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

A. Mysterud[1], K. A. Bartoń[2], B. Jędrzejewska[2], Z. A. Krasiński[3], M. Niedziałkowska[2], J. F. Kamler[2,*], N. G. Yoccoz[4] & N. C. Stenseth[1]

1 Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, Oslo, Norway
2 Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland
3 Białowieża National Park, Białowieża, Poland
4 Department of Biology, University of Tromsø, Tromsø, Norway

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 (Krasińska & Krasiński, 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,

1987; Pucek *et al.*, 1996; Pucek, 2004) and fragmentation of contemporary populations (Perzanowski, Olech & Kozak, 2004). At the beginning of the 20th century, European bison were only found in two geographically distant regions, the Białowieża Primeval Forest (BPF, located on the contemporary Polish–Belarussian borderland) and the Caucasus Mountains (Krasiński, 1978). European bison were eradicated from Białowieża by 1919, as wartimes in these areas were correlated with the massive overharvesting of ungulates (Jędrzejewska *et al.*, 1997; Jędrzejewska & Jędrzejewski, 1998). European bison was subsequently re-introduced there from zoological gardens in 1929. Today, the BPF is among the few places where European bison still live in the wild (Gębczyńska, Gębczyński & Martynowicz, 1991), and contains the largest free-living population of the species (Krasiński, 1978; Pucek, 2004).

A thorough knowledge of limiting and regulating factors is one of several components necessary for successful conservation (for European bison in Ukraine, see Akimov *et al.*, 2001; for north-east Poland, see Krasiński & Krasińska, 1992). However, factors affecting the dynamics of European bison are still recognized insufficiently (but see Krasiński, 1978; Jędrzejewska *et al.*, 1997; Jędrzejewska & Jędrzejewski, 1998; Krasińska & Krasiński, 2004), and the effect of environmental factors on vital rates is poorly known (Gill, 1998). From 1952, when free breeding started and until present, the population in BPF has been monitored. We here provide an updated account of the population development as well as the first detailed analysis of variation in recruitment rates, sex ratio of offspring and mortality rates for this population. We tested the following general hypotheses about ungulate demography and population dynamics for this large-bodied ungulate:

H_1. *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.

H_2. *The winter severity hypothesis*: We predict a negative effect of winter severity (low temperature and deep snow) on recruitment 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).

H_3. *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 (H_{3a}) negative (e.g. Sæther, 1985; Bø & Hjeljord, 1991) or (H_{3b}) positive for ungulate performance (e.g. Pettorelli *et al.*, 2005a,b).

H_4. *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.

H_5. *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 $1500 \, \text{km}^2$, $52°45'$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 ($600 \, \text{km}^2$) and the Belarussian ($900 \, \text{km}^2$) 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 ($105 \, \text{km}^2$), surrounded by managed (i.e. harvested and replanted) tree stands ($495 \, \text{km}^2$). 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 (Krasiński, 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 (Krasiński, Bunevich & Krasińska, 1994). Since that time, bison numbers in the Polish part of BPF have remained at about 250–350 individuals. In the Belarussian part, a herd of *c.* 300 bison is maintained using similar management practices (Krasiński *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, mean group size = 13) 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) (Krasińska & Krasiński, 1995; Krasińska, Krasiński & 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 (Krasiński & 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_{tot}); Number of adult bison, that is 4 years and older (n_{adults}); number of subadult bison, that is 1.5–3.5 years of age (n_{young}); number of bison less than 1 year old (n_{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_{rec}), recruitment rates [$n_{rec\ (year\ t)}$ per $n_{female\ adults\ (year\ t-1)}$]. 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; Krasińska & Krasiński, 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 (NAOdjf), for spring between March and May (NAOmam), for summer between June and August (NAOjja) and for autumn between September and November (NAOson). 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 PCA1-winter) explained 78.7% of the variance, a high value corresponding to warm temperatures and little
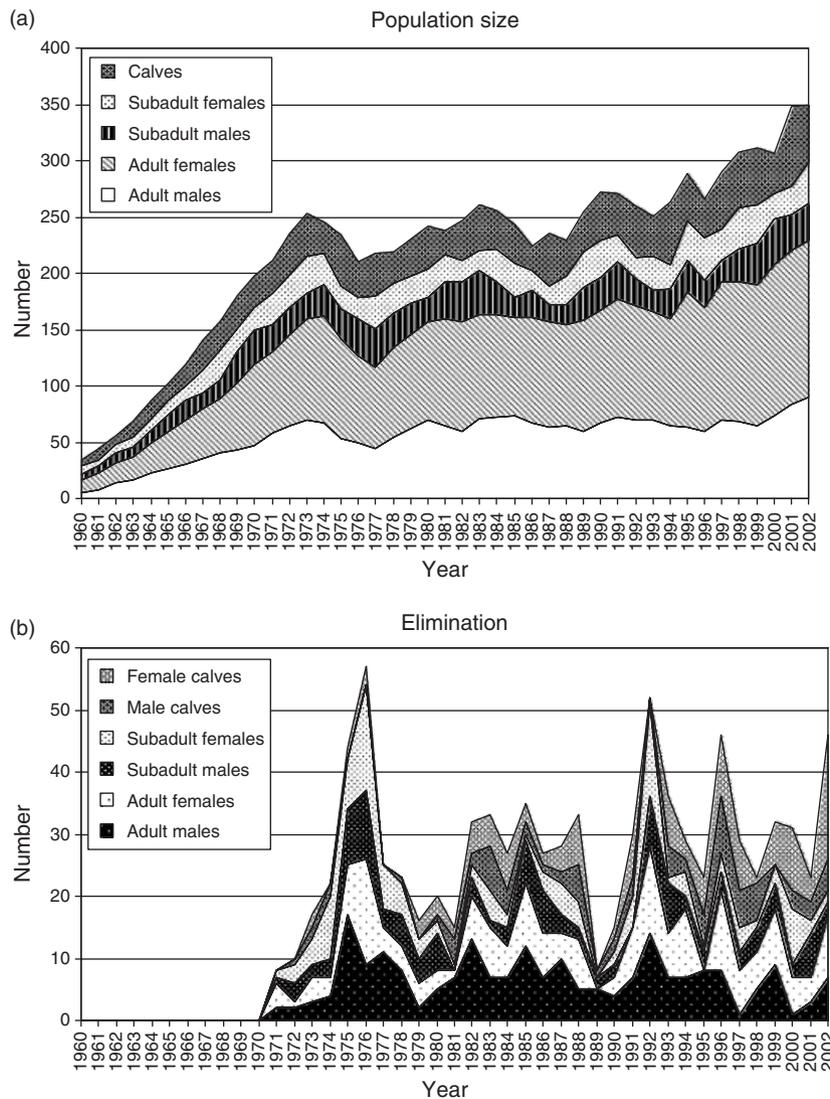
Figure 1 Development in population size and structure (upper graph) and number of animals (lower graph) removed or culled from the European bison herd in the Białowieża Primeval Forest in Poland from 1960 to 2002.

Table 1 Correlation between local (Białowieża Primeval Forest, East Poland) winter weather, the first PCA describing local winter weather and global climate indexes for the NAO (station based and PCA based)

Parameter	PCA1-winter	Temp – January	Temp – February	Temp – March	Prec – January	Prec – February	Prec – March	Snow – January	Snow – February	Snow – March
PCA1-winter	1.000	0.767	0.726	0.680	−0.244	−0.145	0.066	−0.777	−0.841	−0.843
NAO-station based	0.759	0.604	0.598	0.677	0.059	−0.166	0.270	−0.498	−0.531	−0.640
NAO-PCA based	0.742	0.602	0.598	0.474	−0.111	−0.130	0.159	−0.587	−0.598	−0.551

Temp, temperature; Prec, precipitation; Snow, snow depth; PCA, principal component analysis; NAO, North Atlantic Oscillation.

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 Białowieża 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

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 (Krasiński & Raczyński, 1967), we could at least construct a very simplified age structure into the model ($B_{juv} = B_{sa} = 0$; while $B_{ad} = B_{sen}$ 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
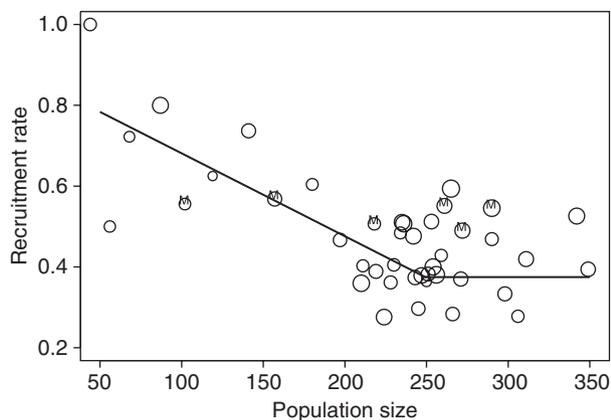

Figure 2 Recruitment rate of European bison in the Białowieża Primeval Forest (East Poland) for the period 1961–2001 as a function of population density for years with masting (marked 'M', heavy crops of oak *Quercus robur* seeds) and without masting. Recruitment rate – *n* young recruited in year *t* per *n* adult females in year *t*–1. The size of the symbols is directly scaled to the temperature in May the previous year, being larger the warmer and better the conditions.

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, λ was 1.194. From 1970 to 2002, λ 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

Table 2 Parameter estimates from the most parsimonious model of recruitment rates, sex ratio of calves and natural mortality of the European bison *Bison bonasus* population in Białowieża Primeval Forest, East Poland

Parameter	Value	SE	95% CI	T	P
Recruitment rate					
Intercept	5.954	1.549		3.844	<0.001
Ln (population size); 0–250 individuals	−1.166	0.277	[−1.726, −0.605]	−4.209	<0.001
Ln (population size); >250 individuals	0		–		
May temperature (previous year)	0.068	0.034	[−0.00063, 0.136]	2.009	0.052
Masting (previous year)	0.359	0.162	[0.031, 0.687]	2.216	0.033
Sex ratio of calves					
Intercept	17.236	9.502		1.814	0.070
Year (continuous)	−0.009	0.005	[−0.018, 0.0006]	−1.823	0.068
NAOjja (previous year)	0.108	0.057	[−0.0045, 0.220]	1.879	0.060
Natural mortality					
Intercept	−3.510	0.063		−55.800	<0.001
PCA1-winter	−0.101	0.030	[−0.158, −0.042]	−3.411	<0.001

NAOmam, PCA-based NAO index for March, April and May; NAOjja, for June, July and August. PCA1-winter – the first PCA for local winter weather – a high value corresponding to mild temperature and little snow. Effect of population density is fitted using a continuous threshold model with the threshold estimated by minimizing the deviance and assuming no effect above the threshold (i.e. regression coefficient=0).
PCA, principal component analysis; NAO, North Atlantic Oscillation; CI, confidence interval.

(Table 3). λ varied between 1.049 for years with severe winter, cold May the year before and no masting in the previous autumn, whereas λ was 1.152 for mild winters with masting and warm May previous year. May temperature and winter weather severity were clearly the more important variables determining population growth. The current management measure of culling to regulate the population can thus be varied accordingly (Table 3). The elasticity of adult survival was always higher than for recruitment, as expected for a large ungulate (Table 3).

Discussion

Knowledge on the detailed population ecology is an important aspect necessary for the successful conservation of
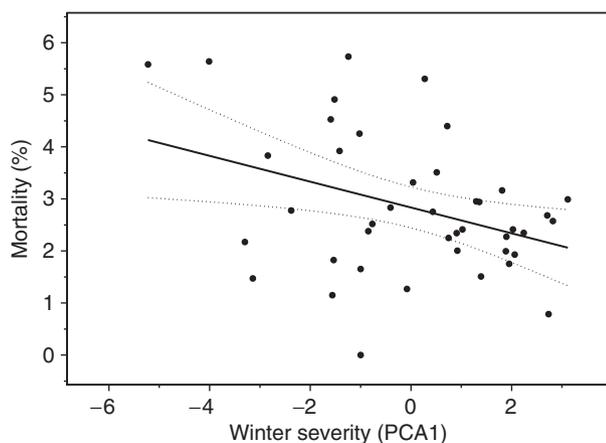

Figure 3 Natural mortality of European bison in the Białowieża Primeval Forest (1960–2002) as a function of winter weather severity, which is indexed using the first principal component analysis (PCA) (accounting for 78.7% of the variance in winter weather), a high value corresponding to high temperatures and little snow, and a low value corresponding to cold, snowy winters.

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 H_1), 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 (H_2) 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; Grøtan *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 H_{3a}), 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 H_4). 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 Krasińska & Krasiński (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 H_5; 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.

Table 3 Demographic rates used in a simple deterministic age-structured population model to guide conservation measures

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

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, Białowieża 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 masting 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 masting 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 (Krasińska & Krasiński, 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

References

Akimov, I., Kozak, I., Kryzanovskij, V. & Perzanowski, K. (2001). Long-term population records - a crucial factor for the success of the re-establishment of European bison (*Bison bonasus*) population in Ukraine. *Ekol. Bratislava* **20**, 62–67.

Aulak, W. (1976). Development and production of ground flora in *Tilio-Carpinetum* Tracz 1962 association as one of the elements of basic trophic level in the forest ecosystems (in Polish with English summary). *Zesz. Nauk. SGGW-AR w Warszawie, Rozprawy Nauk.* **60**, 1–151.

Begon, M., Harper, J.L. & Townsend, C.R. (1996). *Ecology. individuals, populations and communities*. Boston, Oxford, London, Edinburgh and Melbourne: Blackwell Scientific Publications.

Benton, T.G. & Grant, A. (1999). Elasticity analysis as an important tool in evolutionary and population ecology. *Trends Ecol. Evol.* **14**, 467–471.

Bø, S. & Hjeljord, O. (1991). Do continental moose ranges improve during cloudy summers? *Can. J. Zool.* **69**, 1875–1879.

Borowski, S. & Kossak, S. (1972). The natural food preferences of the European bison in seasons free of snow cover. *Acta Theriol.* **17**, 151–169.

Burney, D.A. & Flannery, T.F. (2005). Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol. Evol.* **20**, 395–401.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference. A practical information-theoretic approach*. New York: Springer.

Caboń-Raczyńska, K., Krasińska, M., Krasiński, Z.A. & Wojcik, J.M. (1987). Rhythm of daily activity and behavior of European bison in the Białowieża forest in the period without snow cover. *Acta Theriol.* **32**, 335–372.

Caughley, G. (1966). Mortality patterns in mammals. *Ecology* **47**, 906–918.

Cederlund, G., Sand, H. & Pehrson, Å. (1991). Body mass dynamics of moose calves in relation to winter severity. *J. Wildl. Mgmt.* **55**, 675–681.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**, 1528–1531.

Coulson, T., Gaillard, J.-M. & Festa-Bianchet, M. (2005). Decomposing the variation in population growth into contributions from multiple demographic rates. *J. Anim. Ecol.* **74**, 789–801.

Crawley, M.J. (2003). *Statistical computing. An introduction to data analysis using S-Plus*. Chichester, West Sussex, England: John Wiley and Sons.

Doak, D.F., Morris, W.F., Pfister, C., Kendall, B.E. & Bruna, E.M. (2005). Correctly estimating how environmental stochasticity influences fitness and population growth. *Am. Nat.* **166**, E14–E21.

Eberhardt, L.L. (1977). Optimal policies for conservation of large mammals with special reference to marine ecosystems. *Environ. Conserv.* **4**, 202–212.

Eberhardt, L.L. (2002). A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**, 2841–2854.

Festa-Bianchet, M., Gaillard, J.-M. & Côté, S.D. (2003). Variable age structure and apparent density dependence in survival of adult ungulates. *J. Anim. Ecol.* **72**, 640–649.

Fowler, C.W. (1987). A review of density dependence in populations of large mammals. In *Current mammalogy*: 401–441. Genoways, H.H. (Ed.). New York and London: Plenum Press.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G. & Boisaubert, B. (1996). Body mass of roe deer fawns during winter in 2 contrasting populations. *J. Wildl. Mgmt.* **60**, 29–36.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998). Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol. Evol.* **13**, 58–63.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**, 367–393.

Gębczyńska, Z., Gębczyński, M. & Martynowicz, E. (1991). Food eaten by the free-living European bison in Białowieża Forest. *Acta Theriol.* **36**, 307–313.

Gill, J. (1993). Influence of environmental factors on the deep skin temperature in the European bison, *Bison bonasus* (L.). *Comp. Biochem. Physiol.* **106A**, 653–661.

Gill, J. (1998). Do the abiotic environmental factors influence the reproduction rate in the free-ranging European bison in Białowieża Primeval Forest? *Acta Theriol.* **43**, 417–432.

Glover, R. (1947). The wisent or European bison. *J. Mammal.* **28**, 333–342.

Grøtan, V., Sæther, B.-E., Engen, S., Solberg, E.J., Linnell, J.D.C., Andersen, R., Brøseth, H. & Lund, E. (2005). Climate causes large-scale spatial synchrony in population fluctuations of a temperate herbivore. *Ecology* **86**, 1472–1482.

Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71–75.

Hashimoto, Y., Kaji, M., Sawada, H. & Takatsuki, S. (2003). Five-year study on the autumn food habits of the Asiatic black bear in relation to nut production. *Ecol. Res.* **18**, 485–492.

Hedemann, O. (1939). L'histoire de la forêt de Białowieża (jusqu'a 1798). (in Polish with French summary). *Institut de recherches des Forêts Domaniales, Travaux et comptes rendus, Ser. A* **41**, 1–310.

Hurrell, J.W. (1995). Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science* **269**, 676–679.

Jacobson, A.R., Provenzale, A., von Hardenberg, A., Bassano, B. & Festa-Bianchet, M. (2004). Climate forcing and density dependence in a mountain ungulate population. *Ecology* **85**, 1598–1610.

Jaczewski, Z. (1958). Reproduction of the European bison, *Bison bonasus* (L.) in reserves. *Acta Theriol.* **1**, 334–376.

Jędrzejewska, B. & Jędrzejewski, W. (1998). *Predation in vertebrate communities. The Białowieża Primeval Forest as a case study*. Berlin and Heidelberg: Springer-Verlag.

Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L. & Krasiński, M. (1997). Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriol.* **42**, 399–451.

Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101–108.

Kelly, D. & Sork, V.L. (2002). Mast seeding in perennial plants: why, how, where? *Annu. Rev. Ecol. Syst.* **33**, 427–447.

Kjellander, P., Gaillard, J.-M. & Hewison, A.J.M. (2006). Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia* **146**, 521–530.

Krasińska, M. & Krasiński, Z.A. (1995). Composition, group size, and spatial distribution of European bison bull in Białowieża forest. *Acta Theriol.* **40**, 1–21.

Krasińska, M. & Krasiński, Z.A. (1997). Utilization of the Białowieża National Park by the European bison (in Polish with English summary). *Parki Narodowe i Rezerwaty Przyrody* **16**, 63–77.

Krasińska, M. & Krasiński, Z.A. (2002). Body mass and measurements of the European Bison during postnatal development. *Acta Theriol.* **47**, 85–106.

Krasińska, M. & Krasiński, Z.A. (2004). *Żubr - monografia przyrodnicza (European bison - a natural history monograph)*. (In Polish). Warsawa - Białowieża: SFP Hajstra.

Krasińska, M., Krasiński, Z.A. & Bunevich, A.N. (2000). Factors affecting the variability in home range size and distribution in European bison in the Polish and Belarussian parts of the Białowieża Forest. *Acta Theriol.* **45**, 321–334.

Krasiński, Z.A. (1978). Dynamics and structure of the European bison population in the Białowieża Primeval forest. *Acta Theriol.* **23**, 3–48.

Krasiński, Z.A., Bunevich, A.N. & Krasińska, M. (1994). Characteristics of the European bison populations in the Polish and Belarussian parts of the Białowieża Forest. (In Polish with English summary). *Parki Narodowe i Rezerwaty Przyrody* **13**, 25–67.

Krasiński, Z.A. & Krasińska, M. (1992). Free ranging European bison in Borecka Forest. *Acta Theriol.* **37**, 301–317.

Krasiński, Z.A. & Raczyński, J. (1967). The reproductive biology of European bison living in reserves and in freedom. *Acta Theriol.* **12**, 407–444.

Kruuk, L.E.B., Clutton-Brock, T.H., Albon, S.D., Pemberton, J.M. & Guinness, F.E. (1999). Population density affects sex ratio variation in red deer. *Nature* **399**, 459–461.

Langvatn, R., Mysterud, A., Stenseth, N.C. & Yoccoz, N.G. (2004). Timing and synchrony of ovulation in red deer constrained by short northern summers. *Am. Nat.* **163**, 763–772.

Leopold, A., Sowls, L.K. & Spencer, D.L. (1947). A survey of over-populated deer ranges in the United States. *J. Wildl. Mgmt.* **11**, 162–177.

Loison, A., Langvatn, R. & Solberg, E.J. (1999). Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* **22**, 20–30.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006). *Occupancy estimation and modeling*. Amsterdam: Academic Press.

McShea, W.J. & Schwede, G. (1993). Variable acorn crops - responses of white-tailed deer and other mast consumers. *J. Mammal.* **74**, 999–1006.

Meffe, G.K. & Carroll, C.R. (1997). *Principles of conservation biology*. Sunderland, MA: Sinauer.

Mittlböck, M. & Schemper, M. (1996). Explained variation for logistic regression. *Stat. Med.* **15**, 1987–1997.

Munns, E.N. (1948). Further notes on the European bison. *J. Mammal.* **29**, 300–301.

Mysterud, A. & Østbye, E. (2006). The effect of climate and density on individual and population growth of roe deer *Capreolus capreolus* at northern latitudes - the Lier valley, Norway. *Wildl. Biol.* **12**, 321–329.

Mysterud, A., Stenseth, N.C., Yoccoz, N.G., Ottersen, G. & Langvatn, R. (2003). The response of the terrestrial

ecosystems to climate variability associated with the North Atlantic Oscillation. In *The North Atlantic Oscillation*: 235–262. Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, M. (Eds). Washington: American Geophysical Union.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2000). Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974.

Olech, W. (1987). Analysis of inbreeding in European bison. *Acta Theriol.* **32**, 373–387.

Ostfeld, R.S. & Keesing, F. (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* **15**, 232–237.

Perzanowski, K., Olech, W. & Kozak, I. (2004). Constraints for re-establishing a meta-population of the European bison in Ukraine. *Biol. Conserv.* **120**, 345–353.

Pettorelli, N., Gaillard, J.-M., Mysterud, A., Duncan, P., Stenseth, N.C., Delorme, D. & Van Laere, G. (2006). Using a proxy of plant productivity (NDVI) to find key periods for animal performance: the case of roe deer. *Oikos* **112**, 565–572.

Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatn, R. & Stenseth, N.C. (2005*a*). Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc. Roy. Soc. Lond. Ser. B* **272**, 2357–2364.

Pettorelli, N., Weladji, R.B., Holand, Ø., Mysterud, A., Breie, H. & Stenseth, N.C. (2005*b*). The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to Alpine reindeer performance. *Biol. Lett.* **1**, 24–26.

Pontier, D., Fromont, E., Courchamp, F., Artois, M. & Yoccoz, N.G. (1998). Retroviruses and sexual size dimorphism in domestic cats (*Felis catus* L.). *Proc. Roy. Soc. Lond. Ser. B* **265**, 167–173.

Portier, C., Festa-Bianchet, M., Gaillard, J.-M., Jorgenson, J.T. & Yoccoz, N.G. (1998). Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *J. Zool. (Lond.)* **245**, 271–278.

Pucek, Z. (2004). *European bison. Status survey and conservation action plan*. Gland, Switzerland and Cambridge, UK: IUCN, the Word Conservation Union.

Pucek, Z., Belousova, I.P., Lapshov, V.A., Sipko, T.P. & Kudryavtsev, I.V. (1996). Bison (*Bison bonasus*) - analysis and perspectives of studies: project of an international program of the rare species conservation. *Zool. Zh.* **75**, 1873–1883.

Pucek, Z., Jędrzejewski, W., Jędrzejewska, B. & Pucek, M. (1993). Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. *Acta Theriol.* **38**, 199–232.

R Development Core Team. (2006). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Richards, S.A. (2005). Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* **86**, 2805–2814.

Rouys, S. (2003). Winter movements of European bison in the Białowieża Forest, Poland. *Mammal. Biol.* **68**, 122–125.

Ryan, C.W., Pack, J.C., Igo, W.K., Rieffenberger, J.C. & Billings, A.B. (2004). Relationship of mast production to big-game harvests in West Virginia. *Wildl. Soc. Bull.* **32**, 786–794.

Sæther, B.-E. (1985). Annual variation in carcass weight of Norwegian moose in relation to climate along a latitudinal gradient. *J. Wildl. Mgmt.* **49**, 977–983.

Samojlik, T. & Jędrzejewska, B. (2004). Utilization of Białowieża Forest in the times of Jagiellonian dynasty and its traces in the contemporary forest environment. (in Polish with English summary). *Sylwan* **148**, 37–50.

Sauer, J.R. & Boyce, M.S. (1983). Density dependence and survival of elk in northwestern Wyoming. *J. Wildl. Mgmt.* **47**, 31–37.

Schmidt, K.A. (2003). Linking frequencies of acorn masting in temperate forests to long-term population growth rates in a songbird: the veery (*Catharus fuscescens*). *Oikos* **103**, 548–558.

Schmidt, K.T. & Hoi, H. (2002). Supplemental feeding reduces natural selection in juvenile red deer. *Ecography* **25**, 265–272.

Simberloff, D. (1988). The contribution of population and community biology to conservation science. *Annu. Rev. Ecol. Syst.* **19**, 473–511.

Stenseth, N.C. & Mysterud, A. (2005). Weather packages: finding the right scale and composition for climate in ecology. *J. Anim. Ecol.* **74**, 1195–1198.

Stenseth, N.C., Ottersen, G., Hurrell, J.W., Mysterud, A., Lima, M., Chan, K.-S., Yoccoz, N.G. & Ådlandsvik, B. (2003). Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. Roy. Soc. Lond. Ser. B* **270**, 2087–2096.

Stenseth, N.C., Viljugrein, H., Jędrzejewski, W., Mysterud, A. & Pucek, Z. (2002). Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence. *Acta Theriol.* **47** (Suppl. 1): 39–67.

Stephens, P.A., Buskirk, S.W., Hayward, G.D. & Del Rio, C.M. (2005). Information theory and hypothesis testing: a call for pluralism. *J. Appl. Ecol.* **42**, 4–12.

Stewart, K.M., Bowyer, R.T., Dick, B.L., Johnson, B.K. & Kie, J.G. (2005). Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* **143**, 85–93.

Taylor, V.J. & Dunstone, N. (1996). *The exploitation of mammal populations*. London: Chapman & Hall.

Tuljapurkar, S. & Caswell, H. (1997). *Structured-population models in marine, terrestrial, and freshwater systems*. New York: Chapman & Hall.

Whittingham, M.J., Stephens, P.A., Bradbury, R.B. & Freckleton, R.P. (2006). Why do we still use stepwise modelling in ecology and behaviour? *J Anim Ecol* **75**, 1182–1189.

Wroe, S., Field, J. & Grayson, D.K. (2006). Megafaunal extinction: climate, humans and assumptions. *Trends Ecol. Evol.* **21**, 61–62.