

Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers

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Summary

1. In terrestrial ecosystems many species show large population fluctuations caused by pulsed resources, such as mast seeding. A prime example of a mammal strongly affected by mast seeding of trees is the wild boar *Sus scrofa*, a species that has become a pest in many parts of the world. We investigated the population dynamics of wild boar to assist the development of effective management strategies for this species and possibly for other pulsed resource consumers.

2. We analysed published vital rates of wild boar using Leslie matrix projection models and elasticity analysis. Models were based on vital rates of animals under poor, intermediate and good environmental conditions, which represent combinations of differences in food availability (particularly mast of beech *Fagus sylvatica* and/or oak *Quercus* spp.) and winter climate.

3. Interestingly, we observed a crossover in the ranking of elasticities (e ; the relative impact of each vital rate on population growth rate λ) when comparing different conditions. While the elasticity of λ to adult survival was highest in poor environments [$e(P_{\text{adult}}) = 0.36$, $e(P_{\text{juvenile}}) = 0.22$], the elasticity of λ to juvenile survival was highest under good conditions [$e(P_{\text{adult}}) = 0.16$, $e(P_{\text{juvenile}}) = 0.28$]. Thus juvenile survival becomes increasingly important for population growth as habitat conditions improve.

4. Our analysis of empirical beech mast records gave some indication of an increase of full masts over the last few decades. Modelling different beech mast scenarios showed that an increase in full mast frequency will lead to a rapid increase in λ . The availability of alternative food resources, namely agricultural crops, may also contribute to an expansion of wild boar populations.

5. *Synthesis and applications.* We suggest that, whenever possible, management strategies should be based on separate elasticity analyses for different environmental conditions, especially for species dependent on pulsed resources. For wild boar we suggest the following principal management strategies to stop further population increases: (i) supplementary feeding should be strictly avoided; (ii) under good environmental conditions, reducing juvenile survival will have the largest effect on λ , whereas strong hunting pressure on adult females will lead to most effective population control in years with poor conditions.

Key-words: fecundity, Leslie matrix, pest control, r – K continuum, stochastic λ , survival, tree masting

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Introduction

Many terrestrial ecosystems are characterized by pulsed resources, i.e. the temporary availability of extremely

high food resources (for an overview see Ostfeld & Keesing 2000). Probably the most common resource pulse in these ecosystems is mast seeding, the intermittent, synchronous production of large seed crops by plant populations (Silvertown 1980). Resource pulses can have a strong impact on vital rates and population dynamics of both primary and secondary consumers (Ostfeld & Keesing 2000). Therefore, understanding the responses

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and adaptations of consumers to pulsed resources should be an important pre-requisite for effective management of these species.

A prime example of a mammal showing intense responses to food pulses is the wild boar *Sus scrofa* L. For example, an analysis of long-term records of wild boar densities in the Bialowieza forest in Poland and of hunting bags in Germany showed that the presence or absence of the mast of deciduous trees, such as beech *Fagus sylvatica* L. and oak species *Quercus* L., was the dominating factor determining yearly population growth rates (Briedermann 1990; Jedrzejewska *et al.* 1997).

Management of wild boar and feral domesticated pigs is necessary because this species has become a pest in many parts of the world. The wild boar inhabits vast areas in Europe, southern Asia and northern Africa and has been introduced in North America. Feral offspring of the domesticated form of wild boar are now widespread in Australia, New Zealand and other parts of the world (Bratton 1975; Oliver & Brisbin 1993; Waithman *et al.* 1999). In many parts of Europe, densities of wild boar have been growing notably during the past few decades (Saez-Royuela & Telleria 1986; Neet 1995; Feichtner 1998). This increase has led to substantial damage to agricultural crops and can even cause problems in urban habitats (Geisser & Reyer 2004). Feral pigs in Australia, New Zealand and other countries cause similar damage (Dexter 2003; Hampton *et al.* 2004). Therefore, there is growing interest in the ecology of the wild boar, especially its population dynamics and management.

The increase in wild boar populations may be at least partially the result of the global increase in mean environmental temperatures (global climatic change; Root *et al.* 2003) because it has been shown that high ambient temperatures and low snow cover over winter positively affected yearly population growth (Briedermann 1990; Jedrzejewska *et al.* 1997). Also, there is some indication of a possible increase in the frequency of mast seeding of beech (Hofmann *et al.* 1992). Population growth is further facilitated by the apparent lack of density regulation in this species, as indicated by a study employing experimental manipulation of densities of feral pigs (Choquenot 1998). However, irrespective of the underlying reasons for the increase in population densities of wild boar, we show below that management strategies should be adjusted to year-to-year variation in mast seeding.

Specifically, in this study we addressed the following questions that are relevant for management. Which age classes have the highest impact on population dynamics under different environmental conditions? Do changes in survival rates and fecundities contribute equally to changes in growth rate? To answer these questions, we analysed life-history traits of wild boar. In particular, we used Leslie matrix models (Leslie 1945, 1948), which allow the evaluation of interactions between age-dependent survival rates and fecundities, because this approach

may reveal information about which age classes should be targeted for efficient management measures under certain environmental conditions (for overviews see Benton & Grant 1999; Caswell 2001). This technique also allows analysis of the sensitivities and elasticities of population growth to certain vital rates, i.e. a quantitative assessment of the relative importance of changes in fecundities and survival rates of each age class (caused by environmental variation or harvest) on population dynamics. This modelling approach has not, to our knowledge, been employed for wild boar up to now, even though detailed data on fecundities and yearly survival rates of all age classes under various environmental conditions have been recorded (for an overview see Briedermann 1990). Therefore, we used these and further published data on wild boar to construct Leslie matrix projection models, to calculate sensitivity and elasticity of population growth to vital rates, and to investigate their susceptibility to environmental conditions. One aim of this study was to see whether population growth rate is always most sensitive to a single vital rate (e.g. juvenile survival) or shifts to other vital rates depending on environmental conditions, such as the presence or absence of tree mast. Apart from insights into the life history and population ecology of this species, this evaluation may help to improve the design of effective pest-control measures in areas of rapidly expanding wild boar populations. Moreover, this case study may assist the development of management measures in other species that are consumers of pulsed resources and thus undergo large, rapid population fluctuations.

Materials and methods

WILD BOAR

To analyse population projection models, we used published data on fecundities and survival rates of wild boar (Tables 1 and 2). Our principal source was Briedermann (1990), who combined his own extensive data with studies by Stubbe & Stubbe (1977), Jezierski (1977), Andrzejewski & Jezierski (1978), Ahrens (1984) and other publications. Thus estimates of survival rates and fecundities in Briedermann (1990) are derived from a large database collected over several decades, mainly in Germany and eastern Europe. Importantly, this data set includes estimates of both fecundities and survival rates for different age classes under different environmental conditions (poor, intermediate and good; Table 2), which enabled us to construct not just an average but three different projection matrices, one for each principal environmental condition. Specifically, a combination of high food availability (namely a full mast of beech or oak, with 80–100% of trees seeding) and mild winters should be considered ‘good’ conditions for this species (Briedermann 1990; Okarma *et al.* 1995). In years of full mast, between October and February seeds comprise 70–85% of the stomach contents in wild

Table 1. Reproductive characteristics of wild boar

Litter			Age/weight at birth of first litter	Citation
Range	Mean size \pm SD	<i>n</i>		
1–7	3.69 \pm 1.22	58	30 kg (~10 months)	Fernandez-Llario, Carranza & Mateos-Quesada (1999)
1–7	3.58 \pm 1.33	61	\leq 34 kg	Fernandez-Llario & Mateos-Quesada (1998)
–	4.95 \pm 0.42	–	–	Boitani, Trapanese & Mattei (1995)
–	4.8	17	< 1 years	Moretti (1995)
1–11	5.29 \pm 1.87	251	< 1 years	Briedermann (1990)
–	–	–	8–10 months	Fruzinski (1995)
1–13	6.5	63	–	Oloff 1951 (cited in Briedermann 1990)
1–10	5.7 \pm 2.2	61	8 months	Ahmad <i>et al.</i> (1995)
1–13	5.8	60	–	Martys (1982)

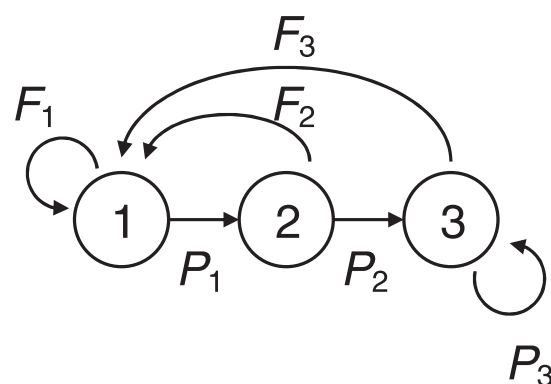
Table 2. Mean litter size, proportion of females participating in reproduction, yearly survival rates and fertilities under different environmental conditions. Survival rates (*P*) and fertilities (*F*) were used as entries for population projection matrices (A_{poor} , $A_{\text{intermediate}}$, A_{good})

	Mean litter size*	Proportion reproducing*	Survival rates† (<i>P</i>)	Fertility (<i>F</i>)
Poor				
Juvenile	3.5	0.30	0.25	0.13
Yearling	4.5	0.80	0.31	0.56
Adult	6.3	0.90	0.58	1.64
Intermediate				
Juvenile	4.0	0.40	0.33	0.26
Yearling	5.5	0.85	0.40	0.94
Adult	6.5	0.90	0.66	1.93
Good				
Juvenile	4.5	0.50	0.52	0.59
Yearling	6.5	0.50	0.60	1.76
Adult	6.8	0.50	0.71	2.29

*Data from table 6/14 in Briedermann (1990).

†Data based on tables 8/2–8/4 in Briedermann (1990); for details see text.

boar, and tree mast is typically followed by high rates of reproduction (Briedermann 1967, 1990; Andrzejewski & Jezierski 1978). Moreover, mild winters with low snow cover facilitate food accessibility and lower energy expenditure, which results in low mortality. The opposite situation, a poor food supply (i.e. failure of mast) and cold winters with frozen ground or high snow covers, seems to be extremely unfavourable, while an average mast (25–50% of trees carrying seeds) and an intermediate winter climate result in intermediate rates of survival and reproduction. Strong effects of environmental conditions, namely of tree seeding and winter climate, on survival and reproduction in this species have also been demonstrated in long-term studies in Poland, Belarus and Switzerland (Okarma *et al.* 1995; Jedrzejewska *et al.* 1997; Geisser 2000). Because experimental manipulation gave no evidence of density dependence of population growth (Choquenot 1998), we did not include density dependence in our models.

**Fig. 1.** Basic life cycle for wild boar corresponding to the population projection matrix. *F*, age-specific fertility; *P*, age-specific survival rate; 1, juveniles (0–1 years); 2, yearlings (1–2 years); 3, adults (> 2 years). Note that animals under 1 year of age are able to reproduce.

FECUNDITY AND REPRODUCTION

Compared with other ungulates, the fecundity (i.e. the average number of females produced by a female of a certain age) of wild boar under good conditions is extremely high (Briedermann 1990; Ahmad *et al.* 1995; Fernandez-Llario & Mateos-Quesada 1998). Females may start to reproduce well under the age of 1 year (Table 1). The onset of female reproduction primarily depends on body weight, and females with a good food supply start to reproduce earlier (Briedermann 1990; Ahmad *et al.* 1995). The minimum weight of free-ranging females for the onset of reproduction is about 30 kg (Fernandez-Llario & Mateos-Quesada 1998; Fernandez-Llario, Carranza & Mateos-Quesada 1999; Table 1) but occasionally females with a weight of only approximately 20 kg are found to be pregnant (A. Mania, personal communication). Based on these observations our analysis included 'juvenile' reproduction (i.e. in the first year of life; Fig. 1) despite the common definition that juveniles do not reproduce. Generally, we differentiated between three age classes with different fecundities (Fig. 1 and Table 2). Our matrix projection models were based on fecundities recorded under different environmental conditions (Briedermann 1990,

table 6/14) derived from embryo counts (corrected for pre-natal mortality by Briedermann 1990) in a large number of culled females. Similar average litter sizes (without distinguishing environmental conditions) for juveniles, yearlings and adults, respectively, have been reported by Fruzinski (1995, 3.9, 4.3 and 6.3) and Neet (1995, 2.17, 5.12 and 6.23).

The proportion of reproducing females differed between age classes and was highest in adults, i.e. 90–95% (Briedermann 1990; Table 2) and 97% (Fruzinski 1995). Although wild boars typically have one litter per year, adult females may have a second litter whenever they fail to raise the first (Martys 1982; Briedermann 1990). In central Europe most young are born between March and April (Martys 1982; Briedermann 1990). These observations justified the use of Leslie matrix models based on a post-breeding census, assuming a birth pulse once a year (Caswell 2001).

SURVIVAL

Estimates of survival rates in wild boar are typically derived from hunted populations and are highly variable (Andrzejewski & Jezierski 1978; Jedrzejewska *et al.* 1997). In a study of non-hunting mortality in Poland, Okarma *et al.* (1995) reported that 61% of carcasses found dead had died from disease or starvation, followed by 16% killed by wolves *Canis lupus* L. Mattioli *et al.* (1995) found that in the northern Apennines, Italy, wild boar was the most important food item for wolves, in particular juveniles at the age of 6–12 months. Local specifics aside, two general patterns concerning survival rates are: (i) juvenile survival is lower than that of yearlings and adults (Briedermann 1990; Fruzinski 1995); (ii) environmental conditions, such as food availability and climatic factors, strongly influence survival (Okarma *et al.* 1995; Jedrzejewska *et al.* 1997). These general patterns are reflected by the survival rates in our projection matrices (Table 2), which were compiled using the ranges of survival rates of each age class given in tables 8/2–8/4 in Briedermann (1990). As Briedermann (1990) presented survival rates of adults for each year, up to age 9, we computed weighted means (using the number of animals in each cohort as weights) to obtain a single survival estimate for this age class (2–9 years) from each table (mainly because only a single fecundity estimate was available for this age class). To investigate effects of different management measures, such as different ages harvested, we also analysed models with survival rates varying from 0.1 to 0.9 in each age class.

PROJECTION MATRIX MODELS

To analyse dynamics of population growth, we used Leslie matrix models (Leslie 1945, 1948). General overviews on the theory and applications of this method are provided by Tuljapurkar & Caswell (1997) and Caswell (2001). Leslie matrix models consider females only, assuming that sex ratios in the field are even. This

assumption is appropriate for most wild boar populations (Durio *et al.* 1995; Fernandez-Llario, Carranza & Mateos-Quesada 1999). Variations in the size and age structure of a population \mathbf{N} between times t and $t + 1$ can be computed from:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$$

where \mathbf{A} is a population projection matrix and \mathbf{N} is a vector describing the age-structured population. We used a three-age class model because fecundity and survival rates differ between juveniles, yearlings and adults (Briedermann 1990; Fruzinski 1995; Neet 1995; Table 2). Thus, our projection matrix was:

$$\mathbf{A} = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} \text{ and } \mathbf{N} = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}$$

where, for age class i , F_i is the fertility (post-breeding model; Caswell 2001). Because we used an extended form of the Leslie matrix, there was a non-zero value at P_3 , which represents the (constant) probability of remaining in the adult age class for all ages above year 2. A basic life cycle for wild boar corresponding to matrix \mathbf{A} is illustrated in Fig. 1. Repeatedly multiplying \mathbf{N} by \mathbf{A} results in a series of vectors that differ by a scalar factor equivalent to the population growth rate λ ($= e^r$, where r is the per capita rate of population increase). The stable age distribution and reproductive values are given by the corresponding right and left eigenvectors \mathbf{w} and \mathbf{v} (Tuljapurkar & Caswell 1997; Caswell 2001). Sensitivity analysis estimates the potential impact of an absolute change in vital rates on λ (Caswell 2001) and can be calculated for any element of \mathbf{A} analytically by:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

where s_{ij} is the sensitivity of λ to the matrix entry a_{ij} , v_i the i th element of the reproductive value vector (\mathbf{v}), w_j the j th element of the stable age distribution (\mathbf{w}), and $\langle \mathbf{w}, \mathbf{v} \rangle$ the scalar product of the vectors. Elasticity (or proportional sensitivity) analysis estimates the effect of a proportional change in the vital rates on population growth rate λ . The proportional change in λ caused by proportional change in the matrix entry can be calculated by:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

where e_{ij} is the elasticity of the matrix entry λ to the matrix entry a_{ij} . Elasticity analysis has become an important tool in developing conservation and management strategies, as vital rates with the highest elasticities have the largest potential impact on population growth rate. All calculations were carried out with programs written in MATLAB 7.0 (The MathWorks Inc., Natick,

Massachusetts, USA), partly using code provided in Caswell (2001, chapters 9·1·1, 9·2, 14·4·1·1 and 14·5·1).

SIMULATION OF FLUCTUATIONS IN FOOD RESOURCES

Several empirical studies have demonstrated that the dominant environmental factor affecting year-to-year variation in population growth in central European wild boar populations is fluctuation in the seed production of beech and oak, the dominant deciduous trees in Europe (Briedermann 1990; Okarma *et al.* 1995; Jedrzejewska *et al.* 1997; Feichtner 1998). Therefore we focused on the degree of tree masting as the primary (but not the only) cause leading to good, intermediate or poor environmental conditions.

We analysed characteristics of the temporal patterns of tree masting using two long-term records of seeding in beech from northern Germany (NG, Schleswig-Holstein, years 1677–1962 with a complete record for the years 1857–1962; Hase 1964) and from eastern Germany (EG, all years from 1808 to 2000; Hofmann *et al.* 1992). Focusing on beech seems justified, as this is the most abundant tree in central European deciduous forests. The relative size of beech mast crops was transformed to scores from 0 to 2, where 0 means no seeding, 1 indicates some seeding and 2 indicates intense seeding (i.e. full mast).

Several properties were common to both time series: time lags between subsequent full masts ranged from 2 to 15 years in NG (median 7) and from 3 to 12 years in EG (with one exception of 58 years; median 6·5) and were approximately Poisson distributed. In both series a full mast was almost always followed by a year with lack of mast (40 cases), occasionally by an intermediate seeding (six cases) but never by another full mast. This pattern of recurrent 2–0 sequences in scores created a significant negative autocorrelation at a lag of 1 year (NG, $r = -0·37$, $P < 0·01$; EG, $r = -0·17$, $P < 0·05$; computed from autocorrelation functions for complete subsets of the time series). The only clear difference between the two data sets concerned the relative frequency of lack-of mast vs. intermediate mast years, which comprised 40% and 47%, respectively, in NG but 73% and 15%, respectively, in EG. This difference may, however, merely reflect a difference in the thresholds used for scoring by the original observers. Using the Lomb-Scargle periodogram (Ruf 1999) for unevenly sampled time series (to allow the inclusion of stretches of time lacking observations), we found no evidence for any significant periodicities in either data set. Nor did any series provide evidence of a statistically significant increase or decrease in the frequency of full masts over time. However, in the last 17 years recorded in EG full masts occurred at a high median frequency of 3 years.

Based on this analysis we then simulated time series of mast as follows. First, a sequence of full mast years at intervals drawn from Poisson-distributed random numbers with selectable means (mean full mast occur-

rence was chosen step-by-step between 3 and 12 years) was generated. Secondly, each year following a full mast year was set to score 0. Thirdly, the remaining intermittent years were randomly assigned scores 0 or 1, with a given proportion of lack-of-seed years (score 0) selected in each run.

To compute a stochastic matrix model, these series of scores were used to generate a simulated time series of 10 000 years with matrices A_{poor} , $A_{\text{intermediate}}$ and A_{good} (Table 2) assigned to scores 0, 1 and 2, respectively, using realistic parameters (i.e. assuming a full mast on average every seventh year and a proportion of 34% years with lack of mast as determined in our analysis of empirical data). From this sequence of 'years' with fluctuating environmental conditions we computed the stochastic growth rate and stochastic elasticity/sensitivity using the MATLAB code given in Caswell (2001), for a comparison with mean growth rates and mean elasticity/sensitivity (mean over 10 000 years; cf. Benton & Grant 1996; Tuljapurkar 1997).

We also used the above type of simulation to assess effects of the full range of variation in tree masting sequences and possible long-term changes in masting frequency on growth rates. Specifically, we evaluated the sensitivity of growth rate on (i) the frequency of full mast years and (ii) the proportion of complete mast failures. For this purpose we generated sequences of 10 000 years each, varying either the duration of intervals between full masts from 3 to 12 years or the proportion of mast failures from approximately 10% to 90% (holding full mast intervals fixed at 3, 7 or 11 years).

Results

PROJECTION MATRIX MODELS FOR DIFFERENT ENVIRONMENTAL CONDITIONS

Analysing projection matrices with realistic estimates of vital rates under the three principal environmental conditions considered (Table 2) resulted in pronounced differences in expected growth rates of wild boar populations (Table 3). Under poor environmental conditions (lack of mast and cold winters) the asymptotic growth

Table 3. Asymptotic population growth rate (λ), stable age distribution (\mathbf{w}) and reproductive value (\mathbf{v}) in wild boar under different environmental conditions; \mathbf{w} and \mathbf{v} are given in proportions

	Poor	Intermediate	Good
λ	0·85	1·09	1·63
\mathbf{w}			
Juvenile	0·61	0·63	0·65
Yearling	0·18	0·19	0·21
Adult	0·21	0·18	0·14
\mathbf{v}			
Juvenile	0·10	0·13	0·18
Yearling	0·29	0·31	0·36
Adult	0·61	0·56	0·46

rate of the population was $\lambda = 0.85$. The asymptotic growth rate was higher ($\lambda = 1.09$) under intermediate conditions and further increased under good environmental conditions, i.e. full mast of seed trees and mild winter climate ($\lambda = 1.63$; Table 3).

As expected, the stable age distribution (**w**) of the population slightly shifted in favour of juveniles under good conditions (juveniles $+0.04 = 4\%$, adults -0.07 , compared with poor conditions; Table 3). However, the general age structure, with almost two-thirds juveniles, was similar under all scenarios. Although the reproductive value (**v**) of adults was always higher than that of yearlings or juveniles, it decreased by 0.15 under good conditions compared with poor conditions. Accordingly, reproductive values of juveniles and yearlings increased under good conditions by 0.08 and 0.07, respectively (Table 3).

Interestingly, the elasticities (*e*) of λ to vital rates showed profound changes under different environmental scenarios. While under poor conditions the survival of adults, $e(P_3)$, had the largest potential impact on asymptotic population growth, survival of juveniles, $e(P_1)$, was the vital rate contributing most to population growth under good environmental conditions (Fig. 2). The elasticity of λ to adult survival showed the largest shift and declined under good conditions (from 0.36 to 0.16), while elasticity of λ to fertility in juveniles, $e(F_1)$, increased strongly (from 0.04 to 0.14), even more than the elasticity of λ to survival $e(P_1)$ (from 0.22 to 0.28) in this age class. The elasticities of λ to yearling fertility also increased under good environmental conditions (from 0.05 to 0.13; Fig. 2).

The stochastic sensitivity and elasticity (Table 4) computed from simulated 10 000-year sequences of alternating matrices (simulating natural environmental fluctuations, i.e. the intervals between full mast years varying around a 7-year interval) showed nearly identical results to elasticities from the mean matrix under these varying conditions (Table 4). The estimated stochastic growth rate was significantly smaller than the asymptotic growth rate determined from the eigenvalue of the mean population projection matrix in the same simulation (Table 4).

We further varied survival rates beyond the ranges used in the matrices above because hunting may affect survival strongly, and also selectively, if particular age classes are targeted. Thus we were interested in calculating the possible range of λ given large differences in survival rates (Fig. 3). While holding survival rates for two age classes fixed at the values given in Table 2, survival was varied between 10% and 90% in the remaining third age class. This analysis showed that, under poor conditions, only very high survival rates (e.g. 80% adults, 70% yearlings and 50% juveniles) would result in growth rates of $\lambda > 1$ (Fig. 3, upper panel). As environmental conditions improved, the slope of λ vs. juvenile survival showed a clear increase, which reflected the strong influence of this age class on population growth under good conditions (Fig. 3, lower panel; cf. sensitivities

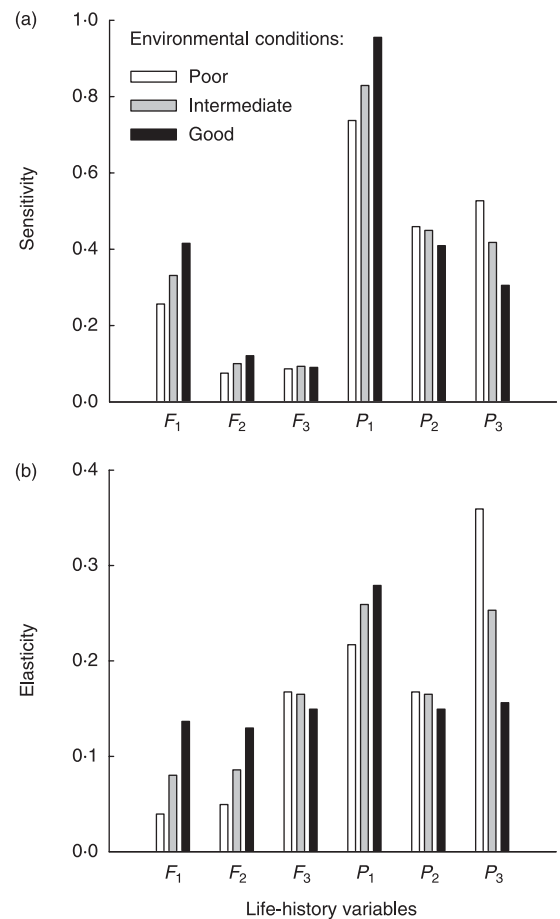


Fig. 2. (a) Sensitivity and (b) elasticity of λ to changes in life-history variables in wild boar under different environmental conditions. For life-history variables see Fig. 1.

in Fig. 2). A consequence of the large contribution of juveniles to population growth under good environmental conditions was that even a mortality of 90–100% (as a result of hunting) among adult females would not lead to a decline of population size if favourable conditions persisted (Fig. 3, lower panel).

EFFECTS OF THE TEMPORAL PATTERN OF ENVIRONMENTAL FLUCTUATIONS

Our analysis of empirical beech mast records gave some indication of an increase of full masts in the last two decades in one of the time series. Also, supplementary feeding and agriculture may buffer the negative impact of mast failures by reducing the frequency of years with poor conditions. Therefore we modelled two possible scenarios of changes in the temporal pattern of fluctuations in food resources: (i) variation in the frequency of years with full mast and (ii) variation in the number of years with mast failure (Fig. 4). These parameters are not completely independent, however, because short intervals between full masts limit the possible range of years with a lack of crops. We observed similar ranges of effects of both simulations on the stochastic growth rate λ_s , with a somewhat stronger influence of changing

Table 4. Stochastic vs. mean population growth rate and elasticities/sensitivities of λ to changes in life-history variables in wild boar. Data based on a simulated series of population projection matrices for poor, intermediate and good environmental conditions over 10 000 years (proportion of mast failure, 0.34; frequency of full masts, 7 years; for details see text). CI, confidence interval (only for stochastic λ). For life-history variables see Fig. 1

	Stochastic $\lambda_s = 1.05$	Mean $\lambda_m = 1.07$
95% CI	1.046–1.058	
Elasticities		
$e(F_1)$	0.074	0.077
$e(F_2)$	0.081	0.085
$e(F_3)$	0.168	0.167
$e(P_1)$	0.249	0.253
$e(P_2)$	0.167	0.167
$e(P_3)$	0.261	0.251
Sensitivities		
$s(F_1)$	0.316	0.329
$s(F_2)$	0.096	0.102
$s(F_3)$	0.091	0.095
$s(P_1)$	0.797	0.816
$s(P_2)$	0.438	0.449
$s(P_3)$	0.412	0.418

frequencies of full masts than the replacement of poor by intermediate years (Fig. 4). For each 0.1 increase in the proportion of full masts, λ_s increased by 0.034, while for each 0.1 increase in proportion of years with mast failures λ_s decreased by -0.025 . It should be noted that a maximum frequency of full masts, every third year, would lead to an extremely high long-term population growth rate of $\lambda_s = 1.124$. Comparably high values of λ_s , however, were reached at lower full mast frequency but high proportions of years with intermediate conditions (Fig. 4).

Discussion

PROJECTION MODELS FOR DIFFERENT ENVIRONMENTAL CONDITIONS

The deterministic growth rates calculated from matrices representing different habitats varied from 0.85 (poor) to 1.63 (good), which seems plausible, as the year-to-year variation in natural populations, probably augmented by some sampling error, may even exceed that range (e.g. $\lambda = 0.3\text{--}3.0$; computed from a 30-year time series in Feichtner 1998). Thus our three matrix models seem to represent reasonable combinations of (positively correlated) vital rates in wild boar, and may serve as a valid base on which to address both basic and applied questions concerning the population ecology of this species.

Under fluctuating conditions, such as variation in food resources and climate, the relative importance of each vital rate for population growth may change (Benton & Grant 1996; Caswell 2001). Interestingly,

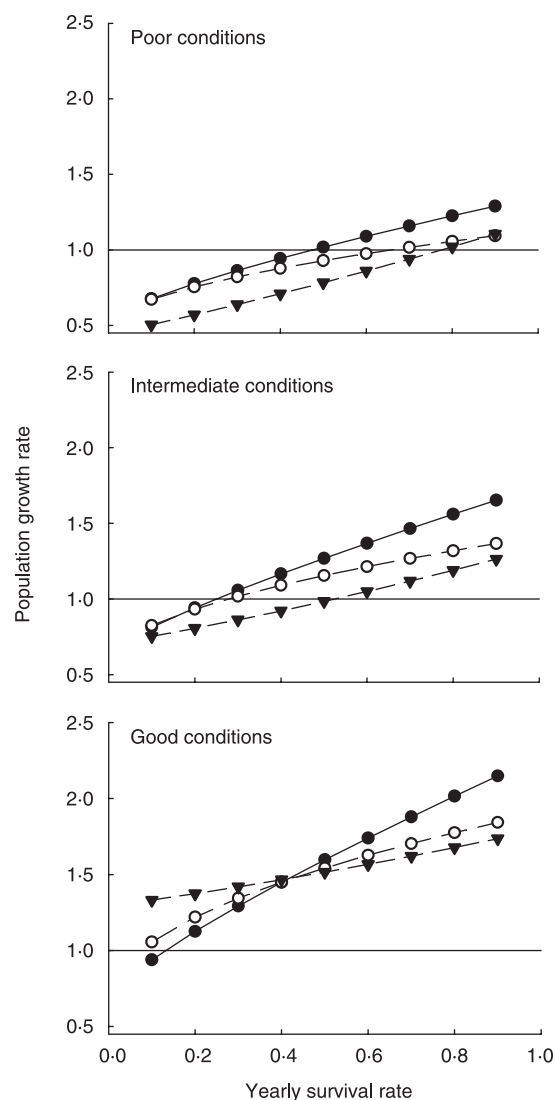


Fig. 3. Influence of survival on growth rate (λ) of wild boar populations for three age classes under different environmental conditions. Dots, juveniles; open circles, yearlings; triangles, adults. The horizontal lines mark the baseline of $\lambda = 1$.

our analysis indeed revealed such a change in the ranking of elasticities (Fig. 2). While the elasticity of λ to juvenile survival $e(P_1)$ was the highest among all vital rates under good conditions, the elasticity of λ to adult survival $e(P_3)$ was highest in a poor environment, and both elasticities were almost equal in intermediate habitats. These changes in the ranking of elasticities may be viewed as moves along the fast–slow continuum scale of mammalian life histories (Oli & Dobson 2003; Oli 2004).

As outlined by Oli & Dobson (2003), the ratio of overall fertility (\bar{F}) to the onset of reproduction (α) may be useful for ordering species along this fast–slow continuum. Typically, in ‘fast’ mammals the ratio \bar{F}/α is > 0.6 and in ‘slow’ mammals \bar{F}/α is < 0.15 (Oli & Dobson 2003). On this scale wild boar indeed adjust their life-history tactics from an intermediate type under poor environmental conditions (\bar{F}/α ratio = 0.52) to a fast life history under intermediate (\bar{F}/α ratio = 0.68) and

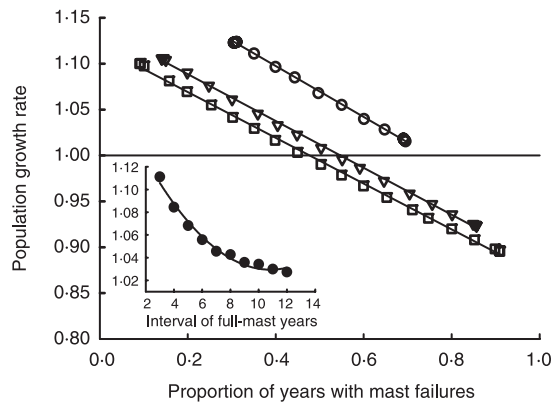


Fig. 4. Influence of different tree masting time series on stochastic population growth rate (λ_s) in wild boar. Lines show full mast intervals: open circle, 3 years; open triangle, 7 years; open rectangle, 11 years. The inset graph illustrates the effect of increasing full mast frequency (given a realistic proportion of 34% mast failures). Its abscissa shows interval duration (rather than the proportion of full mast years) in order to emphasize that empirical data indicate that the minimum interval between full masts is never less than 3 years. The horizontal line marks the baseline of $\lambda = 1$.

good (\bar{F}/α ratio = 1.06) conditions (calculated from equation 14 in Oli & Zinner 2001). Interestingly, the summed elasticity of λ to changes in fertility exceeded the elasticity of λ to either juvenile or adult survival (P_1 , P_3 ; cf. Fig. 2) under good conditions (high \bar{F}/α ratio) but not under poor conditions (low \bar{F}/α ratio). This finding clearly supports the prediction by Oli & Dobson (2003) that the sensitivity of λ to perturbations in fertility should increase as the \bar{F}/α ratio increases (i.e. towards the fast end of the continuum).

Rapid shifts between slow and fast life-history tactics in wild boar may reflect the adaptation of this species to an important but unpredictable food resource, i.e. the mast of beech or oak. While under conditions of poor food availability, juvenile fecundity decreases and, thus, the trade-off between early reproduction and survival is shifted in favour of survival, fecundity of adult animals is less influenced by environmental conditions. This age class represents a reservoir of individuals with high survival rates that dampens negative effects of unfavourable conditions on population size. Under good conditions, on the other hand, population growth is primarily driven by juveniles, which contribute twofold. First, we observed a more than threefold increase in the elasticity of λ to juvenile fertility (Fig. 2). Juveniles under good conditions have an enormous potential to gain weight (which may explain why pigs have been domesticated; Briedermann 1990) and puberty in wild boar depends more on weight than on age (Briedermann 1990; Fernandez-Llario, Carranza & Mateos-Quesada 1999). Secondly, the elasticity of λ on juvenile survival under good conditions was higher than any other elasticity. Thus juveniles have the potential to cause large and rapid increases in λ .

It seems that documented cases of crossovers in elasticities, as observed here, are relatively rare (Mills,

Doak & Wisdom 1999). Typically, population growth and elasticities are derived from a single mean or 'best-guess' matrix for many species, because data on vital rates under fluctuating environmental conditions are often not available. For example, Oli & Dobson (2003) computed elasticities of λ to changes in different vital rates for 142 natural populations of mammals, but only in six cases was more than one set of life-history variables used (Oli & Dobson 2003). From our analysis it is clear that in wild boar conclusions based on elasticities from a single matrix of vital rates, for instance that for intermediate conditions, would be quite misleading if mean long-term environmental conditions (such as the frequency of mast years) should change. Also, management measures that seem optimal, given a certain ranking of elasticities, in one year, may be inappropriate in another (see below). These results support the view that, while elasticity analysis is a useful tool for applied ecology, elasticities should be interpreted with considerable care, especially when they are obtained from a single mean matrix (Mills, Doak & Wisdom 1999; Ehrlén, van Groenendaal & de Kroon 2001; Mills, Doak & Wisdom 2001).

If long-term environmental conditions stay constant, on the other hand, the pure effects of stochasticity on the properties of wild boar populations seem moderate. Mean and stochastic elasticities in our simulations were highly similar (Table 4), which seems quite typical (Benton & Grant 1996; Caswell 2001; but see Tuljapurkar, Horvitz & Pascarella 2003). This similarity was unaffected by the somewhat unusual type of environmental noise in beech mast that contained a significant negative autocorrelation. As expected on theoretical grounds (Caswell 2001), the deterministic λ_m computed from the mean matrix in our simulation of environmental fluctuations was slightly higher than the actual stochastic λ_s (Table 4). Our estimate of a λ_s of 1.05, i.e. steady population growth under a realistic sequence of environmental fluctuations, was probably affected by the fact that Briedermann's (1990) set of vital rates was mainly obtained from populations in eastern Germany, which underwent a long-term population increase. Different combinations of vital rates obtained from other populations may easily lead to lower growth rates, i.e. $\lambda = 0.98$ (Oli & Dobson 2003; based on vital rates published in Jezierski 1977 and Ahmad *et al.* 1995).

CONSEQUENCES OF CHANGES IN FOOD AVAILABILITY AND CLIMATE

The classifications of our three matrix models were based on both food availability and winter climate (Briedermann 1990) but the time pattern of our stochastic fluctuations simulated typical temporal sequences of tree masting only. This was justified by several analyses of long-term data sets showing a clear association between beech or acorn crop availability, winter survival and yearly population growth rates (Okarma *et al.* 1995; Jedrzejewska *et al.* 1997; Feichtner 1998). The abundance

of tree seeds appears to be a limiting ecological factor in several species (reviewed by Silvertown 1980). For example, in the edible dormouse *Glis glis* L. entire populations skip reproduction in years with a failure of beech and/or oak mast (Bieber 1998; Pilastro, Tavecchia & Marin 2003; Fietz *et al.* 2004). While the arboreal dormouse may predict the seeding of trees, at least within 1 year, from the presence of seed buds on branches (one of their food items) in spring, wild boar probably respond entirely opportunistically to this fluctuation in food resources. Also, the bearded pig *Sus barbatus* Müller, a species under threat in parts of its range, is known to be strongly affected by seeding in dipterocarps (Hancock, Milner-Gulland & Keeling 2005). Pulsed resources may also affect densities of secondary consumers, such as mammalian and avian predators, that respond to population fluctuations in mast consumers (for an overview see Ostfeld & Keesing 2000). Rapid population growth in these predators can have a strong impact on other prey, including rare or endangered species (e.g. effects of stoats on endemic birds in New Zealand; Ostfeld & Keesing 2000). Thus pulses of heavy seed production are widespread and may have important consequences for the population dynamics of several species within an ecosystem.

Our evaluation of long-term beech mast time series showed that the temporal sequence of masting is largely random, except that full mast years are generally followed by a year of very low levels of seed production (Piovesan & Adams 2001). Seed production is induced by certain climatic conditions, i.e. moist, cool summers followed by a dry early summer in the next year (Piovesan & Adams 2001), which apparently occur at random intervals. Interestingly, masting of trees seems to be a large-scale phenomenon that occurs synchronously in the northern hemisphere (Piovesan & Adams 2001). Hence, wild boar and other populations within large areas will be affected simultaneously. Our evaluation of the impact of changes in seeding pattern on population growth in wild boar indicated that an increase in the frequency of full mast years should lead to a rapid acceleration of population growth (Fig. 4).

We do not intend to suggest, however, that the seeding of beech and oak is the single environmental factor determining population dynamics in this species, nor that it fully explains the past increase in the number of wild boar in many areas. Historical hunting bag statistics indicate that population densities in central Europe have apparently been stable during most of the last two centuries but have increased dramatically during the past five to six decades (W. Arnold, personal communication). However, we found no statistically significant increase of beech masting frequency over that period in the time series analysed here. Also, it should be noted that our modelling of stochastic environments was based on good, intermediate and poor conditions, which reflected not only food availability but also additional factors such as winter temperatures and snow cover (Briedermann 1990). Thus, our analyses incorporate climatic

influences, namely a clear positive effect of mean annual temperatures on vital rates, and consequently on population growth (Briedermann 1990; Jedrzejewska *et al.* 1997). These effects suggest that one of the decisive factors contributing to the widespread increase in wild boar population densities may have been the well-known rise in global mean annual air temperatures over the last century (global warming; Root *et al.* 2003). In addition, the simultaneous intensification of agriculture has provided increased food resources for wild boar, which buffers environmental fluctuations and further augments reproductive output (Andrzejewski & Jezierski 1978).

IMPLICATIONS FOR MANAGEMENT

Increasing population densities of wild boar have led to growing damage rates of agricultural crops (Andrzejewski & Jezierski 1978; Ahmad *et al.* 1995; Geisser 2000; Geisser & Reyer 2004), may increase the spread of swine fever or other diseases in domesticated pigs (Dexter 2003; Kern *et al.* 1999; Fritzmeier *et al.* 2000) and cause environmental impacts as a result of feeding on endangered birds and plants (Bratton 1975; Briedermann 1990). These problems accentuate the need for effective control of wild boar populations.

As food availability affects population growth strongly (Briedermann 1990; Okarma *et al.* 1995; Feichtner 1998), it is clear that supplementary feeding of wild boar populations should be avoided. Additional food in particular accelerates the onset of reproduction (Andrzejewski & Jezierski 1978; Briedermann 1990), a factor that generally has a high impact on population growth, at least in 'fast' animals (Oli, Slade & Dobson 2001; Oli & Dobson 2003). Accordingly, our simulation of increasing frequencies of tree masts or decreasing frequencies of poor years (as a result of the availability of agricultural crops or winter feeding) showed a strong impact on population growth. Supplementary feeding of wild boar is still common in many parts of Europe, to distract animals from crops (Andrzejewski & Jezierski 1978; Geisser 2000; Geisser & Reyer 2004). However, studies have revealed that claims of damages to crops caused by wild boar were positively correlated with the number of feeding stations in the area (Geisser 2000; Geisser & Reyer 2004) and that, while feeding may distract animals temporarily, it only augments long-term population growth (Andrzejewski & Jezierski 1978).

Our study has direct relevance for hunting strategies in wild boar. It is clear that, rather than relying on a general management strategy derived from an average elasticity analysis, hunting, as a measure to control populations, should be adjusted to changing environmental conditions (cf. Mills, Doak & Wisdom 1999). In growing populations under good environmental conditions, particularly following a full mast of trees, yearly survival of juveniles should be reduced most, to approximately 15% (including natural postnatal mortality), assuming 60% survival in yearlings and 70%

in adults, in order to limit growth rate to $\lambda \leq 1$ (Fig. 3). High hunting pressure on juveniles as an effective measure to control population growth was also recommended by Briedermann (1990) and Neet (1995). However, in many parts of Europe juveniles are rarely hunted because of tradition and difficulties in finding them (Boitani, Trapanese & Mattei 1995). Our analysis shows that preferential hunting of adults in favourable habitats would be ineffective, because even if survival of adults was below 10% (assuming 50% survival in juveniles and 60% survival in yearlings) population growth would not drop to $\lambda = 1$ (Fig. 3). For poor environments, on the other hand, our elasticity analysis indicated that decreasing adult survival would lead to the most effective reduction of population growth and should be considered, for instance, if the aim is to reduce or even remove a population from a certain area.

Regarding the practicability of these recommendations, it should be noted that the three age classes chosen for our analyses are easy to distinguish visually in the field. Also, data on the current mast situation in beech and oak and winter climate (e.g. snow cover) are simple to register. Thus, our recommendations are applicable management measures. However, reducing yearly survival rates of juveniles to approximately 15% in favourable habitats might be a difficult task to fulfil. In that case, simultaneously increasing hunting pressure on all other age classes will be necessary. Moreover, should important environmental factors, such as mean annual temperatures and masting frequency of trees, continue to increase (cf. Hofmann *et al.* 1992), controlling growth and spreading of wild boar populations will require major increases in total hunting effort and harvest rates.

In conclusion, we suggest that management strategies in species that are strongly affected by mast seeding or other pulsed resources should, whenever possible, be based on the analysis of vital rates obtained under various environmental conditions, such as peak and minimum food abundance. In species showing large population fluctuations because of resource variation, management measures merely based on 'average' vital rates will almost certainly be less effective.

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