Population ecology and conservation of endangered megafauna: the case of European bison in Białowieża Primeval Forest, Poland

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Keywords
climate; density dependence; mortality; North Atlantic Oscillation; reproduction; vital rates; winter weather severity.

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Abstract
The European bison *Bison bonasus* is an example of nearly extinct ‘charismatic megafauna’. The Białowieża Primeval Forest in Poland is among the few places where they still live in the wild. The management of this free-living herd has to reconcile to the conservation needs of a species and the economic and environmental objectives of their habitat: protected as well as commercial woodlands of Białowieża. Here we present a detailed account of the population development and analyse variation in vital rates based on monitoring that started in 1952 and continued until 2002. The population was allowed to grow freely until 1970, when removal started with the aim to stabilize population size. We found that recruitment rate, but not mortality, was density dependent, suggesting that the population density was not very high relative to resource levels. Winters with much snow and cold temperature had a strong negative effect on survival. May temperature of the previous year positively affected recruitment rates. Masting (oak seed) also positively affected recruitment rates, which provides a rare account of masting affecting the performance of a large ruminant. Sex ratio of offspring was even and was not strongly affected by density or climate. We use an age-structured matrix model to show how this knowledge of intrinsic and extrinsic factors affecting vital rates may help managerial decisions by providing explicit links between given environmental conditions and the population growth rates.

Introduction
Humans have persecuted large herbivore species for meat, fur and trophies since prehistorical times until present (Taylor & Dunstone, 1996). Overharvesting in combination with climate change and habitat loss are likely causes of the extinctions (Meffe & Carroll, 1997; Burney & Flannery, 2005; Wroe, Field & Grayson, 2006). Other species have survived in low numbers and are currently subject to intense conservation effort to save the populations and their original genetic variation. Clearly, successful conservation of such species requires knowledge from several scientific disciplines (Simberloff, 1988; Meffe & Carroll, 1997), including also population ecology. Large mammals often occur in low densities due to food limitation. Since reserve sizes are usually severely restricted for large mammals, absolute population sizes are often small, but still sizes often need to be regulated due to resource limitation. Regulating their numbers within sustainable levels may be facilitated through insight into the causes of annual variation in vital rates, and how much variation in specific vital rates in turn affects annual population growth rates. Thus, in many cases, a detailed understanding of variation in and importance of vital rates is an important step towards a scientifically based conservation plan.

One example of nearly extinct ‘charismatic megafauna’ is the European bison *Bison bonasus* or wisent (Glover, 1947; Munns, 1948; Jaczewski, 1958; Pucek et al., 1996). These huge animals – adult females and males reach weights of 400 and 700 kg, respectively (Krasinski & Krasinski, 2002) – once roamed over large areas of Europe. Nowadays, they are scattered in small populations and face problems of inbreeding, mainly due to the historical bottleneck of population numbers in the early 20th century (e.g. Olech,
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H1. The density hypothesis: We predict reduced recruitment rates, increased mortality (Fowler, 1987; Gaillard et al., 2000) and sex ratios skewed towards females (Kruuk et al., 1999; Mysterud et al., 2000) at high density.

H2. The winter severity hypothesis: We predict a negative effect of winter severity (low temperature and deep snow) on recruitment rates and survival rates (e.g. Cederlund, Sand & Pehrson, 1991) and increasingly female-biased sex ratios of newborns with increasing winter severity (Mysterud et al., 2000).

H3. The early summer climate hypothesis: For the spring/summer climate it is more difficult to derive clear predictions, as high temperatures in May and June may be either (H3a) negative (e.g. Sæther, 1985; Bo & Hjeljord, 1991) or (H3b) positive for ungulate performance (e.g. Pettorelli et al., 2005a,b).

H4. The masting hypothesis: Oak Quercus robur seed crops in BPF are extremely variable from year to year, with masts at 6–9-year intervals (Jędrzejewska & Jędrzejewski, 1998). It has been shown that wild boar Sus scrofa reproduce more successfully after years with masting, but so far the effect of masting on other ungulates, including European bison, has not been studied. We predict higher recruitment rates, less mortality and more male-biased offspring sex ratios after years of masting.

H5. The September rainfall hypothesis: Specifically for the European bison population in BPF, an earlier account found that rainfall in September was the most important abiotic factor (Gill, 1998). The number of calves dropped with increasing rainfall in September and the sex ratio of offspring became more female biased (Gill, 1998).

On the basis of the testing of these hypotheses, we propose modifications to the current conservation and management measures, especially with regard to the yearly offtake of animals and the extent of supplementary winter feeding.

Materials and methods

Study area and its natural history

The BPF (about 1500 km²), 52°45’N, 24°E, which straddles the Polish–Belarussian border, is one of the best preserved deciduous and mixed forests of European lowland (Jędrzejewska & Jędrzejewski, 1998). The Polish (600 km²) and the Belarussian (900 km²) parts of the forest are separated by a 2.5-m-wire fence, built along the former Soviet border in 1981. Since that time, the European bison inhabiting the Polish and Belarussian parts have had no contact with each other. This study concentrates on the bison inhabiting the Polish part of BPF. The study area consists of oldgrowth and protected forests in Białowieża National Park (105 km²), surrounded by managed (i.e. harvested and replanted) tree stands (495 km²). The mean age of tree stands exceeds 100 years in the national park and averages 75 years in the managed forests. Throughout the Polish part of BPF, coniferous and mixed forests dominated by pine Pinus silvestris and spruce Picea abies cover 52% of the area, wet forests with black alder Alnus glutinosa and ash Fraxinus excelsior cover 20%, and rich deciduous tree stands dominated by oak, hornbeam Carpinus betulus, lime Tilia cordata and maple Acer platanoides cover 16%. Finally, birch Betula verrucosa and Betula pubescens and aspen Populus tremula stands cover 12% of the area. The only open areas within BPF are sedge Carex spp. and reed Phragmites spp. marshes found in narrow (0.1–1-km-wide) river valleys and several small glades with adjacent villages. The terrain of BPF is flat with an elevation of 134–186 m a.s.l.

The climate of BPF is transitional between continental and Atlantic types, with clearly marked cold and warm seasons. During the last 40 years, the mean temperatures of January and July were −4.2 and 18.6 °C, respectively. The mean annual precipitation was 631 mm (range 438–931) and maximum snow cover averaged 34 cm (range 4–95).

In BPF, the European bison coexist with four species of ungulates, moose Alces alces, red deer Cervus elaphus, roe deer Capreolus capreolus and wild boar, and two species of large carnivores, lynx Lynx lynx and wolves Canis lupus, of which the latter may sporadically prey on bison (Jędrzejewska & Jędrzejewski, 1998).

At the end of the 19th century, BPF contained the last remaining population of lowland European bison. The
species has been protected there as a royal game since the 14th century. The population eventually became extinct in 1919, after a few years of heavy poaching during World War I and the subsequent political chaos. In 1929, an international captive breeding programme was initiated, based on animals collected from zoological gardens and brought to enclosures in BPF. In 1952, the first captive-raised bison were released into BPF. This population grew rapidly, reaching 100 animals in 1965 and 200 bison in 1971 (Krasinski, 1978). Annual removal from the herd started in 1970 for translocation purposes. In the early 1980s, the National Park personnel began to cull the herd (20–40 bison year\(^{-1}\)) on an annual basis to stabilize numbers (Krasinski & Krasinska, 1994). Since that time, bison numbers in the Polish part of BPF have remained at about 250–350 individuals. In the Belarusian part, a herd of c. 300 bison is maintained using similar management practices (Krasinski et al., 1994). All contemporary European bison are the descendents of 12 animals; therefore high inbreeding remains a serious threat to species survival (Pucek, 2004).

In spring and summer, the basic food of European bison in BPF consists of grasses, sedges and herbs (Borowski & Kossak, 1972). They forage 60% of daytime hours (Caboń-Raczyńska et al., 1987). Mixed groups (including adult females, subadults and young) have an average home range of 69 km\(^2\) during summer. Adult males (single or in small bachelor groups) move in ranges of similar size (mean 70 km\(^2\)) (Krasinski & Krasinska, 1995; Krasinska, Krasinski & Bunevich, 2000). Throughout winter, bison are provided with abundant supplementary food. Hay is placed in c. 15 feeding stations. In BPF, supplementary winter feeding of bison has existed since the 1700s, although historically bison had access to hay stacks in riverside meadows since the 1400s (Hedemann, 1939; Samojlik & Jędrzejewska, 2004). Contemporarily, winter feeding strongly affects the behaviour of the bison. Their movements are reduced, home ranges shrink and social structure changes into a few large aggregations at the feeding sites (Krasinski & Raczyński, 1967; Rouys, 2003).

**Bison data**

Observations of free-ranging bison in Białowieża Forest were carried out since the start of free breeding (1952). Annual counts of bison were conducted each winter by personnel of Białowieża National Park. In December–February (most often in January), when bison were aggregated around feeding stations, all stations were visited at the same time after the first snow fall, and the animals attending them were counted with visual identification of sex and age. Moreover, during the fieldwork, all records of bison (animals or their tracks seen) not staying at the feeding sites were noted. The number of animals counted was noted in the national park records as population status for 31 December year \(t\). Ageing was based on visual identification in the field, which was only suitable for group animals in the main life stages (juveniles, yearlings/subadults and adults).

Mortality of the bison herd was monitored year round by the national park personnel, who recorded all animals that were found dead. Furthermore, forestry services of BPF informed the park about any dead bison encountered in the forest. The park personnel visited all carcasses in an attempt to identify the cause of death, which was possible in about 70% of cases.

Annual culling of the population is conducted in winter by the national park services and a number to be culled each year is proposed by the park and finally accepted by the Ministry of Environment.

The population parameters recorded each year and analysed in this paper were:

1. **Population size and sex and age structure**: Total number of bison at the end of the year \(n_{\text{tot}}\); Number of adult bison, that is 4 years and older \(n_{\text{adult}}\); Number of subadult bison, that is 1.5–3.5 years of age \(n_{\text{subadult}}\); number of bison less than 1 year old \(n_{\text{calves}}\). Animals in all age classes were separated by sex (Fig. 1).

2. **Recruitment**: Female bison only produce one offspring per breeding event. Number of bison recruited \(n_{\text{rec}}\), recruitment rates \(n_{\text{rec}} \text{ (year } t \text{) per } n_{\text{female adults (year } t-1)}\). After the mating season in August–September, calves are born in May–July; therefore the winter counts record the calves when they are 6–8 months old.

3. **Mortality**: Total loss from population = number of (naturally) dead bison + number of live-captured bison + number of culled bison + number of lost (missing) bison. In this study, special attention was paid to the natural mortality of bison, the main causes of which were disease and injuries, each accounting for 21% of all dead bison, followed by senescence and poaching (each 7%, average values from 1952 to 2002; Krasinska & Krasinski, 2004).

**Data on climate and seed crop**

Data on monthly averages of temperature, precipitation and snow depth from 1960 to 2002 were available from the meteorological station in Białowieża village, located at the centre of BPF. The number of monthly weather parameters is very high, which is problematic from a model selection perspective (Burnham & Anderson, 2002). Also, monthly values may be misleading if mortality is not restricted to specific months (Mysterud et al., 2003; Hallett et al., 2004; Stenseth & Mysterud, 2005). We therefore also used seasonal indices for the North Atlantic Oscillation (NAO; Hurrell, 1995; Stenseth et al., 2003): for winter between December and February (NAO\(_{\text{wint}}\)), for spring between March and May (NAO\(_{\text{spr}}\)), for summer between June and August (NAO\(_{\text{sum}}\)) and for autumn between September and November (NAO\(_{\text{aut}}\)). For winter months, simple correlations showed close relationships between temperature and snow depth (Table 1). For that reason, we used principal component analysis (PCA) to obtain an overall picture of the winter climate, and hence more tractable from a model selection perspective. The first PCA (hereafter termed PCA\(_{\text{1-wint}}\)) explained 78.7% of the variance, a high value corresponding to warm temperatures and little
snow and, conversely, a low index corresponding to cold, snowy winters (Table 1). For the summer season, there was little correlation between months, and we used averages for May and June temperatures, which is regarded as important for spring conditions in Europe (e.g. Gaillard et al., 1996; Pettorelli et al., 2005a,b; Pettorelli et al., 2006). We therefore used the first PCA (PCA1) for winter, and retained the monthly averages for summer.

Quantitative data on oak seed crop in 1960–2000 (with the exception of 7 years, for which only qualitative data were available) were provided by the Bialowieża Forest Administration (Jędrzejewska & Jędrzejewski, 1998; Stenseth et al., 2002). The indices of crops (in kg) were the annual purchases (for re-plantation purposes) of acorn from the local people, who gathered them in the exploited part of BPF. The amount of acorn purchased relates to the seed crop. It

### Table 1

<table>
<thead>
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</tr>
</thead>
<tbody>
<tr>
<td>PCA1-winter</td>
<td>1.000</td>
<td>0.767</td>
<td>0.726</td>
<td>0.680</td>
<td>–0.244</td>
<td>–0.145</td>
<td>0.066</td>
<td>–0.777</td>
<td>–0.841</td>
<td>–0.843</td>
</tr>
<tr>
<td>NAO-station based</td>
<td>0.759</td>
<td>0.604</td>
<td>0.596</td>
<td>0.677</td>
<td>–0.059</td>
<td>–0.166</td>
<td>0.270</td>
<td>–0.498</td>
<td>–0.531</td>
<td>–0.640</td>
</tr>
<tr>
<td>NAO-PCA based</td>
<td>0.742</td>
<td>0.602</td>
<td>0.596</td>
<td>0.474</td>
<td>–0.111</td>
<td>–0.130</td>
<td>0.159</td>
<td>–0.587</td>
<td>–0.598</td>
<td>–0.551</td>
</tr>
</tbody>
</table>

Temp, temperature; Prec, precipitation; Snow, snow depth; PCA, principal component analysis; NAO, North Atlantic Oscillation.
cannot, however, be excluded that this assessment is somewhat influenced by current prices, making the actual value of the index less reliable. Moreover, for the 7 years with no quantitative data, information on masting/non-masting was available. We therefore categorized all the data into masting and non-masting years.

Statistical analyses

Variation in recruitment rates (proportion of adult females having calf on foot in January), mortality (number of animals found dead relative to total population size) and sex ratio of juveniles (proportion of male calves) were analysed using generalized linear models with a binomial error and a logit link (i.e. logistic regression). To check for possible overdispersion, we used the residual deviance that should approach the model degrees of freedom (d.f.). For recruitment rates, the final model was overdispersed (residual deviance = 91.690, d.f. = 35), which will lead to too narrow confidence intervals. We therefore rather used a quasibinomial error, which takes into account this overdispersion (i.e. using quasilikelihood to fit the model). Standard diagnostic tools were applied to the final models.

We used the Akaike information criterion corrected (AICc) for sample size for selecting an appropriate model for hypothesis testing (Burnham & Anderson, 2002; Johnson & Omland, 2004; see also Stephens et al., 2005). When using the quasibinomial error, we calculated QAICc adjusting for overdispersion by dividing the residual deviance (i.e. −2 loglikelihood) with the overdispersion parameter calculated from the most complex model as the sum of squares Pearson residuals divided by the number of degrees of freedom (Burnham & Anderson, 2002). Models with the lowest AICc (or QAICc) value are considered to be the most parsimonious models, that is the best compromise between explaining most of the variation and simultaneously using as few parameters as possible. We used the subset years (1961–2001) for which all covariates were available in the model selection procedure. Using a forward or backward stepwise model selection strategy was not a good option in our case because the end result may be dependent on which variable is entered first (or last) in the model (e.g. Whittingham et al., 2006). We rather considered all models and ordered them according to their (Q)AICc values. Such a brute force approach may not be optimal in the sense that a very large number of models is considered (Burnham & Anderson, 2002), but we had no particular reasons to restrict our search to a small set of models, and are confident this approach is preferable to other alternatives (e.g. stepwise selection). The importance of the predictor variables was then assessed on the basis of proportion of models including those variables, and weighting the presence of a variable by the relative likelihood = AICc weights of the models (termed ‘importance’). Such an approach was advocated by Burnham & Anderson (2002, p. 167; see also MacKenzie et al., 2006). The significance of the most important variables may be assessed on the basis of 95% confidence intervals of regression parameters obtained from the best model judged by the AICc (or QAICc). Although this ignores the model selection process (see MacKenzie et al., 2006 for a similar approach), there is no simple way of using model averaging for estimating regression coefficients because regression coefficients have different interpretation in different models (e.g. consider a model with only additive effects vs. a model with interaction terms) or when parameters appear in only a subset of models (cf. Burnham & Anderson, 2002, pp. 155–167; and Richards, 2005). To estimate the amount of variation explained by the best model, we calculated the squared correlation between the observed proportions and the predicted proportions (based on the model; Mittlböck & Schemper, 1996; Pontier et al., 1998).

We constructed a deterministic age-structured model for the female segment of the bison population. Demographic rates of ungulates can be relatively well described by age groups; juveniles (juv), subadults (sa; 1–3 years in our case), prime-aged (pa) and senescent (sen) individuals (Caughley, 1966; Gaillard, Festa-Bianchet & Yoccoz, 1998), according to the ‘standard’ ungulate life cycle; cf. Gaillard et al. (2000). Unfortunately, we were not able to estimate all these parameters. Because the European bison usually start reproducing at 4 years of age (Krasinski & Raczyński, 1967), we could at least construct a very simplified age structure into the model (Bφm = Bsa = 0; while Bpa = Bsa is variable and estimated from the statistical analysis above). Note that age at first reproduction is often variable for ungulates (e.g. Langvatn et al., 2004), and we could not account for this. Sex ratio was fairly even (see Results). Together, this yielded a simple Leslie–Usher matrix model (Tuljapurkar & Caswell, 1997). We parametrized this model for different environmental scenarios on the basis of predictions from the best models of recruitment rates and mortality rates. We then obtained the asymptotic population multiplication rate (λ) for each matrix and performed an elasticity analysis (Tuljapurkar & Caswell, 1997; Benton & Grant, 1999; Coulson, Gaillard & Festa-Bianchet, 2005; Doak et al., 2005). Elasticity of λ is the change in λ resulting from a proportional change in a demographic rate. We analysed elasticity for changes in recruitment and adult survival.

Analyses were carried out in S-Plus version 6.2 (Crawley, 2003) and R version 2.2.1 (R Development Core Team, 2006). We always report differences between levels with ‘treatment’ contrasts, i.e. comparing levels of a factor with one specific level – a reference level.

Results

Recruitment rates, sex ratio of juveniles and natural mortality

Recruitment rates were best predicted \((R^2 = 0.588)\) by population density [importance (imp) = 1.00], temperature in May (imp = 0.91) and masting (imp = 0.74) the previous year. Recruitment rates decreased markedly as population size increased (Fig. 2), from above 70% down to below 40%
at high population density. Recruitment rates were higher after autumns with masting (Table 2, Fig. 2). The PCA1 for winter (imp = 0.55) was fairly often in the higher ranked models, but was not significant when added to the model including the other most important factors (\(T = 1.664, P = 0.105\)). The NAO in summer (imp = 0.19), and the interaction term between masting and population density (imp = 0.12) entered much fewer of the higher ranked models.

Over the whole period, a total of 741 males and 770 females was recorded recruited, giving a sex ratio of 49% males, that is very close to 50:50. Sex ratio was best predicted (\(R^2 = 0.157\)) by the summer NAO of the previous year (imp = 0.73) and year as a continuous trend (imp = 0.59), while population density (imp = 0.18), June temperature (imp = 0.18) and September precipitation (imp = 0.18) of the previous year, masting (imp = 0.24) and spring NAO the year before (imp = 0.24) ranked lower. Although the retained model included spring and summer NAO indices, the confidence intervals for these effects were quite wide (Table 2). We therefore failed to find a clear pattern of sex ratio variation and impacts of climatic variability in bison. There was no indication of overdispersion in this model (residual deviance = 20.233, d.f. = 33).

Variability in natural mortality was between 0 and 6% of the total population. Mortality rates were best predicted (\(R^2 = 0.145\)) by winter severity alone (imp = 1.00), while population density (imp = 0.44), masting (imp = 0.25), temperature in May (imp = 0.18) and NAO in autumn (imp = 0.13) and spring (imp = 0.06) were less important. With an increase in the PCA1-winter (warm, less snowy winter), mortality decreased (Table 2; Fig. 3). Thus, mortality was higher in cold winters with much snow. Even though population density had a fairly high importance and one may argue it should be included, the estimated effect was in opposite of prediction (estimate = 0.319; se = 0.271). There was no indication of overdispersion in this model (residual deviance = 39.255, d.f. = 39).

### Population growth rate and elasticity

The population was allowed to grow freely until 1970, when elimination was started to regulate the population, first by relocations, and since 1980 also by culling (Fig. 1). From 1960 to 1970, \(\lambda\) was 1.194. From 1970 to 2002, \(\lambda\) was on average 1.018 (Fig. 1). We then used the matrix model and parametrized it with the above data for eight situations: mild versus severe winter, warm versus cold May, and for years with and without masting for the high-density period.
wildlife such as the European bison. We have presented the first extensive analysis of vital rates of this highly endangered species. There was marked density dependence in recruitment rates (supporting H1), while there was no evidence that density affected mortality, thus suggesting an early stage of density effects (more below). After snowy, cold winters, reproduction was lower and mortality increased; thus, the winter severity hypothesis (H2) was supported. It was well documented that severe winters negatively affect individual body mass (Cederlund et al., 1991; Loison, Langvatn & Solberg, 1999) and the population growth of ungulates (Jacobson et al., 2004; Grotan et al., 2005; Mysterud & Østbye, 2006) in northern areas. The PCA based on local weather provided a better function for winter severity than the NAO index. Temperature in May the previous year positively affected recruitment rates (supporting H3a), suggesting that an early spring is favourable to the bison. Spring and summer conditions are indeed known to be important to ungulates (e.g. Pettorelli et al., 2005a; Stewart et al., 2005). Interestingly, we found evidence that recruitment rate was higher after years with masting (supporting H4). Both factors (May temperature and acorn crop of the last year) reflect improved feeding conditions for the bison, which – in the case of adult females – translate to higher breeding success. In warm springs, the herb layer on the forest floor develops earlier and is more abundant (Aulak, 1976), which makes bison leave their winter feeding sites earlier and forage on natural food. The intense feeding of bison on acorn in autumn was observed by Krasinska & Krasinski (1997), who noticed that in years of good crops bison shifted their ranges to include tree stands with old oaks.

We failed to replicate the result that September rainfall should influence recruitment rates and sex ratio in European bison (not supporting H5; Gill, 1993). The latter may possibly be because Gill (1998) calculated the recruitment rates as a percentage of the whole population rather than relative to adult female numbers as used here.

### Discussion

Knowledge on the detailed population ecology is an important aspect necessary for the successful conservation of wildlife such as the European bison. We have presented the first extensive analysis of vital rates of this highly endangered species. There was marked density dependence in recruitment rates (supporting H1), while there was no evidence that density affected mortality, thus suggesting an early stage of density effects (more below). After snowy, cold winters, reproduction was lower and mortality increased; thus, the winter severity hypothesis (H2) was supported. It was well documented that severe winters negatively affect individual body mass (Cederlund et al., 1991; Loison, Langvatn & Solberg, 1999) and the population growth of ungulates (Jacobson et al., 2004; Grotan et al., 2005; Mysterud & Østbye, 2006) in northern areas. The PCA based on local weather provided a better function for winter severity than the NAO index. Temperature in May the previous year positively affected recruitment rates (supporting H3a), suggesting that an early spring is favourable to the bison. Spring and summer conditions are indeed known to be important to ungulates (e.g. Pettorelli et al., 2005a; Stewart et al., 2005). Interestingly, we found evidence that recruitment rate was higher after years with masting (supporting H4). Both factors (May temperature and acorn crop of the last year) reflect improved feeding conditions for the bison, which – in the case of adult females – translate to higher breeding success. In warm springs, the herb layer on the forest floor develops earlier and is more abundant (Aulak, 1976), which makes bison leave their winter feeding sites earlier and forage on natural food. The intense feeding of bison on acorn in autumn was observed by Krasinska & Krasinski (1997), who noticed that in years of good crops bison shifted their ranges to include tree stands with old oaks.

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### Table 3

Demographic rates used in a simple deterministic age-structured population model to guide conservation measures.

<table>
<thead>
<tr>
<th>Environmental conditions</th>
<th>Winter</th>
<th>Masting</th>
<th>May temp (°C)</th>
<th>Recruitment rates</th>
<th>Mortality rates</th>
<th>Elasticity</th>
<th>Adult survival</th>
<th>Lambda (λ)</th>
<th>Suggested modifications in management practices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(Mortality %)</td>
<td>(%)</td>
<td></td>
<td></td>
<td></td>
<td>Supplementary winter feeding</td>
</tr>
<tr>
<td>Severe</td>
<td>No</td>
<td>10</td>
<td>0.273</td>
<td>0.048</td>
<td>0.072</td>
<td>0.710</td>
<td>1.049</td>
<td></td>
<td>Normal</td>
</tr>
<tr>
<td>Mild</td>
<td>No</td>
<td>10</td>
<td>0.273</td>
<td>0.021</td>
<td>0.072</td>
<td>0.710</td>
<td>1.078</td>
<td></td>
<td>Reduced</td>
</tr>
<tr>
<td>Severe</td>
<td>Yes</td>
<td>10</td>
<td>0.343</td>
<td>0.048</td>
<td>0.082</td>
<td>0.673</td>
<td>1.068</td>
<td></td>
<td>Normal</td>
</tr>
<tr>
<td>Mild</td>
<td>Yes</td>
<td>10</td>
<td>0.343</td>
<td>0.021</td>
<td>0.082</td>
<td>0.673</td>
<td>1.098</td>
<td></td>
<td>Reduced</td>
</tr>
<tr>
<td>Severe</td>
<td>No</td>
<td>17</td>
<td>0.496</td>
<td>0.048</td>
<td>0.097</td>
<td>0.611</td>
<td>1.103</td>
<td></td>
<td>Much reduced</td>
</tr>
<tr>
<td>Mild</td>
<td>No</td>
<td>17</td>
<td>0.496</td>
<td>0.021</td>
<td>0.097</td>
<td>0.611</td>
<td>1.134</td>
<td></td>
<td>Limited/none</td>
</tr>
<tr>
<td>Severe</td>
<td>Yes</td>
<td>17</td>
<td>0.578</td>
<td>0.048</td>
<td>0.104</td>
<td>0.585</td>
<td>1.121</td>
<td></td>
<td>Much reduced</td>
</tr>
<tr>
<td>Mild</td>
<td>Yes</td>
<td>17</td>
<td>0.578</td>
<td>0.021</td>
<td>0.104</td>
<td>0.585</td>
<td>1.152</td>
<td></td>
<td>Limited/none</td>
</tr>
</tbody>
</table>

The specific model for European bison in BPF was parameterized for the high-density phase (>250 individuals in population). Recruitment rates – n young recruited in year t per n adult females in year t−1. Mortality rate – only natural mortality (not culling), n dead bison as a percentage of total population number. Lambda (λ) – increase rate of the population size.

BPF, Białowieza Primeval Forest; PCA, principal component analysis; NAO, North Atlantic Oscillation; temp, temperature.
It may be important to keep the ungulate population at intermediate densities, because if the population reaches high density, the effects of severe weather may be more pronounced (Sauer & Boyce, 1983; Portier et al., 1998; Coulson et al., 2001). A large variation in numbers is often not desired from either a demographic or a genetic aspect. In the case of large herbivorous mammals, the conflict between commercial forestry (and thus damage caused to young plantations) and species conservation also has to be taken into account. So far, managers in Białowieża seem to have been quite successful in stabilizing the population by culling, but they are very interested in obtaining quantitative measures of the carrying capacity of the local habitat for the European bison. Ecological carrying capacity is usually defined as the level at which reproduction is balanced by mortality (Begon, Harper & Townsend, 1996). One might consider plotting population growth rate versus population size and extrapolate to the population size level at which \( \lambda = 1 \). However, this is not feasible in our case, as the bison are fed during winter. Indeed, the current conservation efforts of winter foddering may lower the effect of both density dependence and winter severity as well as the possible interaction between the two. Remembering this constraint, one may obtain some information about the density relative to resource levels by comparing how vital rates respond to density increase. Indeed, the relationship between vital rates and population density is especially important, as managers can regulate density but do little about climate or masting.

The occurrence of density dependence in vital rates in large mammals is well documented (Fowler, 1987; Gaillard et al., 2000). The negative effect of population density on recruitment rates in the European bison in Białowieża fits well into this picture. Recently, there has been increased focus on the observation that different vital rates respond at different stages of a density increase (Eberhardt, 1977; Gaillard et al., 2000; Eberhardt, 2002). This is not a new idea (see e.g. Leopold, Sowls & Spencer, 1947), but more data are currently available and allow us to understand the specific sequence of events regarding how different vital rates respond when population density increases. For herbivores above 150 kg, the most sensitive parameter is age of first reproduction, while mortality of calves increases before reproduction in adult females is affected. Finally, the least sensitive parameter to increase with density is adult mortality (Gaillard et al., 2000; Eberhardt, 2002; Festa-Bianchet, Gaillard & Côté, 2003). The lack of detailed age determination for European bison makes it difficult to separate between whether age of first reproduction has increased or that also adult reproduction has responded to this density increase. The decrease of recruitment rates with increased density is marked, suggesting that adult female reproduction is also affected. However, because we found no evidence that natural mortality was affected by density, this may suggest that the population currently shows moderate density effects.

Masting is defined as the synchronous intermittent production of large seed crops in perennial plants (e.g. Ostfeld & Keesing, 2000; Kelly & Sork, 2002). Regardless of whether mast seeding results from weather conditions or is an evolved plant reproductive strategy, the pulse of resources through mastfeeding have ecosystem effects (Ostfeld & Keesing, 2000), affecting populations of a number of species from insects, birds (Schmidt, 2003) to bears (Hashimoto et al., 2003). In Białowieża, seed crops of oak and hornbeam are characterized by dramatic interannual fluctuations with the synchronous masting occurring at intervals of 6–9 years (Jędrzejewska & Jędrzejewski, 1998). In mast years, populations of rodents such as yellow-necked mice Apodemus flavicollis and bank voles Clethrionomys glareolus (Pucek et al., 1993; Jędrzejewska & Jędrzejewski, 1998; Stenseth et al., 2002) as well as an ungulate, the wild boar (Jędrzejewska et al., 1997; Jędrzejewska & Jędrzejewski, 1998), exhibit high overwinter survival and begin to grow rapidly the following spring. Several mammalian and avian predators respond to these population fluctuations (Jędrzejewska & Jędrzejewski, 1998). Hence, the masting seems to lead to trophic cascading effects. Accounts showing an effect of mast on vital rates of a large ruminant are rare, but reported previously for roe deer (Kjellander, Gaillard & Hewison, 2006) and white-tailed deer Odocoileus virginianus (McShea & Schwede, 1993; Ryan et al., 2004). However, the effect of masting was much less important for population growth compared to winter severity and May temperature (Table 3). That masting can also be beneficial to ruminants should be no surprise, as the term ‘masting’ comes from the German word for fattening livestock on abundant seed crops (Kelly & Sork, 2002).

Our findings have at least three important implications for the conservation of the European bison population in BPF. Firstly, in the long-term management and conservation strategy, ad libitum winter feeding with hay should slowly cease to allow for the recovery of the natural functioning of the population year round. Our results show that by monitoring the autumn crop of oak seed, the extent of winter feeding may be adjusted to the abundance of natural food supply in autumn and winter. In masting years, the amount of provided hay could be reduced (severe winters, cold May) or greatly reduced (mild winters, warm May).

Secondly, the results have suggested that at the current level of densities and with current management rules (winter foddering), the natural mortality rates are so low that they cannot balance the recruitment rates, and – if not culled – the population would continue to increase. Although necessary to keep the population within limits, culling may unintentionally cause the reduction of already low genetic variability of the population. In the recent decades, not only weak, sick and injured bison are culled, but also a number of apparently fit individuals are eliminated. On the basis of our results, it is not possible to recommend specific changes to the culling practices. However, it seems that adjustment of winter feeding to climatic conditions and acorn supply will allow for natural selection to operate more freely on the bison population (cf. Schmidt & Hoi, 2002). The number culled annually should not be fixed, but might be smaller in
severe winters and after years with cold May temperatures, especially those after poor acorn crops, and bigger in mild winters after masting and warm May temperatures the previous year (Table 3). Population genetics research on bison is greatly needed to work out the culling scenarios that would not decrease the genetic variability of the population (Krasiańska & Krasiański, 2004).

Finally, the third interesting conservation implication of this study is the importance of oak oldgrowth as a source of high-quality autumn and winter food for the bison population. In BPF, the habitat management for bison has so far been focused on the restoration of river side and forest meadows, which are frequently utilized in summer. Protection of old, fructificating oak stands is thus a crucial measure of managing the habitat for European bison.

Acknowledgements

The Polish–Norwegian cooperation was financed by the project BIOTER – Centre of Excellence in Biodiversity Conservation and Mammal Research, financed by the European Commission (5FP, EVK2-CT-2002-80011, to Mammal Research Institute PAS). The financial support of the Research Council of Norway to A. M. (YFF project) was greatly appreciated. We are grateful to Petter Kjellander and one anonymous referee for very useful comments on a previous draft.

References


