals provided any genetic contribution to the founder population upon their release into the wild in 1952, and of the 7 founders, 2 individuals contributed 85% to the genetic make-up of the lowland line of the species (Krasińska & Krasiński 2007). Since then, the bison population in Białowieża (both the Polish and the Belarussian parts) has increased to 820 (December 2008 total count); however, the species is still listed as Endangered according to IUCN criteria (IUCN 2007). A border fence effectively isolates the Polish from the Belarussian bison populations (Daleszczyk & Bunevich 2009). Having passed through such a narrow bottleneck, the European bison is genetically depauperate and shows low levels of heterozygosity (Tokarska et al. 2009, 2011, Wójcik et al. 2009). Although there is no evidence of inbreeding depression, balanoposthitis disease, a necrotic inflammation on the prepuce, is prevalent (Krasińska & Krasiński 2007). This disease has yet to make a detectable impact on the rate of population increase.

Finally, since the restoration began, European bison have been extensively managed through artificial selection. They are regularly provided with supplementary winter feed aimed at reducing damage to regenerating forest stands and agricultural crops, while also limiting bison dispersal. This leads to unnatural bison aggregations and influences social organisation and space use. The European bison population in the Białowieża Primeval Forest has also been culled regularly since the 1970s (3 to 17% of the population annually; Krasińska & Krasiński 2007) to keep the population within some hypothesised carrying capacity of the environment and to remove invalid animals.

European bison live in an environment that offers periods of both resource deficiency and high resource abundance. For example, pulses of highly nutritious food sources strike the forest every 6 to 9 yr by way of enormous quantities (e.g. 1922 kg ha⁻¹) of acorns dropped in summer by oak trees *Quercus robur* (Jędrzejewska & Jędrzejewski 1998, Jędrzejewska et al. 2004). Masting affects European bison recruitment rates, although previous studies have not found any effect on calf sex ratios (Mysterud et al. 2007).

In contrast to its American counterpart, the European bison may no longer exhibit natural evolutionary strategies because it is derived from captive-bred stock, because of its high level of inbreeding and/or because of the intensive management that has strongly influenced its social organization, spatial structure and dispersal via artificial selection. We aimed to test whether the European bison conformed to natural evolutionary strategies by looking at the sex allocation of this expanding population. We used data on population size, body condition, annual climatic conditions and pulses of key foods to determine the causes of observed variation in calf sex ratio throughout the past 50 yr. We predicted that, following the Trivers-Willard theory, an increase in population density would lead to a decrease in individual female bison condition and a concomitant decrease in male calves born (Trivers & Willard 1973). We also predicted that pulses of nutrient-rich food (acorn mast years) would improve the condition of adult females, resulting in an increase in the proportion of male calves born. We acknowledge that the age of male ruminants and male sperm quality may lead to a higher proportion of male calves (Saether et al. 2004, Gomendio et al. 2006); however, no information is available on which males of this polygynous species dominated breeding in the Białowieża bison population. We are also aware that the Trivers-Willard theory predicts change at the level of the individual rather than the population, but we base our population level findings on similar population level results for other species (Reuterwall 1981, Mysterud et al. 2000, Bjørneraas et al. 2009).

MATERIALS AND METHODS

Study area

Białowieża Primeval Forest (BPF, 52° 30'–53° 0' N, 23° 30'–24° 15' E) spans 1500 km² across the Polish–Belarussian border and is one of the best preserved lowland deciduous forests in Europe. Since 1981, the forest has been split by a border fence created by the

former Soviet Union. This fence separated the forest into 2 distinct management units.

The forest consists of mixed deciduous woodlands (93.6% of the area), interspersed with open areas (glades with meadows, riparian zones with sedges and reed marshes; Jędrzejewska & Jędrzejewski 1998). The climate of Białowieża is transitional between Atlantic and continental, with clearly marked cold and warm seasons. The mean annual temperature is 6.8°C, and ranges from –4.8°C in January to 18.4°C in July. Snow cover lasts for an average of 92 d yr⁻¹, with a maximum recorded depth of 95 cm. Mean annual precipitation is 631 mm.

Bison population size and sex structure

The European bison has been intensively monitored since its reintroduction to the wild in 1952. Data on population size and composition, including adult and calf sex ratio, were collected by observational total count surveys conducted each winter between 1952 and 2007 by the Białowieża National Park staff (Table 1). From December to February each year (less than 6 mo from birth dates), when bison aggregate around feeding stations, experienced researchers and managers count all bison observed at feeding stations. Data on population structure is also obtained. During this count, feed (hay) is distributed in lines through the forest, and observers count, age and sex the attending bison. Any bison that do not approach these feeding sites (usually a small number of males based on radio telemetry; R. Kowalczyk unpubl. data) are recorded by snow-tracking and then visual observations. This method has been employed since 1952 and is simultaneously repeated several times, with the largest estimate taken as the final annual census. Data on calf sex ratio cover the period from 1957 (when the first calf was born after bison were reintroduced to the wild) to 2008, and includes 1834 calves (871 males and 963 females). Population density was calculated as the population estimate divided by the area of the forest.

The European bison rutting season begins in August and ends in October when polygynous males fight for access to females in oestrus (Kraśnińska & Kraśniński 2004). Cows give birth to a single calf in spring after a gestation period averaging 264 d (Kraśniński & Raczyński 1967). Almost all births occur between May and July (Kraśniński & Raczyński 1967, Kraśnińska & Kraśniński 2007). Overall, the calf sex ratio is not considered to depart from a 1:1 ratio (Kraśnińska & Kraśniński 2007, Mysterud et al. 2007).

Table 1. *Bison bonasus*. Values of Akaike Information Criterion corrected for small sample sizes (AICc), Akaike weights (w) and cumulative Akaike weights (cum_w) for the models of bison sex ratio variation (proportion of male calves), assuming a binomial error. PopDens: population density index; Condition.prev: female condition in the previous winter; WinterTemp: average temperature in January each year; Temperature: mean temperature over the year; AcornMast: 2-level factor coding for acorn mast versus non-mast years; I: interactions; Acorn3: 3-level factor coding for acorn mast year versus year-after-mast versus other non-mast years. The top set of models (1 to 18) was run on the subset of years where condition data were available (22 yr between 1982 and 2007), and the bottom set (1' to 12') was run on all 48 yr from 1960 to 2007. **Bold** characters indicate models representing 95% of the cumulated Akaike weight

Model rank	Covariates	Null deviance	Residual deviance	Parameters	Δ AICc	w	cum_w
1	PopDens + WinterTemp	15.66	9.52	3	0.0	0.22	0.22
2	Condition.prev + WinterTemp	15.66	10.82	3	1.3	0.11	0.33
3	PopDens	15.66	13.95	2	2.1	0.08	0.41
4	PopDens + AcornMast	15.66	11.55	3	2.4	0.07	0.48
5	Condition.prev + PopDens	15.66	11.93	3	2.4	0.07	0.55
6	Condition.prev + AcornMast	15.66	12.16	3	2.7	0.06	0.61
7	PopDens + AcornMast + WinterTemp	15.66	9.18	4	2.7	0.06	0.66
8	Condition.prev	15.66	14.92	2	2.7	0.06	0.72
9	PopDens + WinterTemp + I(WinterTemp²)	15.66	9.24	4	2.8	0.06	0.78
10	PopDens + Condition.prev + WinterTemp	15.66	9.33	4	2.8	0.05	0.83
11	PopDens + AcornMast + Condition.prev	15.66	9.79	4	3.3	0.04	0.87
12	Intercept	15.66	15.66	1	3.7	0.03	0.91
13	PopDens + Acorn3	15.66	10.75	4	4.3	0.03	0.93
14	PopDens + AcornMast + PopDens × AcornMast	15.66	11.33	4	5.2	0.02	0.95
15	PopDens + AcornMast + Temperature	15.66	11.43	4	5.3	0.02	0.96
16	PopDens + AcornMast + Condition.prev + WinterTemp	15.66	8.36	5	5.3	0.02	0.98
17	PopDens + Acorn3 + WinterTemp	15.66	9.16	5	6.1	0.01	0.99
18	PopDens + AcornMast + Condition.prev + Temperature	15.66	9.43	5	6.3	0.01	1.00
1'	PopDens + AcornMast	50.04	35.27	3	0.0	0.27	0.27
2'	PopDens	50.04	38.87	2	1.3	0.14	0.41
3'	PopDens × AcornMast	50.04	34.92	3	1.6	0.12	0.53
4'	PopDens + Acorn3	50.04	34.55	4	1.6	0.12	0.65
5'	PopDens + AcornMast + WinterTemp	50.04	34.81	4	1.9	0.10	0.76
6'	PopDens + AcornMast + Temperature	50.04	35.17	4	2.3	0.09	0.85
7'	PopDens + WinterTemp	50.04	38.10	3	2.8	0.07	0.91
8'	PopDens + Acorn3 + WinterTemp	50.04	34.09	4	3.2	0.05	0.97
9'	PopDens + WinterTemp + I(WinterTemp ²)	50.04	37.51	4	4.6	0.03	0.99
10'	WinterTemp	50.04	46.44	2	8.9	0.00	1.00
11'	AcornMast	50.04	47.74	2	10.2	0.00	1.00
12'	Intercept	50.04	50.04	1	10.3	0.00	1.00

Body mass

No animals were handled as part of this study. We used data from individuals culled by park staff, as approved by the park management plan, to investigate temporal trends in body mass under the assumption that increased body mass relates to better animal condition. Białowieża's bison population has been regulated by approximately 11% on average annually since 1971 through culling or removal for translocation purposes (Kraśnińska & Kraśniński 2002). Between 1971 and 2007, 826 bison were culled, of which 435 were female (including calves, sub-adults and adults). Of the adult female bison, 67% were culled for reduction purposes rather than to remove sick or invalid individuals from the popu-

lation (Kraśnińska & Kraśniński 2007). Thus, we assumed that culled individuals represent a random sample of adult females and that any variation in body mass is likely to be indicative of the entire population. All females culled due to poor condition were excluded from our analyses. We used data from 1990 to 2008 (125 in total); the data were scarce prior to that due to the low number of bison culled or because the carcasses were not collected.

Data analysis

Bison sex ratio was modelled as the proportion of male calves in the population censused using logistic regressions, i.e. generalized linear models with a

logit link and assuming a binomial error distribution (Crawley 2007). In order to weight the data according to the sample size in every year, the response variable was specified as a 2-column matrix with the number of males and female calves, respectively. The covariates used to explain variation in calf sex ratio were bison population density, condition of culled female bison, mean winter temperature and mean annual temperature, and presence of a mast crop in the current year or in the previous year. Models were selected using the Akaike Information Criterion corrected for small sample sizes (AICc; Anderson 2008). The best model is the one with the lowest AICc. Models were compared using their difference in AICc (ΔAIC_c) compared to that of the best model. Models with ΔAIC_c near 0 are considered to have considerable support from the data, i.e. they are considered highly plausible (Anderson 2008). Here we estimated the probability of every model using Akaike weights, and we considered the pool of models of which cumulated probabilities represent 95% of the total Akaike weight. All models were checked using standard residuals-based diagnostic tools, and the absence of temporal autocorrelation was verified by plotting the autocorrelation function of the residuals of the model (Crawley 2007). In a first step, we selected models for sex ratio variation using only the 22 yr for which female condition data were available. In a second step, we made use of the full data set available (48 yr) to explore more accurately the effect of environmental covariates (excluding condition) on sex ratio. In a distinct analysis, we tested the existence of temporal trends in sex ratio using a generalised additive model (GAM). The GAM allows for non-linearity in the temporal trend using thin plate regression splines (Wood 2006).

We defined the condition of culled females as the difference between a female's body mass and the expected body mass for an average female of the same age. As bison body mass increases non-linearly with age, we used a GAM to model the relationship and to predict the average body mass at a given age. We also used a GAM to test the existence of temporal trends in female condition. In both models, we included a random 'year' effect to account for non-systematic year-to-year variation in body mass or condition (Crawley 2007).

RESULTS

The European bison population in BPF has undergone 3 distinct periods of flux: an initial population increase at low density following release into the wild from captive breeding centres between 1957 and 1973 (increase from 6 to 253 ind.); a relatively stable population at moderate density between 1974 and 1993 (range: 210–271 ind.); and finally an increasing population at high density between 1994 and 2007 (from 265 to 439 ind.; Fig. 1). The calf sex ratio fluctuated considerably from year to year, in part due to small sample size in some years, and ranged between 0.3 and 0.68 (but see standard errors in Fig. 1). Calf sex ratio tended to be male-biased prior to 1975 and female-biased after 1985, as shown by the temporal trend in Fig. 1. The proportion of each age class remained relatively constant throughout the study period (Fig. 2).

Female body mass reached its maximum around the age of 22 yr (Fig. 3). The condition index derived as the residuals from the body mass–age relationship shows that female condition declined significantly over the period 1992 to 2008 (Fig. 3), coinciding with the second phase of density increase in the Białowieża bison population (Fig. 1).

The correlation between female condition and population density was limited (-0.18), so both covariates could be considered simultaneously as candidates in

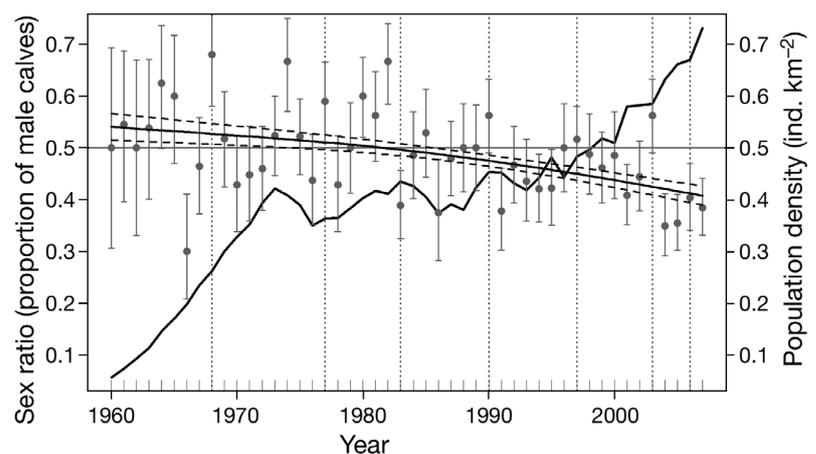


Fig. 1. *Bison bonasus*. Summary plot of the population density (black solid line) and calf sex ratios (grey dots showing mean \pm 1SD) of the Białowieża Primeval Forest European bison population between 1960 and 2007. The horizontal grey line indicates an even sex ratio. The black solid and dashed curves represent the temporal trend in sex ratio as estimated by a generalised additive model (model fit and standard error, respectively). Acorn mast years are also shown by grey vertical dashed lines. Population index shows 3 periods of population dynamics: an increasing population at low density (1960–1973); a stable population at intermediate density (1974–1993); and an expanding population at high density (1994–2007)

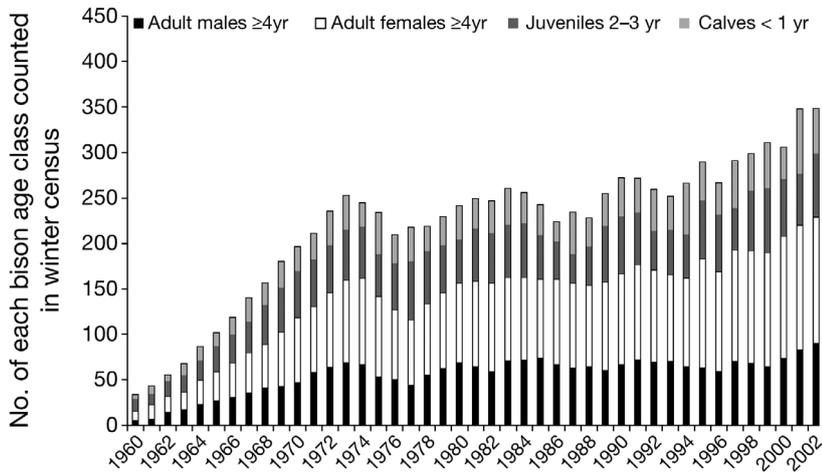


Fig. 2. *Bison bonasus*. Age class composition of European bison censused in Poland's Białowieża Primeval Forest

the model of calf sex ratio. When restricting the data to the 22 yr for which female condition data were available, Akaike weights suggested that the sex ratio of calves is best explained by population density (negative effect on the proportion of males) and by winter temperatures (negative effect; see Model 1, Table 1). However, replacing population density by female condition performed nearly as well (Model 2, $\Delta AIC_c = 1.3$; Table 1). Models including the effect of acorn masting (positive effect of masting on the proportion of males in the following winter and a slight negative effect in the winter after that) were also supported, but with a probability 3 times lower than the best model. When using data from all years, 5 models received particularly strong support according to their Akaike weights, which included the effects of

population density (negative effect on the proportion of male calves), acorn mast (positive effect in the following winter and slightly negative in the year after) and average temperature of the previous winter (negative effect). Models including acorn mast broken into 2 categories (mast year versus non-mast year; e.g. Models 1' and 5'; see Table 1) had probabilities 2 times higher than similar models using 3 levels (mast year, year after mast and other non-mast year; Models 4' and 8'). The 3-level model suggested an increase in the proportion of males in the winter following the mast, a slight female bias in the year following that, and no effect thereafter. Hence,

bison calf sex ratios are male-biased in mast years (Fig. 4b), but evidence for delayed effects in the year after mast is more limited. There was some support for a negative interaction between masting and population density, with the positive effect of masting disappearing at high population density (Model 3'). Models including mean annual temperatures (negative effect) were plausible but ranked low (model probability 3 times lower than equivalent models without temperature; see Table 1). Mean annual temperature therefore does not appear to be a strong predictor of bison calf sex ratios. The results of Model 1' (best model using data from all years; Table 1) are presented in Fig. 4 and show the decrease in the proportion of male calves with population density (Fig. 4a) and the positive effect of acorn mast (Fig. 4b).

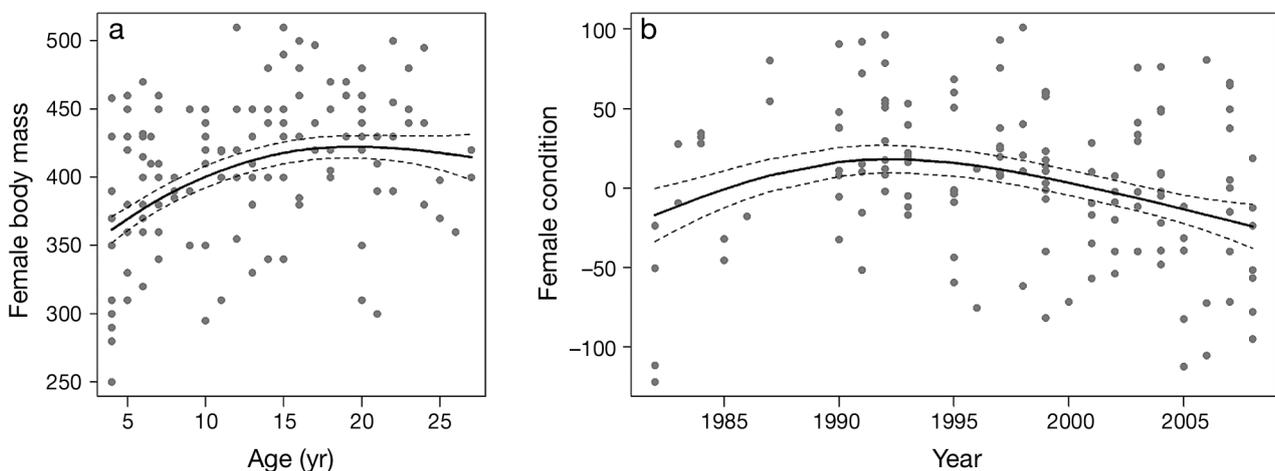


Fig. 3. *Bison bonasus*. (a) Relationship between female body mass and age in Białowieża Primeval Forest; (b) temporal trend in female condition (measured body mass – average body mass at a given age) showing a decline after 1992. Body mass was taken from individuals culled in winter between 1990 and 2008

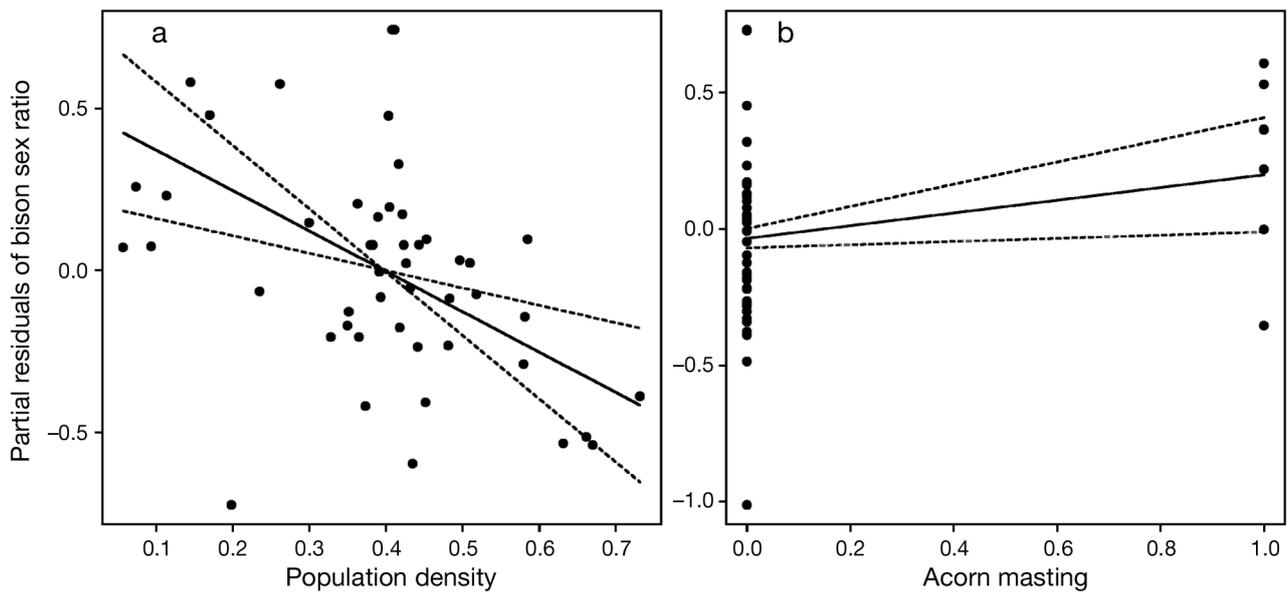


Fig. 4. *Bison bonasus*. Calf sex ratio (proportion of males) of the European bison population in relation to (a) population density; (b) acorn production (0 = non-mast year, 1 = mast year) based on the Model 1 variables (see Table 1). The plots show partial regression terms (solid line) and partial residuals of the proportion of male calves (dots) against each predictor. Dashed lines represent SE

DISCUSSION

We used evolutionary biology theory to analyze and evaluate conservation management strategies. Intensive management may alter the evolutionary trajectory of small populations, such as Białowieża European bison population, in the same manner as removing coalitions of male lions *Panthera leo* may reduce predation attempts on African buffalo *Synceus caffer* and thereby alter their anti-predator adaptations (Hayward et al. 2007). As the European bison population density in BPF increased, female body mass decreased and parasite loads increased, indicating a corresponding decline in condition. In the 1980s, $23 \pm 9\%$ of sampled European bison were affected by parasites; however, by 2006, $66 \pm 16\%$ were affected by parasites and increases in the num-

bers of all sampled parasites except *Dicrocoelium dendriticum* were observed (Table 2; Demiaszkiewicz & Lachowicz 2007). However, increasing parasite load may result not only from increasing densities, but also from strong winter concentration of bison arising from supplementary feeding in fixed locations (Radwan et al. 2010, Pyziel et al. 2011). Blood serum and morphological changes also suggest that Białowieża's bison have declined in condition over the past 20 yr (Wołk & Krasińska 2004). This decline in female body condition appears to have led to a female-biased sex ratio, as predicted by sex allocation theory (Trivers & Willard 1973).

The difference in calf sex ratio between a mast year and the year following an acorn mast crop are unexpected compared to our predictions. We hypothesized that the calf sex ratio would be male-biased in the year

following an acorn mast crop because pregnant females would be in better condition for the duration of their pregnancy. Masting occurs during the second half of September, by which time most females are pregnant. Masting leads to an increased number of calves born (Myserud et al. 2007), but not to an increase in the proportion of males born in the following year (Fig. 1), as we had hypothesized. However, there was an increased propor-

Table 2. Extent of parasite loads in European bison in Białowieża Primeval Forest (Poland) based on the percentage of culled bison parasitized by each species. (-): Years for which no data were collected for those species of parasite. Data from Demiaszkiewicz & Lachowicz (2007)

Parasite	1986	1999	2001	2004	2006
<i>Fasciola hepatica</i>	44	-	-	50	100
<i>Dicrocoelium dendriticum</i>	41	-	-	23	31
<i>Parafasciolopsis fasciolaemorpha</i>	6	-	-	9	27
<i>Ashworthius sidemi</i>	0	0	25	100	100
<i>Setaria labiatopapillosa</i>	25	-	-	41	71

tion of males born in the year of the mast (Fig. 4b). We hypothesize that the North Atlantic Oscillation (NAO), which initiates masting in oaks, also has a positive effect on the body condition of female bison and that it is thus the NAO, rather than the acorn mast, which drives the male-biased calf sex ratio. This seems likely, given that the maternal energy balance at or soon after conception influences birth sex in black rhinoceros *Diceros bicornis*, wild horses *Equus caballus* and parrots (Clout et al. 2002, Cameron & Linklater 2007, Berkeley & Linklater 2010). An alternative explanation could be the differential mortality of calves between birth in spring and the population census in winter if males are more food limited than females.

Mast years tend to be correlated with climatic variables, such as temperature or precipitation, and have often followed years with hot summers and mild winters (Sork 1993, Kelly & Sork 2002, Abrahamson & Layne 2003, Overgaard et al. 2007). Pre-breeding environmental conditions (Mysterud et al. 2007) probably influence the body condition of females and result in higher fecundity or biased calf sex ratios. It seems that variation in environmental condition due to climatic changes (e.g. increased frequency of mast years; Overgaard et al. 2007) may influence bison fecundity and sex ratio in the future.

The female bias in the sex ratio became increasingly apparent during the last period of rapid population growth (Fig. 4a). This corresponds to the period for which we have data on female body condition and supports our conclusions that a decline in body condition, associated with increasing population density, has driven the observed female-bias in the calf sex ratio. Incidentally, data from the European bison population in the Belarussian side of BPF also show a female bias at higher population density levels (R. Kowalczyk unpubl. data).

Managers of the European bison in BPF have taken a very 'hands-on' approach to its conservation since its restitution in the wild, via selective breeding, culling sick or injured individuals, provisioning food, creating artificial habitat by mowing meadows and creating additional sources of water (Krasińska & Krasiński 2007). Nonetheless, despite being highly inbred and highly managed, there is no evidence that this intensive management has affected the way the European bison sex ratio is expected to respond to environmental variation. Further research is required to ascertain the mechanism driving variation in the European bison sex ratio and to determine when the ratio deviates from parity (e.g. fewer males conceived, higher pre- or post-natal mortality of males compared to females; Monard et al. 1997).

Acknowledgements. M.W.H. and T.C. were funded by a Marie Curie Transfer of Knowledge Fellowship BIORESC of the European Community's Sixth Framework Programme under contract number MTKD-CT-2005-029957. The study was supported by the budget of the Mammal Research Institute PAS in Białowieża. We are grateful to the inter-library loan service of the University of New South Wales, Australia, for collecting several important papers.

LITERATURE CITED

- Abrahamson WG, Layne JN (2003) Long-term patterns of acorn production for five oak species in xeric Florida uplands. *Ecology* 84:2476–2492
- Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York, NY
- Berkeley EV, Linklater WL (2010) Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *S Afr J Wildl Res* 40:53–57
- Bjorneraas K, Solberg EJ, Herfindal I, Saether BE (2009) Large-scale spatiotemporal variation in calf sex ratio in moose (*Alces alces*): an effect of density-dependent decrease in maternal condition? *Can J Zool* 87: 346–355
- Cameron EZ, Linklater WL (2002) Sex bias in studies of sex bias: the value of daughters to mothers in poor condition. *Anim Behav* 63:F5–F8
- Cameron EZ, Linklater WL (2007) Extreme sex ratio variation in relation to change in condition around conception. *Biol Lett* 3:395–397
- Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, NJ
- Clout MN, Elliott GP, Robertson BC (2002) Effects of supplementary feeding on the offspring sex ratio of kakapo: a dilemma for the conservation of a polygynous parrot. *Biol Conserv* 107:13–18
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. *Q Rev Biol* 61:339–374
- Cockburn A, Legge S, Double MC (2002) Sex ratios in birds and mammals: Can the hypotheses be disentangled? In: Hardy ICW (ed) Sex ratios: concepts and research methods. Cambridge University Press, Cambridge, p 266–286
- Crawley MJ (2007) The R Book. John Wiley & Sons, Chichester
- Daleszczyk K, Bunevich AN (2009) Population viability analysis of European bison populations in Polish and Belarussian parts of Białowieża Forest with and without gene exchange. *Biol Conserv* 142:3068–3075
- Demiaszkiewicz AW, Lachowicz J (2007) Rise of helminth infections in European bison in Białowieża Forest. In: Olech W (ed) Role of ex-situ breeding in bison restitution. Goluchow, Krakow, p 12–16
- Frank SA (1990) Sex allocation theory for birds and mammals. *Annu Rev Ecol Syst* 21:13–55
- Gomendio M, Malo AF, Soler AJ, Fernandez-Santos MR and others (2006) Male fertility and sex ratio at birth in red deer. *Science* 314:1445–1447
- Hayward MW, Hofmeyr M, O'Brien J, Kerley GIH (2007) Testing predictions of the prey of the lion (*Panthera leo*) derived from modeled prey preferences. *J Wildl Manag* 71:1567–1575
- IUCN (International Union for Conservation of Nature) (2007) 2007 Red List of Threatened Species. IUCN, Gland

- Jędrzejewska B, Jędrzejewski W (1998) Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. Springer, Berlin
- Jędrzejewska B, Pucek Z, Jędrzejewski W (2004) Seed crops and forest rodents. In: Jędrzejewska B, Wójcik JM (eds) Essays on mammals of Białowieża Forest. Mammal Research Institute, Polish Academy of Science, Białowieża, p 129–138
- Kelly DJ, Sork VL (2002) Mast seeding in perennial plants: why, how, where? *Annu Rev Ecol Syst* 33:427–447
- Kerley GIH, Kowalczyk R, Cromsigt JPGM (2011) Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? *Ecography* (in press)
- Koskela E, Mappes T, Niskanen T, Rutkowska J (2009) Maternal investment in relation to sex ratio and offspring number in a small mammal—a case for Trivers and Willard theory? *J Anim Ecol* 78:1007–1014
- Kowalczyk R, Taberlet P, Coissac E, Valentini A, Miquel Ch, Kamiński T, Wójcik JM (2011) Influence of management practices on large herbivore diet—case of European bison in Białowieża Primeval Forest (Poland). *For Ecol Manag* 261:821–828
- Krasińska M, Krasiński ZA (2002) Body mass and measurements of the European bison during postnatal development. *Acta Theriol* 47:85–106
- Krasińska M, Krasiński ZA (2004) Life of the European bison. In: Jędrzejewska B, Wójcik JM (eds) Essays on mammals of Białowieża Forest. Mammal Research Institute, Polish Academy of Science, Białowieża, p 35–42
- Krasińska M, Krasiński ZA (2007) The European bison: a nature monograph. Mammal Research Institute, Polish Academy of Science, Białowieża
- Krasiński ZA, Raczyński J (1967) The reproduction biology of European bison living in reserves and freedom. *Acta Theriol* 12:407–444
- Monard AM, Duncan P, Fritz H, Feh C (1997) Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behav Ecol Sociobiol* 41:243–249
- Mysterud A, Yoccoz NG, Stenseth NC, Langvatn R (2000) Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J Anim Ecol* 69: 959–974
- Mysterud A, Barto K, Jędrzejewska B, Krasiński ZA and others (2007) Population ecology and conservation of endangered megafauna: the case of European bison in Białowieża Primeval Forest, Poland. *Anim Conserv* 10: 77–87
- Overgaard R, Gemmel P, Karlsson M (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. *Forestry* 80:555–565
- Pucek Z (2004) European bison - history of a flagship species. In: Jędrzejewska B, Wójcik JM (eds) Essays on mammals of Białowieża Forest. Mammal Research Institute, Polish Academy of Science, Białowieża, p 25–34
- Pyziel AM, Kowalczyk R, Demiaszkiewicz AW (2011) The annual cycle of shedding *Eimeria* oocysts by European bison (*Bison bonasus*) in the Białowieża Primeval Forest, Poland. *J Parasitol* 97:737–739
- Radwan J, Demiaszkiewicz AW, Kowalczyk R, Lachowicz J and others (2010) An evaluation of two potential risk factors, MHC diversity and host density, for infection by an invasive nematode *Ashworthius sidemi* in endangered European bison (*Bison bonasus*). *Biol Conserv* 143: 2049–2053
- Reuterwall C (1981) Temporal and spatial variability of the calf sex ratio in Scandinavian moose *Alces alces*. *Oikos* 37:39–45
- Rutberg AT (1986) Lactation and fetal sex ratios in American bison. *Am Nat* 127:89–94
- Saether BE, Solberg EJ, Heim M, Stacy JE, Jakobsen K, Olstad R (2004) Offspring sex ratio in moose *Alces alces* in relation to paternal age: an experiment. *Wildl Biol* 10: 51–57
- Samojlik T, Jędrzejewska B (2005) The bison—rich treasure of the forests. In: Samojlik T (ed) Conservation and hunting: Białowieża Forest in the time of kings. Mammal Research Institute, Polish Academy of Science, Białowieża, p 75–88
- Silk JB (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 121:56–66
- Silk JB (1984) Local resource competition and the evolution of male-biased sex ratios. *J Theor Biol* 108:203–213
- Sork VL (1993) Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.). *Vegetatio* 108:133–147
- Tokarska M, Kawałko A, Wójcik JM, Pertoldi C (2009) Genetic variability in the European bison (*Bison bonasus*) population from Białowieża forest over 50 years. *Biol J Linn Soc* 97:801–809
- Tokarska M, Pertoldi C, Kowalczyk R, Perzanowski K (2011) Genetic status of the European bison *Bison bonasus* after extinction in the wild and subsequent recovery. *Mammal Rev* 41:151–162
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–92
- Waldram MS, Bond WJ, Stock WD (2008) Ecological engineering by a mega-grazer: white rhino impacts on a South African savanna. *Ecosystems* 11:101–112
- Wójcik JM, Kawałko A, Tokarska M, Jaarola M, Vallenback P, Pertoldi C (2009) Post-bottleneck mtDNA diversity in a free-living population of European bison *Bison bonasus*—implications for conservation. *J Zool* 277:81–87
- Wolk E, Krasińska M (2004) Has the condition of European bison deteriorated over last twenty years? *Acta Theriol* 49:405–418
- Wood SN (2006) Generalized additive models: an introduction with R. Chapman & Hall/CRC, Boca Raton, FL