Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2012, **49**, 833–841 doi: 10.1111/j.1365-2664.2012.02160.x

Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar

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Summary

1. Harvest models are often built to explore the sustainability of the dynamics of exploited populations and to help evaluate hunting management scenarios. Age-structured models are commonly used for ungulate population dynamics. However, the age of hunted individuals is usually not recorded, and hunting data often only include body weight and sex limiting the usefulness of traditional models.

2. We propose a new modelling approach that fits data collected by hunters to develop management rules when age is not available. Using wild boar *Sus scrofa scrofa* as a case study, we built a matrix model structured according to sex and body weight whose output can be directly compared with the observed distribution of hunted individuals among sex and body weight classes.

3. In the face of the current wide scale increase in populations of wild boar, the best feasible option to stop or slow down population growth involves targeting the hunting effort to specific sex and body weight classes. The optimal harvest proportion in the target body weight classes is estimated using sensitivity analyses.

4. The number of individuals shot in each sex and body weight class predicted by our model was closely associated with those recorded in the hunting bag. Increasing the hunting pressure on medium-sized females by 14·6% was the best option to limit growth rate to a target of 0·90.

5. *Synthesis and applications*. We demonstrate that targeting hunting effort to specific body weight classes could reliably control population growth. Our modelling approach can be applied to any game species where group composition, phenotypic traits or coat colour allows hunters to easily identify sex and body weight classes. This offers a promising tool for applying selective hunting to the management of game species.

Key-words: body weight-structured model, exploited populations, hunting, optimal harvesting, population dynamics, *Sus scrofa scrofa*, wildlife management.

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Introduction

Humans affect both the size and structure of many animal and plant populations through hunting, fishing or agriculture. Such 'exploited populations' share specific demographic patterns not found in populations free from human disturbance (Beverton & Holt 1957). The consequences of population exploitation in terms of population dynamics have been well described (Allendorf & Hard 2009), particularly in fisheries (Darimont *et al.* 2009).

Although exploitation can be used to control population size and expansion (McShea, Underwood & Rappole 1997), it has to be sustainable (Freckleton *et al.* 2003). Models designed to explore the sustainability of harvest management under different scenarios are based on the theory of exploited populations (Lebreton 2005a). These models require parameter estimates and must be validated using independent data such as hunting statistics if they are to be efficient and realistic (Nichols, Lancia & Lebreton 2001). As both the type and quality of data vary among case studies, a variety of models have been proposed. Age-structured models (Caswell 2001) are commonly used for mammals (Eberhardt 1991), while stage-structured models are often used for plants (Salguero-Gomez & de Kroon 2010). Whether age- or stage-structured models are preferable depends on both the relevance of age as a structuring factor and the availability of data to validate model predictions against empirical data collected by hunters. In our study, we used sex and body weight as structuring factors because they are commonly recorded by hunters for a variety of game species, whereas age is less often recorded. We thus built a sex- and weight-structured model. We considered both live and dead individuals explicitly so that we could compare the observed distribution of the hunting bag among sexes and weight classes to a model-based distribution.

The wild boar *Sus scrofa scrofa* (Linnaeus 1758) is a particularly relevant case study in that context. As with most ungulate populations in temperate areas (Gill 1990), its abundance and distribution has increased in most European countries over the last decades (Apollonio, Andersen & Putman 2010). The number of wild boar shot annually in France has increased from 36 429 in 1973 to 401 083 in 2001 (Maillard *et al.* 2010), at a rate of 9% a year. The main causes of this increase are greater mast production (i.e. acorn and beechnut) induced by land abandonment (Loison, Toïgo & Gaillard 2003), milder winters that favour survival (Melis *et al.* 2006), artificial feeding of wild boar to reduce crop damage, and hunting restrictions that favour the survival of larger individuals with higher fecundity. Moreover, there is no fixed hunting quota for wild boar, although maximum and minimum numbers of wild boar that can be shot each year are fixed in about half of France. This unique situation for wild boar (compared to other ungulates) is common throughout Europe and has led to higher costs to agriculture because of damage to crops (Groot Bruinderink & Hazebroek 1996). Compensation for damage caused by wild boar in France rose from 2 to 18 million Euros between 1973 and 2001, a nearly tenfold increase (Maillard *et al.* 2010).

Hunting pressure is already high in most wild boar populations (Toïgo *et al.* 2008) but the number of hunters is decreasing (Riley *et al.* 2003; Bedarida 2008). Therefore, the abundance of wild boar cannot be controlled by only increasing the hunting effort (i.e. purely quantitative management). Qualitative management targeting particular classes of individuals within a population might offer a solution because demographic performance, and hence contribution to population growth, depends on body weight. The size of the wild boar populations might be reduced by selectively increasing hunting pressure on specific weight classes. We developed an optimal harvesting strategy using demographic sensitivity analyses to determine the proportion of wild boar that should be culled in different sex and weight classes to reach a target population growth rate.

Materials and methods

STUDY AREA AND DATA COLLECTION

The study site is located in north-eastern France in the 11 000 ha forest of Châteauvillain-Arc-en-Barrois (48°02N, 4°56E). These forests are mainly composed of oak *Quercus petraea*, beechnut *Fagus sylvatica* and hornbeam *Carpinus betulus*.

Capture–mark–recapture (CMR) data were collected annually from 1982–1983 to 2006–2007. Wild boars were trapped each year from March to September, individually marked if not already marked, and then released. From 1982 to 2007, 2139 individuals (1143 males and 996 females) were marked. For each capture or recapture of an individual, both the weight and sex were recorded. Besides this live recapture data, hunters contributed records of the date of death of individuals shot from October to February. In addition, the dressed body mass (i.e. body mass without the digestive system, heart, lungs, liver, reproductive tract and blood) was recorded for each individual shot and retrieved. No information was available for individuals that died from natural causes and some individuals shot by hunters were not retrieved (crippling loss).

Wild boars live in matrilineal social groups, while males are solitary (Kaminski *et al.* 2005): this behaviour makes the determination of sex straightforward. A female group is led by a large sow (generally weighing more than 50 kg), which is followed by juveniles that are markedly smaller. Moreover, juveniles are striped until 4 months of age and then wear a reddish coat until they reach about 30 kg (Moretti 1995). Hunters can thus easily assess sex and approximate body mass before shooting.

The modelling process involved three steps: (i) build a sex- and body weight-structured matrix model; (ii) estimate demographic parameters; and (iii) develop management scenarios.

LIFE CYCLE AND MATRIX MODEL

We built a matrix model (Caswell 2001) by firstly considering three classes of body weight for each sex, for females: < 30 kg (small), between 30 and 50 kg (medium) and > 50 kg (large). As the 30-kg threshold corresponds to the body mass required for sexual maturity (Servanty *et al.* 2009), we assumed that females < 30 kg did not reproduce. The 50-kg threshold corresponds to a hunting rule (hunters must pay a financial penalty if they shoot females over 50 kg). The three weight classes for males were < 45 kg (small), between 45 and 75 kg (medium) and > 75 kg (large). Secondly, we considered two states (alive and just shot) for each sex × body weight class. The population vector had 3 body weights × 2 sexes × 2 states corresponding to a 12×12 matrix. The population vector was considered each year at the end of the hunting season and before reproduction (prebreeding census); the model was female dominant (Caswell 2001) (Table 1).

In each body weight class, net fecundity was obtained as the product of the proportion of breeding females (medium: BPm; large: BPl), the number of juveniles produced (medium: Fm; large: Fl) and the postnatal survival probability Spn (i.e. from birth to weaning) (Fig. 1). We assumed a balanced sex ratio at birth (Servanty *et al.* 2007). Juveniles stayed in the small weight class (with a probability of piOs) or moved to the medium-sized class (1 − piOs). Older wild boars either remained in the same weight class during the year (small or medium) (with respective probabilities pSS and pimm for females and mpSS and mpimm for males) or moved to the next one. We assumed that there was no backward transition towards a lighter weight class. During the first part of the year, without hunting, the survival probability in each weight class was denoted as Ss for small individuals, Sm for medium individuals and Sl for large individuals. These survival probabilities, defined by $S = 1 - NM$ with NM corresponding to natural mortality, corresponded to mortality sources other than hunting (i.e. starvation, diseases, injuries or collisions). We assumed that natural mortality was negligible during the hunting period in the second part of the year. This is not a very stringent assumption because the multiplicative relationship between natural survival and survival to hunting approximately holds even with some overlap in time between the two sources of mortality (Lebreton 2005b). The proportion of individuals shot in each body weight class was denoted as hs, hm and hl for small, medium and large individuals, respectively. The weight class–specific proportion of animals shot during the hunting season was defined by $h = \frac{MH}{1-NM}$, where MH corresponds to the mortality owing to hunting. Consequently, the survival probability at the end of the year corresponded to natural survival ($S = 1 - NM$) times the probability of not being shot during the hunting season ($1 - h$) (Lebreton 2005b).

PARAMETER ESTIMATION

Capture–mark–recapture and recovery data (Williams, Nichols & Conroy 2002) were simultaneously analysed using multistate models (see Lebreton *et al.* 2009 for a review) to estimate separately natural mortality (or equivalently survival) from hunting mortality (Lebreton, Almeras & Pradel 1999). We described the fate of an individual using ten states. States 1, 2 and 3 corresponded to individuals alive in the small, medium and large weight classes, respectively. States 4, 5 and 6 corresponded to individuals just shot, again in the three weight classes, respectively. States 7, 8 and 9 corresponded to individuals that had recently died from natural causes, again in the three weight classes, respectively. The state 'dead from a natural cause' was not observable because no information was available for individuals that did not die from hunting. Hunting-related mortality such as crippling loss was included in natural mortality. In turn, the estimated hunting mortality was thus a minimum. State 10 corresponded to individuals already dead. The state 'already dead' was not observable either but brought together all the dead individuals. The parameters in the multistate model were survival probabilities (Appendix S1 in Supporting Information) and transition probabilities from one weight class to the next (Appendix S2 in Supporting Information). Regarding the observation process, if an individual was alive, it could be recaptured with probability p or not recaptured with probability $1 - p$; if an individual has just died from hunting, it could be recovered with probability r or not recovered with probability $1 - r$ (see Appendix S3 in Supporting Information). We analysed males and females separately because of the strong differences in size and hunting pressure between sexes (Toïgo *et al.* 2008). We first tested the goodness-of-fit (GOF) (Pradel, Wintrebert & Gimenez 2003) using U-CARE software (Choquet *et al.* 2009a). As the effort put on both captures and tag recoveries was constant over the course of the study, recapture and recovery probabilities were assumed to be constant over time. Model selection was based on the Akaike information criterion (Burnham & Anderson 2002). These analyses were implemented in E-SURGE (Choquet, Rouan & Pradel 2009b). Data on female reproductive status were collected and used to estimate weight-specific breeding proportions (BP) (Servanty *et al.* 2009) and fecundity (F) (Table 2).

Postnatal survival Spn and the probability that juveniles remained in the small weight class (piOs) were estimated by expert opinion (see Servanty *et al.* 2011 for further information about Spn; Eric Baubet, unpublished data for piOs) (Table 2).

MODEL VALIDATION

To validate the model, we first compared the asymptotic growth rate $\lambda_{current}$ obtained from our model with the growth rate from an age-structured model previously developed for this population (Gamelon *et al.* 2011). We then used a simple linear regression through the origin to assess the relationship between the predicted and the observed numbers of wild boars shot in each of the 6 weight × sex classes, using R 2.10.1 (R Development Core Team 2009) and Gordon's (1981) formula for the coefficient of determination (R^2) adapted for linear regression through the origin (Kozak & Kozak 1995).

OPTIMAL HARVESTING

The relative importance of each demographic parameter was quantified using elasticity and sensitivity analyses (Caswell 2001), with specific reference to generation time, a major determinant of the overall sensitivity pattern (Gaillard *et al.* 2005). Generation time corresponds to the weighted mean age of the mothers in a population when they gave birth and was calculated as the inverse of the elasticity of the asymptotic population growth rate to a proportional change in all recruitment parameters (Brooks & Lebreton 2001).

For each body weight class, we approximately determined the proportion h′ that would need to be shot to reach a specific target growth rate λ_{target}, based on the first-order Taylor development of the growth rate around its current value (Brooks & Lebreton 2001):

$$h' = h + \frac{-(\lambda_{current} - \lambda_{target})}{S(h)}$$

in which $S(h)$ is the sensitivity of the asymptotic population growth rate to h for each weight class. In each management scenario, the hunting pressure was thus kept equal to the baseline value h for all weight classes except one. For the focal weight class, h′ was estimated based on the formula above. The optimal harvesting scenario corresponds to the scenario that minimizes the hunting pressure (i.e. providing the lowest value of h′) for a maximal reduction of population growth rate. We chose a λ_{target} of 0·90 to assess the optimal harvesting of the studied population. The asymptotic growth rate, the stable body weight class distribution, sensitivities and elasticities were obtained by implementing our model in Software ULM (Legendre & Clobert 1995).

Table 1. Sex- and weight-structured population matrix combining live and dead (shot by hunters) wild boar. Live individuals correspond to rows 1–6 with small, medium-sized and large females (denoted *f*) for rows 1, 2 and 3 and with small, medium-sized and large males (denoted *m*) for rows 4, 5 and 6. Wild boar shot by hunters correspond to rows 7–12 with small, medium-sized and large females (*f*) for rows 7, 8 and 9 and with small, medium-sized and large males (*m*) for rows 10, 11 and 12. See Table 2 for parameter definitions and values

			Alive						Dead
			♀			♂			
			Small	Medium-sized	Large	Small	Medium-sized	Large	
Alive	♀	Small	Ssf × pSS × (1 − hsf)	BPm × Fm × 0·5 × Spn × piOs × Ssf × (1 − hsf)	BPl × Fl × 0·5 × Spn × piOs × Ssf × (1 − hsf)	0	0	0	
		Medium-sized	Smf × (1 − pSS) × (1 − hmf)	BPm × Fm × 0·5 × Spn × (1 − piOs) × Smf × (1 − hmf) + pimm × Smf × (1 − hmf)	BPl × Fl × 0·5 × Spn × (1 − piOs) × Smf × (1 − hmf)	0	0	0	
		Large	0	(1 − pimm) × Slf × (1 − hlf)	Slf × (1 − hlf)	0	0	0	
	♂	Small	0	BPm × Fm × 0·5 × Spn × mpiOs × Ssm × (1 − hsm)	BPl × Fl × 0·5 × Spn × mpiOs × Ssm × (1 − hsm)	Ssm × mpSS × (1 − hsm)	0	0	
		Medium-sized	0	0	0	Smm × (1 − mpSS) × (1 − hmm)	mpimm × Smm × (1 − hmm)	0	
		Large	0	0	0	0	Slm × (1 − mpimm) × (1 − hlm)	Slm × (1 − hlm)	0…0
Dead	♀	Small	Ssf × pSS × hsf	BPm × Fm × 0·5 × Spn × piOs × Ssf × hsf	BPl × Fl × 0·5 × Spn × piOs × Ssf × hsf	0	0	0	… 0…0
		Medium-sized	Smf × (1 − pSS) × hmf	BPm × Fm × 0·5 × Spn × (1 − piOs) × Smf × hmf + pimm × Smf × hmf	BPl × Fl × 0·5 × Spn × (1 − piOs) × Smf × hmf	0	0	0	
		Large	0	(1 − pimm) × Slf × hlf	Slf × hlf	0	0	0	
	♂	Small	0	BPm × Fm × 0·5 × Spn × mpiOs × Ssm × hsm	BPl × Fl × 0·5 × Spn × mpiOs × Ssm × hsm	Ssm × mpSS × hsm	0	0	
		Medium-sized	0	0	0	Smm × (1 − mpSS) × hmm	mpimm × Smm × hmm	0	
		Large	0	0	0	0	Slm × (1 − mpimm) × hlm	Slm × hlm	

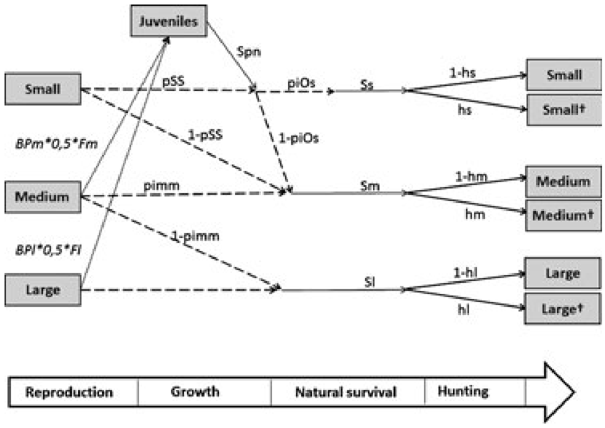

Fig. 1. Model of female wild boar life cycle. The sex ratio is 0·5. Individuals killed by hunting are represented by †. See Table 2 for parameter definitions and values.

Results

PARAMETER ESTIMATION

For females, the GOF test indicated no lack of fit (χ^2 (47) = 31·848, P = 0·956). For males, the GOF test indicated some lack of fit (χ^2 (30) = 57·804, P = 0·003), which was accounted for by using a coefficient of over-dispersion equal to 57·804/30 = 1·93. For both males and females, the best model included among–body-weight-class differences for natural survival NM and probability of being shot during the hunting season MH (Table 3). Estimates of the mortality and transition probabilities are given in Table 2.

MODEL VALIDATION

As expected, the asymptotic growth rate λ_{current} obtained from our body weight-structured model (1·048) was close to that obtained from an age-structured model for the same population (1·047). The asymptotic growth rate was estimated to be 1·926 without hunting, that is, the population would in theory have almost doubled every year without hunting.

The numbers of individuals shot in each sex x body weight class predicted by our model were closely associated with those observed (R^2 = 0·773 and slope of 1·0137 (SE: 0·112), P = 0·0003, Fig. 2). Small males and females were the most heavily hunted classes, followed by medium-sized and large females; medium-sized and large males were the less frequently hunted classes.

Table 2. Parameters and values used in the model

Parameter	Biological meaning	Estimation
Ssf	Natural survival of small females (without hunting)	0·978
Smf	Natural survival of medium-sized females (without hunting)	0·855
Slf	Natural survival of large females (without hunting)	0·859
hsf	Proportion of small females killed by hunting	0·449
hmf	Proportion of medium-sized females killed by hunting	0·345
hlf	Proportion of large females killed by hunting	0·678
Ssm	Natural survival of small males (without hunting)	0·962
Smm	Natural survival of medium-sized males (without hunting)	0·777
Slm	Natural survival of large males (without hunting)	0·904
hsm	Proportion of small males killed by hunting	0·511
hmm	Proportion of medium-sized males killed by hunting	0·541
hlm	Proportion of large males killed by hunting	0·789
BPm	Breeding probability of medium-sized females	0·90
BPl	Breeding probability of large females	0·97
Fm	Mean number of juveniles produced by medium-sized females	4·859
Fl	Mean number of juveniles produced by large females	6·116
Spn	Postnatal survival	0·75
piOs	Probability of juvenile females entering the small class during the year	0·60
pSS	Probability of small females remaining in this class during the year	0·121
pimm	Probability of medium-sized females remaining in this class during the year	0·431
mpiOs	Probability of juvenile males entering the small class during the year	0·6
mpSS	Probability of small males remaining in this class during the year	0·253
mpimm	Probability of medium-sized males remaining in this class during the year	0·322

OPTIMAL HARVESTING

Parameters of medium-sized females showed the highest elasticities and sensitivities (Table 4). The sum of elasticities of recruitment parameters was 0·490, leading to a generation time of 2·04 years. As the model was female dominant, the three management scenarios proposed were based on female hunting controls only (Table 5). A 35·6% increase in hunting pressure on small females (leading to a new hsf′ of 0·809) while keeping the same hunting pressure on the other two body weight classes made it possible to reach the 0·90 target (Table 5a). A growth rate close to 0·90 could also be reached by increasing the hunting pressure on medium females by 14·6% (Table 5b). Alternatively, the 0·90 growth rate target could also be reached through a 31·7% increase in hunting pressure on large females

Table 3. Model selection results. Number of parameters (Np) and difference in AIC between each tested model and the best model (ΔAIC) for effects of body weight classes (3*w* for small, medium and large) on survival probability (*S*, including mortality owing to hunting MH and natural mortality NM) for males (M) and females (F). *AIC* of the best models are 2276·845 (males) and 4501·307 (females)

Model	Biological meaning	Np	ΔAIC
M			
S(MH)_3w-(NM)_3w	MH and NM depend on 3 weight classes	23	0
S(MH)_3w-(NM)	MH depends on 3 weight classes; NM constant	13	256·262
S(MH)-(NM)	MH constant; NM constant	11	440·438
S(MH)-(NM)_3w	MH constant; NM depends on 3 weight classes	12	440·813
F			
S(MH)_3w-(NM)_3w	MH and NM depend on 3 weight classes	24	0
S(MH)_3w-(NM)	MH depends on 3 weight classes; NM constant	14	375·786
S(MH)-(NM)_3w	MH constant; NM depends on 3 weight classes	13	537·264
S(MH)-(NM)	MH constant; NM constant	12	537·403

while keeping the same hunting pressure on small and medium-sized females (Table 5c). The optimal harvesting thus corresponded to the second scenario (Table 5b), which minimized the hunting for a maximal reduction in population growth rate. Nevertheless, in terms of individuals and not h′, the 0·90 growth rate target could be reached by only killing 20 more large females while keeping the same hunting pressure on small and medium-sized females.

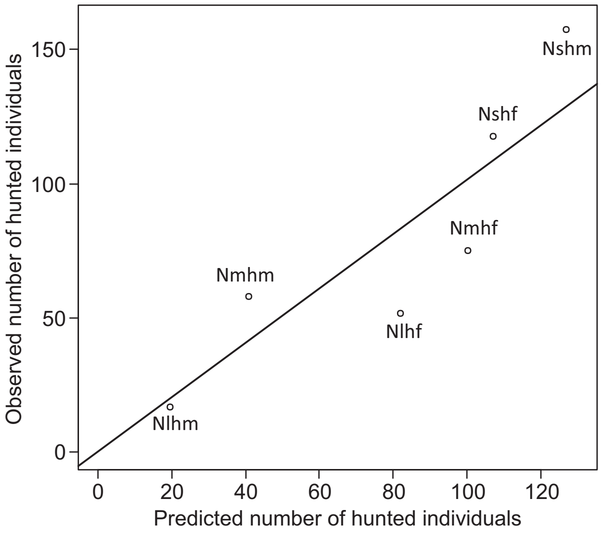

Fig. 2. Relationship between the mean numbers of wild boar for each sex and weight class hunted in Châteauvillain-Arc-en-Barrois and those predicted by the model ($R^2 = 0·773$; slope = 1·0137 (SE: 0·112), $P = 0·0003$). The analysis was restricted to the years 1993–1999. *Nshf*, *Nmhf* and *Nlhf* correspond to the number of small, medium-sized and large females, respectively, shot by hunters, and *Nshm*, *Nmhm* and *Nlhm* correspond to the number of small, medium-sized, and large males, respectively, killed by hunting.

Table 4. Elasticities and sensitivities of demographic parameters. Male parameters are not displayed because their elasticities and sensibilities are null. See Table 2 for parameter definitions and values

Parameter	Elasticities	Sensitivities
hsf	−0·179	−0·418
hmf	−0·335	−1·019
hlf	−0·303	−0·469
Spn	0·490	0·686
Ssf	0·2191	0·235
Smf	0·637	0·781
Slf	0·144	0·176
BPm	0·384	0·448
BPl	0·106	0·115
Fm	0·384	0·166
Fl	0·106	0·036

Discussion

Age-structured models (Caswell 2001) are frequently used to model vertebrate population dynamics, in particular ungulates (Gaillard & Yoccoz 2003). Age is often the main structuring factor of population dynamics, and in large herbivores, three age classes are usually retained (Gaillard *et al.* 2000). However, many species cannot easily be described using age classes (Hastings & Botsford 2006). Therefore, stage-structured models might be more useful as is often the case in plant ecology (Salguero-Gomez & de Kroon 2010). In ungulates, demographic traits strongly depend on body weight (e.g. Festa-Bianchet, Gaillard & Jorgenson 1998 on bighorn sheep *Ovis canadensis*), and body weight therefore influences population dynamics (see Gaillard *et al.* 2000 for a review) and evolution (Pelletier *et al.* 2007 on Soay sheep *Ovis aries*). Body weight thus appears to be a more appropriate structuring factor than age in wild boar populations. Moreover, our focus was on the use of hunting data to allow managers to apply our model through manipulation of hunting pressure. Therefore, we could not use age-structured models simply because age is not recorded when hunters shoot wild boar. Hunters record sex and body weight of the wild boar they shoot, so we built a sex- and body weight-specific model.

Among ungulates, the wild boar is highly fecund and has a short generation time. Wild boar females have a high fecundity for their body weight, with generally five piglets per litter and per year (Servanty *et al.* 2007). Moreover, in our study area in Châteauvillain-Arc-en-Barrois in France, females with a dressed body weight of ≥50 kg were avoided by hunters, so small individuals were the most heavily hunted. The proportion of first-year wild boars in the hunting bag ranged from

Table 5. Reaching an asymptotic growth rate of 0·90 by selectively increasing the harvest rate in each of the three body weight classes. In each scenario, the baseline proportion of individuals shot during the hunting season is denoted as h and the harvest proportion needed in the focal weight class to reach the target asymptotic growth rate of 0·90 is denoted h′. The required increase in the proportion harvested in the focal class is $\Delta h = h' - h$. The corresponding number of individuals to be killed in a population of arbitrary size 1000 individuals is given in the Number column. The last column ΔN provides the required number of individuals to be killed compared to the number of individuals currently killed

	h	h′	Δh	Number	ΔN
(a)					
Small		0·806	0·356	198	88
Medium-sized	0·345			108	
Large	0·678			43	
(b)					
Small	0·449			110	
Medium-sized		0·490	0·146	153	45
Large	0·678			43	
(c)					
Small	0·449			110	
Medium-sized	0·345			108	
Large		0·995	0·317	63	20

0·55 to 0·95 (Gamelon *et al.* 2011). This high hunting pressure was selected for an increased reproductive effort early in life (Gamelon *et al.* 2011), thus accelerating the life cycle (Servanty *et al.* 2011). Consequently, the generation time in this heavily hunted wild boar population was 2·04 years instead of 7 years expected from the allometric relationship linking body mass and generation time among ungulates (Gaillard *et al.* 2008). Wild boar populations under high hunting pressure have a fast turnover (Gaillard *et al.* 2005) and populations can double within a single year. For instance, without hunting, the population at Châteauvillain-Arc-en-Barrois studied here would have increased each year by 92·6%. Such a growth rate is between two and three times higher than those of other ungulates (Gaillard *et al.* 2000).

With such exceptional population dynamics, the control of wild boar populations is dependent on hunting focussing on specific body weight classes. We aimed to develop a management scenario that maximized the impact of hunting on population growth rate while allowing for the steady decrease in the number of hunters. Clearly, the availability of adult males was not limiting fecundity, as demonstrated by the high reproductive output of females in the studied population (Servanty *et al.* 2011). A model that was only partially female dominant (Caswell 2001, p. 570) would thus unavoidably make the harvesting of males less efficient than that of females for controlling population growth of wild boar. Therefore, the focus was on an optimal harvesting strategy for females. Managers should increase the hunting pressure on medium-sized females by about 15% to reduce the wild boar population to an asymptotic growth rate of 0·90. The key role of medium-sized females in the population dynamics has been demonstrated by the elasticity analysis. In our model, females weighing between 30 and 50 kg included 1-year-old females, which play an important role in the demography of heavily hunted wild boar populations (Gamelon *et al.* 2011).

This management option is specific to wild boar in European countries. However, the structure of our model is widely applicable to the management of other exploited populations, provided information on sex and phenotypic attributes can be recorded by hunters. Population management is dominated by a pattern-oriented approach based on surveys of population size, while a process-oriented approach based on the estimation and modelling of demographic flows (e.g. Coulson, Milner-Gulland & Clutton-Brock 2000) would be more powerful. The only limitation is that the process-oriented approach requires costly long-term monitoring. While the construction of our model requires a process-oriented approach, the monitoring tool we provided based on the number of individuals shot by hunters is a pattern-oriented approach (Nichols & Williams 2006). At least in an applied ecology context, these approaches should be viewed as complementary rather than opposing strategies.

Obtaining reliable estimates of sex- and weight-specific demographic parameters is a crucial step in our approach. Both survival and reproductive parameters may vary within and among populations depending on hunting pressure and resource availability (Servanty *et al.* 2011). However, the high explanatory power of our deterministic model indicates that temporal variation in demographic parameters did not markedly influence the distribution of body weights among male and female wild boars. The high hunting pressure was indeed the strongest determinant of the dynamics of the studied population (Gamelon *et al.* 2011). Although further analyses will be required to assess whether lower levels of exploitation magnify the role of stochastic variation in demographic parameters on population dynamics, our case study suggests that managers can often rely on deterministic models. Indeed, the validation of our model shows that this weight-structured model leads to the same growth as an earlier age-structured model, and moreover shows a strong similarity between predicted and observed numbers of individuals shot in each sex x body weight class. As a perspective, the estimation of survival and reproductive parameters could be based on a combination of population surveys or hunting statistics and of CMR data into an integrated model (Schaub *et al.* 2007). Indeed, population counts contain hidden information on demographic parameters, and this information can make estimates of demographic parameters more precise (Besbeas, Freeman & Morgan 2002).

The inclusion of both living and killed individuals of each sex and body weight class allowed a quantitative comparison between the observed and predicted numbers of individuals shot in each category during the hunting season and therefore provided a direct way to assess the suitability of the model. Once the model has been correctly parameterized, wildlife managers can evaluate the consequences of a given hunting rule and then implement the appropriate management strategies to meet the objectives. Focussing the hunting pressure on specific sex and weight classes corresponds to a kind of selective hunting. However, most examples of selective hunting in game species have focussed on the resulting changes in phenotypic traits, as well illustrated by selective hunting in deer populations in relation to antler size (e.g. Strickland *et al.* 2001). Recent studies have proposed that selective hunting of game populations can be useful for population management (Webb *et al.* 2012). The population model we propose here provides a reliable tool to apply this approach. Antler size in deer and horn size in bovids could offer suitable metrics for classifying individuals in categories easily recognizable by hunters in a similar way to our use of body weight in this study.

In conclusion, the 0·90 growth rate target in the studied population could be reached by killing 20 more large females only, that is, harvesting among the most fecund females, while keeping the same hunting pressure on small and medium-sized females. Our approach thus provides managers with a qualitative harvest plan that allows controlling wild boar populations without increasing the overall hunting pressure. As the number of hunters is declining in several European countries, increasing hunting pressure to control any fast-growing game populations is irrelevant. A suitable alternative is to target the most influential categories of individuals. Our modelling approach offers a suitable way to identify such individuals in a large range of situations.

Acknowledgements

We are grateful to all those who helped trap and mark wild boar, especially Serge Brandt, as well as those who collected harvested wild boars, particularly P. Van den Bulck and G. Corbeau. We warmly thank Jim Mitchell for correcting our English and for his helpful comments that improved our paper. We also thank Guillaume Chapron and one anonymous referee for constructive comments on a previous draft. We are grateful to the Office National des Forêts and to F. Jehlé, who allowed us to work on the study area.

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Received 16 November 2011; accepted 17 May 2012
Handling Editor: Johan du Toit

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Matrix showing mortality due to hunting, natural mortality and survival (denoted by a letter) at $t + 1$ (columns) through transitions from state at time t (rows) to state at time $t + 1$ (columns).

Appendix S2. Transition probabilities for females from a given weight-class at time t to another weight-class at time $t + 1$.

Appendix S3. Matrix showing recapture probability (p) and recovery probability (r); states are in row and observations in column (0: individual is not seen, 1, 2, 3: this individual is recaptured in the small, medium and large body weight-class, respectively; 4, 5, 6: this individual is hunted in the small, medium and large body weight-class, respectively), at the same occasion t.