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Influence of harvesting pressure on demographic tactics: implications for wildlife management

Sabrina Servanty[1,2,3]*, Jean-Michel Gaillard[4], Francesca Ronchi[5], Stefano Focardi[5], Éric Baubet[6] and Olivier Gimenez[1]

[1]*Centre d'Écologie Fonctionnelle et Évolutive, UMR 5175, campus CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France;* [2]*USGS Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, MD 20708-4039, USA;* [3]*Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, CO 80523-1484, USA;* [4]*Université de Lyon, F-69000, Lyon; Université Lyon 1; CNRS, UMR5558, Laboratoire de Biométrie et Biologie Evolutive, F-69622, Villeurbanne, France;* [5]*Istituto Superiore per la Protezione e Ricerca Ambientale, via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia, Italy; and* [6]*Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés Sangliers, Montfort 01330 Birieux, France*

Summary

1. Demographic tactics within animal populations are shaped by selective pressures. Exploitation exerts additional pressures so that differing demographic tactics might be expected among populations with differences in levels of exploitation. Yet little has been done so far to assess the possible consequences of exploitation on the demographic tactics of mammals, even though such information could influence the choice of effective management strategies.

2. Compared with similar-sized ungulate species, wild boar *Sus scrofa* has high reproductive capabilities, which complicates population management. Using a perturbation analysis, we investigated how population growth rates (λ) and critical life-history stages differed between two wild boar populations monitored for several years, one of which was heavily harvested and the other lightly harvested.

3. Asymptotic λ was 1·242 in the lightly hunted population and 1·115 in the heavily hunted population, while the ratio between the elasticity of adult survival and juvenile survival was 2·63 and 1·27, respectively. A comparative analysis including 21 other ungulate species showed that the elasticity ratio in the heavily hunted population was the lowest ever observed.

4. Compared with expected generation times of similar-sized ungulates (more than 6 years), wild boar has a fast life-history speed, especially when facing high hunting pressure. This is well illustrated by our results, where generation times were 3·6 years in the lightly hunted population and only 2·3 years in the heavily hunted population. High human-induced mortality combined with non-limiting food resources accounted for the accelerated life history of the hunted population because of earlier reproduction.

5. *Synthesis and applications*. For wild boar, we show that when a population is facing a high hunting pressure, increasing the mortality in only one age-class (e.g. adults or juveniles) may not allow managers to limit population growth. We suggest that simulations of management strategies based on context-specific demographic models are useful for selecting interventions for population control. This type of approach allows the assessment of population response to exploitation by considering a range of plausible scenarios, improving the chance of selecting appropriate management actions.

Key-words: comparative analysis, demography, hunting, life history, life table response experiment, prospective analysis, retrospective analysis, *Sus scrofa*, ungulate, wild boar

*Correspondence author. E-mail: sab.servanty@free.fr

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Introduction

Demographic tactics are shaped by different selective pressures generated by changes in food resources, climate, predation or inter- and intraspecific competition (Southwood 1988). Human exploitation (fishery, hunting or harvesting) adds selective pressures that can strongly influence the life histories of individuals (Milner, Nilsen & Andreassen 2007; Allendorf *et al.* 2008). Between-population differences in the levels of exploitation lead to contrasting demographic tactics through changes in generation time (Crampe *et al.* 2006; Nilsen *et al.* 2009), a key variable for both demography (Lebreton & Clobert 1991) and evolution (Gaillard *et al.* 2005). Thus, a high rate of exploitation of adults relative to juveniles leads to an increased reproductive effort early in life (Festa-Bianchet 2003; Proaktor, Coulson & Milner-Gulland 2007) as expected from theory (e.g. Schaffer 1974). Such a demographic shift may occur through two mechanisms: evolutionary changes in gene frequencies over many generations (Stearns 2000) or change across the lifetime of an individual (Chevin, Lande & Mace 2010).

The evolutionary consequences of size-selective exploitation were first identified in fisheries (Law 2000). Empirical evidence of the consequences of exploitation on terrestrial mammals remains scarce because long-term monitoring of hunted populations is mostly lacking (but see Coltman *et al.* 2003). To date, intensively studied ungulate populations have not been hunted and are located on islands (Clutton-Brock, Guinness & Albon 1982; Clutton-Brock & Pemberton 2004), in fenced areas (Gaillard *et al.* 1993) or in remote mountain areas (Jorgenson *et al.* 1997; Toïgo *et al.* 2007; Festa-Bianchet & Côté 2008). Thus, it is not known whether the patterns in life-history variation observed in those populations would apply to intensively hunted populations.

In age-structured populations, reproductive parameters respond more rapidly than adult survival (AS) to changes of environmental conditions (Gaillard *et al.* 2000). However, the response to increased hunting pressure should vary depending on the species' ability to increase reproductive effort early in life. Thus, ungulates facing predation do not reproduce at earlier ages, leading to declines in population size (Wittmer *et al.* 2005; Festa-Bianchet *et al.* 2006; Nilsen *et al.* 2009).

Here, we compare the demography of two wild boar *Sus scrofa* L. populations with contrasting hunting pressure. Wild boar populations have grown in number during the last three decades (Schley & Roper 2003) and have expanded their ranges, negatively impacting other wildlife and agriculture (Massei & Génov 2004). Their agricultural damage cost more than € 19 000 000 in 2006 in France (Guibert 2008) and more than € 7 000 000 in 2004 in Italy (Carnevali *et al.* 2009).

The life history of the wild boar is unusual among ungulates (Focardi *et al.* 2008). Females produce five offspring per litter (Servanty *et al.* 2007), whereas similar-sized ungulates generally produce two (Hayssen, Van Tienhoven & Van Tienhoven 1993). Moreover, wild boar females may give birth for the first time at 1 year old (Mauget 1982), whereas females in other ungulates do not produce offspring before 2 years old (Hayssen, Van Tienhoven & Van Tienhoven 1993). Furthermore, compared with similar-sized ungulates, annual fluctuations in the proportion of breeding females are high and lead population size to vary (Bieber & Ruf 2005; Servanty *et al.* 2009).

We investigated how asymptotic population growth rates (λ) and critical life-history stages varied between two wild boar populations subject to different hunting pressure. We performed a prospective perturbation analysis to assess the functional dependence of λ on variations in demographic parameters and a retrospective perturbation analyses to quantify relative contributions of changes in demographic parameters to variation in λ (Caswell 2000). Finally, we simulated different harvest scenarios with the aim of preventing population growth, starting from the situation observed in each population.

Material and methods

Wild boar have no natural predators once they are weaned. The French population is located in Haute-Marne in the 11 000 ha Châteauvillain-Arc en Barrois forest (48°02′N; 4°55′E). This deciduous forest is mainly composed of oak *Quercus petraea* (Liebl. 1784, 41%) and beech *Fagus sylvatica* (L., 30%). The climate is intermediate between continental and oceanic types. The forest is divided into two sections (i) the 8500-ha core managed by The Office National des Forêts and divided by forest trails into plots of about 15 ha and (ii) the 2500-ha periphery including private and communal areas. Wild boar are intensively hunted each year between October and February. They are driven towards hunters surrounding a 250- to 500-ha area by beaters and dogs. Before 1986–87, 166 ± 68 wild boar were shot every year; subsequently, the harvest was 482 ± 213. Individual boar has a 40% chance of being shot every year, rising up to 70% for adult males (Toïgo *et al.* 2008). The annual harvest comprises 38·9% (±5·3) yearling males, 33·8% (±3·3) yearling females, 9·3% (±3·1) subadult females, 9·1% (±3·6) subadult males, 5·9% (±1·4) adult females and 3·0% (±1·0) of adult males. Since 1982, during March to September, wild boar have been monitored through capture–mark–recapture (CMR) over an area covering 1400–2000 ha. Between 1982 and 2007, 1372 males (1248 juveniles, 111 yearlings and 13 adults) and 1258 females (1084 juveniles, 112 yearlings and 62 adults) were marked using ear-tags. During the hunting season, employees of the Office National de la Chasse et de la Faune Sauvage and people living adjacent to the forest check shot boars for individual tags.

The Italian population is located within the 6000 ha fenced Preserve of Castelporziano (41°44′N, 12°24′E). This area is a typical Mediterranean coastal ecosystem (Focardi *et al.* 2008) including the holly oak *Quercus ilex* (L., 27%) and deciduous oak forests (34%) with *Q. cerris* (L.) and *Q. frainetto* (Tenore 1813), often associated with an undergrowth of *Carpinus orientalis* (Miller). The climate is Mediterranean with dry summers and rainfall concentrated in October–November. Temporary pools and a few wetlands are used by wildlife during summer droughts. The frequent occurrence of summer droughts might influence the reproductive performance of wild boar (Fernández-Llario & Carranza 2000). The harvest plan aims to keep the proportion of yearlings to adults constant. Harvest is by government employees only: live-trapping in August–September (mainly juveniles and yearlings) and hunting of adults in September–March. The hunting pressure has been low since 1988 (about 11·2% of the total population removed each year, composed of 48·9% yearlings, 11·3% subadult males, 10·4% subadult females, 14·7% adult males and 14·7% adult females, Focardi *et al.* 2008). Since 1995, the population has been monitored using CMR. Between 1995 and 2006, 642 males (483 juveniles, 108 yearlings and 51 adults) and 586 females (454 juveniles, 77 yearlings and 55 adults) have been marked.

Several lines of evidence indicate that the differences in demographic patterns observed between the two populations can reliably be attributed to differences in hunting pressure. First, the ratio between the number of hunted marked individuals and the total number of marked individuals (an index of the hunting pressure, Lebreton 1977) was much lower in the Italian (0·091) than in the French (0·646) population. Secondly, although environmental resources were greater and more predictable in the French population, the high reproductive output of yearlings observed in this population is more likely to be explained by the high hunting pressure than by high food availability (Servanty *et al.* 2009). Indeed, the observed threshold body mass required for females to become reproductive for the first time was lower at Châteauvillain than in a carefully designed experiment on females captured as wild piglets and fed in captivity on an *ad libitum* diet (Pépin & Mauget 1989). This demonstrated that high food availability alone cannot induce early reproduction in wild boar. By contrast, the intense hunting pressure experienced by this wild boar population (i.e. the heaviest hunting pressure ever measured for a large mammal, Toïgo *et al.* 2008) probably explained the observed low threshold body mass for earliest reproduction (see also Table 3 in Servanty *et al.* 2009).

MATRIX PERTURBATION ANALYSIS

We used a prebreeding census matrix (Caswell 2001). Based on previously reported annual age-specific variation in demographic parameters (Focardi *et al.* 2008; Toïgo *et al.* 2008; Servanty *et al.* 2009), we distinguished three age-classes: yearlings (Y, 1 year of age), subadults (Sa, 2 years of age) and adults (A, ≥3 years of age). We assumed a balanced sex ratio at birth. We included in the model (see Fig. 1): (1) Yearling recruitment (YR) taken as the product of the proportion of yearling females breeding, the mean number of females produced at birth by yearling females, juvenile survival (i.e. the product of the survival probability of females between birth and weaning and the survival probability of females from weaning to 1 year of age); (2) Subadult recruitment (SaR) taken as the product of the proportion of subadult females breeding, the mean number of females produced at birth by subadult females and the juvenile survival; (3) Adult recruitment taken as the product of the proportion of adult females breeding, the mean number of females produced at birth by adult females and the juvenile survival; (4) Yearling survival (YS) taken as the survival probability of females from 1 year of age to 2 years of age; and (5) AS taken as the survival probability for females from 2 years of age and older.

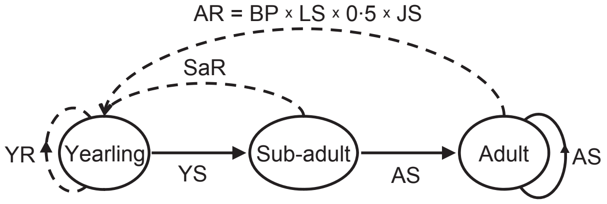

Fig. 1. Life cycle graph of wild boar. Three main age-classes are considered: Yearling (at 1 year of age), Subadult (at 2 years of age) and Adult (at 3 years of age and older). Solid lines represent the probability of surviving until the next age (see text): YS, yearling survival; AS, adult survival (for individuals aged 2 years and older). Dashed lines represent the recruitment (see text): YR, yearling recruitment; SaR, subadult recruitment; AR, adult recruitment; BP, breeding proportion; LS, litter size; JS, juvenile survival.

In both populations, we updated previous CMR analyses (Focardi *et al.* 2008; Toïgo *et al.* 2008) to obtain estimates of overall survival (i.e. survival including both non-hunting and hunting mortality; see Appendix S1, Supporting Information for more details). In the French population, we estimated the probability of retrieving a mark after boar has been shot rather than fixing it to 0·9 as in previous analyses (Toïgo *et al.* 2008). We did not have empirical estimates of survival from birth to weaning because juveniles were already weaned when first captured. We used expert opinion to set this survival rate at 0·75 (Servanty *et al.* 2005), a high value supported by sparse observations (Jezierski 1977).

In the French population, we obtained age-class-specific estimates of mean litter size and an estimate of the proportion of breeding females from examination of reproductive tracts of females shot in January–February (Servanty *et al.* 2009). The proportion of breeding females was slightly underestimated because some females, especially juveniles, become reproductive after the hunting season (Gethöffer, Sodeikat & Pohlmeyer 2007). In the Italian population, we estimated mean litter size and proportion of breeding females from a sample of reproductive tracts from females shot in January–March, providing us with almost unbiased estimates because the birth season occurs from March to April. As a result of small sample size per age-class in some years, we restricted the study period to 1999–2005 in the French population and to 2002–2006 in the Italian population.

We tested whether the age-specific proportions of breeding females differed between populations. We performed unequal variance *t*-tests to compare age-class-specific mean litter sizes. We obtained the λ, the stable age distribution (Caswell 2001).

Using prospective analysis, we assessed the effect of proportional changes in any demographic parameter on λ by calculating elasticities. The parameter with the highest potential impact on λ is the one with the highest elasticity.

Using retrospective analysis, we identified which demographic parameter had the highest contribution to observed variation in λ (1) in each population and (2) between populations. To assess the relative contribution of demographic parameters to observed variation in λ in each population, we used the variance decomposition proposed by Horvitz, Schemske & Caswell (1997). Empirical studies have highlighted that demographic parameters with a high elasticity generally have low temporal variability (Pfister 1998; Gaillard & Yoccoz 2003). The contribution of a given vital rate to the variation in λ was calculated by multiplying the squared elasticity of this trait by the squared coefficient of variation (i.e. standard deviation/mean computed between years) of the same trait and divided by the total variance in λ. The total variance in λ was estimated as the sum across all vital rates of the products of the squared elasticity by the squared coefficient of variation of parameters (Horvitz, Schemske & Caswell 1997). To assess the relative contribution of demographic parameters to observed variation in λ between populations, we performed a fixed-design life table response experiment (LTRE) analysis (Caswell 2001), using the matrix of the Italian population as a reference.

We calculated generation time as the inverse of the relative elasticity of the population growth rate to a change in all recruitment parameters (Brooks & Lebreton 2001).

All calculations were performed in program R 2.8.0 (R Development Core Team 2008) using package popbio (Stubben & Milligan 2007).

Table 1. Mean breeding proportions (BP), litter size (LS) and survival (S) for each age-class in the heavily hunted (Châteauvillain, France) and lightly hunted (Castelporziano, Italy) populations of wild boar. The coefficient of variation (CV) for each demographic parameter and the sample size (N) from which the reproductive parameters were estimated are also provided. For each age-class, recruitment (R) is calculated as BP × 0·5 × LS × JS where JS is the product of the survival from birth to weaning (0·75) and the survival from weaning to 1 year of age that has been estimated by CMR (0·484 in Châteauvillain and 0·745 in Castelporziano)

	Age-class	N	BP	SE_{BP}	CV_{BP}	LS	SE_{LS}	CV_{LS}	S	CV_S	R
Châteauvillain (Heavily hunted)	Adult	92	0·97	0·005	0·05	6·36	0·080	0·12	0·484	0·173	1·120
	Subadult	153	0·90	0·009	0·12	5·40	0·026	0·06	(0·484)	(0·173)	0·882
	Yearling	298	0·51	0·012	0·42	3·88	0·027	0·12	0·484	0·173	0·359
Castelporziano (Lightly hunted)	Adult	97	0·88	0·009	0·1	3·74	0·057	0·15	0·745	0·168	0·919
	Subadult	29	0·79	0·022	0·15	2·8	0·052	0·1	0·745	0·168	0·618
	Yearling	14	0·14	0·019	0·50	1·17	0·047	0·15	0·745	0·168	0·039

CMR, capture–mark–recapture.

SIMULATION MODELLING OF HARVEST

We used the output of the prebreeding matrix in each population as a starting point to simulate how to increase the age-specific proportion of hunted animals to prevent the population from growing. In a first management scenario, we tested the increase in harvested yearling females (i.e. additional harvest on top of the existing one) when subadult and adult females were hunted in the same proportions as before. In the second scenario, we tested the increase in harvested adult females, when yearlings and subadults were hunted in the same proportions as before. Simulations were implemented in SAS 9.2 for Windows (SAS Institute Inc., Cary, NC, USA).

Results

Female wild boar in the heavily hunted French population had larger litter sizes (yearling: $t = 20·14$, $P < 0·0001$; subadults: $t = 38·64$, $P < 0·0001$; and adults: $t = 23·02$, $P < 0·0001$) and bred in higher proportion as both yearlings and adults (yearlings: $\chi^2 = 5·82$, $P = 0·016$; subadults; $\chi^2 = 1·86$, $P = 0·17$; and adults: $\chi^2 = 4·12$, $P = 0·041$) than females in the lightly hunted Italian population (Table 1). Survival was not age dependent in either population and was higher in the lightly hunted Italian population than in the heavily hunted French population (Table 1).

PROSPECTIVE ANALYSIS

In the lightly hunted Italian population, wild boar increased at a rate of 24% per year, whereas in the heavily hunted French population, they increased at a rate of 11% per year. Generation time was longer in the lightly hunted Italian population than in the heavily hunted French population (3·64 vs. 2·27 years). As a consequence, the stable age structure differed greatly between populations (Fig. 2). In the heavily hunted population, the ratio of yearlings to adults was 2·8–1, whereas in the lightly hunted population, the ratio was 1·1–1.

In the lightly hunted population, the elasticity of λ to changes in AS was higher than the elasticities of λ to changes in recruitment (Table 2). The sum of elasticities of reproduction (0·275) and that of survival (0·724) showed that changes in survival rates would have the greatest impact on λ. In the heavily hunted population, juvenile survival had the highest elasticity, whereas all other age-specific parameters had similar elasticities (Table 2). The sum of elasticities of reproduction (0·44) and that of survival (0·56) showed that if either survival rates or reproductive rates were modified, the impact on λ would be high relative to the observed elasticities in the lightly hunted population, in which the impact on λ was highest for a given change in AS.

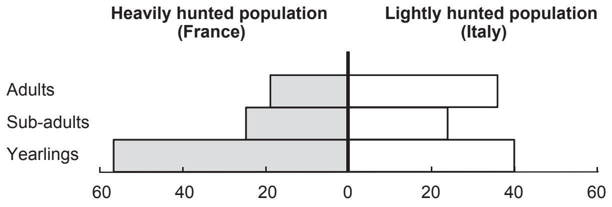

Fig. 2. Predicted stable age structure (%) in the heavily hunted (Châteauvillain) and lightly hunted (Castelporziano) populations of wild boar.

Table 2. Age-class-specific elasticities of the asymptotic population growth rate to changes of demographic parameters in the heavily hunted (Châteauvillain) and the lightly hunted (Castelporziano) populations of wild boar

	Age-class	Recruitment	Survival
Châteauvillain (Heavily hunted)	Adult	0·147	0·260
	Subadult	0·151	(0·260)
	Yearling	0·142	0·3
	Juvenile	0	0·44
Castelporziano (Lightly hunted)	Adult	0·183	0·458
	Subadult	0·082	(0·458)
	Yearling	0·01	0·266
	Juvenile	0	0·275

However, in both cases, the ratio between the elasticity of AS and juvenile survival was low compared with that observed in 21 other ungulate species previously studied (Table 3). Wild boar are almost equally sensitive to perturbations in survival and recruitment; hence, their life history is more typical of short-lived vertebrate species (i.e. fast life history with a high annual turnover of individuals) than of long-lived ones

Table 3. Ratio between the elasticity of adult survival and juvenile survival for 22 ungulate species. When no reference is indicated, elasticity ratio was calculated from data provided in Appendix A of Gaillard & Yoccoz (2003). For species able to reproduce for the first time as yearlings (i.e. wild boar and Soay sheep *Ovis aries*), elasticities of adult survival also included the yearling survival to allow comparison with species that reproduce for the first time as yearlings

Species	Elasticity ratio	Reference
Feral horse *Equus caballus*	17·35	
Mountain goat *Oreamnos americanus*	8·96	
Pronghorn *Antilocapra americana*	8·74	
Red deer *Cervus elaphus*	8·63	
Dall sheep *Ovis dalli*	8·17	
Alpine ibex *Capra ibex*	8·05	
Reindeer *Rangifer tarandus*	7·02	
Caribou *Rangifer tarandus granti*	6·93	
Moose *Alces alces* (population 1)	6·89	
Chillingham cattle *Bos taurus*	6·85	
Bighorn sheep *Ovis canadensis* (population 2)	6·57	
Bighorn sheep (population 1)	5·94	
Greater kudu *Tragelaphus strepsiceros* (population 1)	5·63	
African buffalo *Syncerus caffer*	5·61	Jolles, Cooper & Levin 2005
Greater kudu (population 2)	5·44	
Plain zebra *Equus burchelli*	5·33	Grange *et al.* 2004
Elk *Cervus elaphus*	4·76	Raithel, Kauffman & Pletscher 2007
Mule deer *Odocoileus hemionus* (population 1)	4·68	
African buffalo	4·62	Grange *et al.* 2004
Chinese water deer *Hydropotes inermis*	4·28	Dubost *et al.* 2008
Bison *Bison bison*	4·25	Fuller *et al.* 2007
Moose (population 2)	4·14	
Moose (population 4)	4·00	
Mule deer (population 2)	3·85	
Wildebeest *Connochaetes taurinus*	3·56	Grange *et al.* 2004
Soay sheep	3·47	
Roe deer (population 2)	3·27	
Wild boar (lightly hunted population)	2·63	This study
Moose (population 3)	2·57	
Roe deer (population 1)	2·48	
Wild boar (heavily hunted population)	1·27	This study

(i.e. a slow life history with a low annual turnover of individuals). Even when subjected to light hunting pressure, their life-history traits are closer to the fast end of the fast-slow continuum of life-history tactics (Gaillard *et al.* 2005) than has been reported for any other ungulate species. Further, this fast life history is even more pronounced when wild boar are exposed to heavy hunting pressure (Table 3).

RETROSPECTIVE ANALYSIS

The relative contribution of each vital rate to the variation in λ observed during the study period differed between populations (Fig. 3). In the heavily hunted population, the variance in λ was mostly driven by temporal variation in yearling reproduction (i.e. contribution of breeding proportions and litter size; 25·2%) and juvenile survival (38·4%). Temporal variation in adult and subadult reproduction accounted for similar amounts of variance (between 2% and 5%; Fig. 3). In the lightly hunted population, the observed variation in λ was mostly accounted for by AS (52%), followed by juvenile and YS (18·75% and 17·54%, respectively). Although the coefficient of variation of juvenile reproduction was high (Table 1), its contribution to variation in λ was low (0·2%).

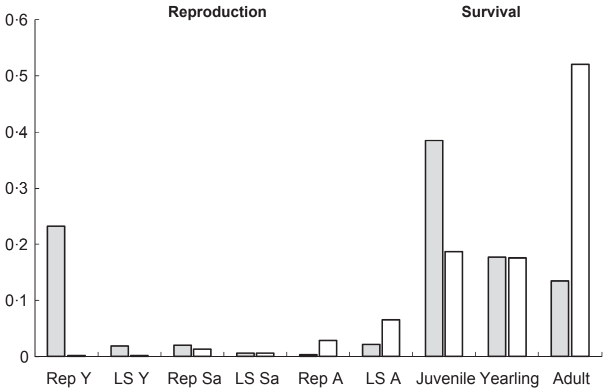

Fig. 3. Relative contributions of demographic parameters to observed changes of population growth rate for each age-class in the heavily hunted (Châteauvillain, grey bars) and lightly hunted (Castelporziano, white bars) populations of wild boar. Rep is the age-specific breeding proportion, LS, litter size; Y, yearlings; Sa, subadults; A, adults.

Life table response experiment showed that changes in survival contributed the most to declines in population growth in response to heavy hunting pressure. When a population was subject to an increase in hunting pressure, the impact of survival on λ was partially offset by increases in recruitment, most notably in YR (Fig. 4). Wild boar appear to be able to compensate for elevated mortality to some extent by increasing yearling reproductive output.

SIMULATION MODELLING OF HARVEST

Based on our estimates of the demographic parameters (Table 1), we showed that in the lightly hunted Italian population, increasing the harvest rate of the remaining adult females was more efficient than increasing the removal of yearlings in controlling population growth (Fig. 5). Population growth stopped when the proportion of adult females harvested was increased by 44% or when the proportion of yearling females harvested was increased by 60%, assuming harvest rates among other groups was unchanged. Conversely, in the heavily hunted French population, population growth stopped when harvest rates of yearling females were increased by 23% or adults by 42% (Fig. 5).

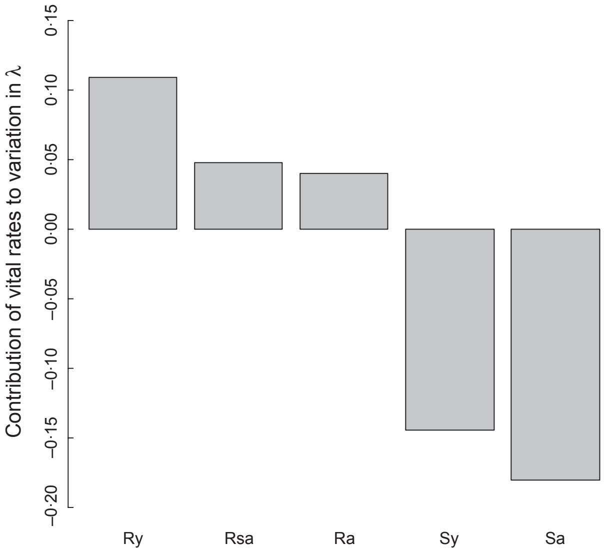

Fig. 4. Contributions of the matrix elements of the heavily hunted French population to the variation in λ when the lightly hunted Italian population is the reference matrix. R, recruitment; S, survival; y, yearling; a, adult.

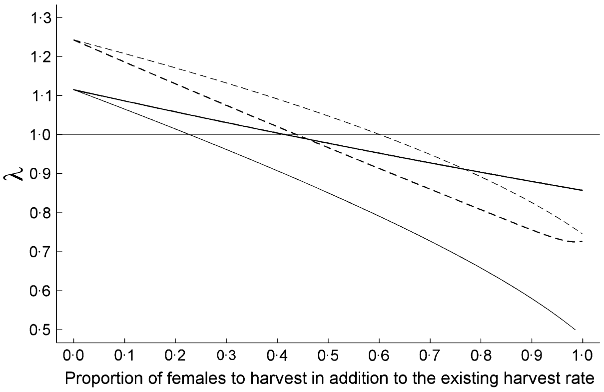

Fig. 5. Simulations of two different management scenarios to prevent growth of the heavily hunted French population (solid lines) and the lightly hunted Italian population (dashed lines). One scenario looks at increasing harvest of adult females only (black lines), while the other looks at increasing harvest of yearling females only (grey lines). The horizontal line represents the stable population (λ = 1).

Discussion

Our results highlight very different demographic patterns between conspecific populations with contrasting hunting pressure. Differences in survival and recruitment affected population growth rate in each population. Both of the wild boar populations showed positive population growth; in the French population, this was despite high hunting mortality (Toïgo *et al.* 2008). The small difference in population growth between populations with contrasting hunting pressure was because of the marked increase in YR in the population subject to strong hunting pressure. Furthermore, underlying demographic patterns differed between populations both in the functional dependence of population growth rates to demographic parameters (Table 2) and in the relative contribution of demographic parameters to the observed changes of population growth rate (Figs 3 and 4; see also Nilsen *et al.* 2009).

The demography of the lightly hunted Italian population was typical of long-lived species, with population growth rate being most sensitive to AS (Gaillard *et al.* 2000). However, the ratio between elasticities of adult and juvenile survival (2·63) was lower than that of most other similar-sized ungulates (Gaillard & Yoccoz 2003; Table 3). In the heavily hunted French population, growth rate was most sensitive to juvenile survival and the potential impact of changes in recruitment rates; the age-class survival probabilities after 1 year were similar. In this population, the ratio between elasticities of adult and juvenile survival (1·27) was the lowest observed among 21 ungulate species, which had a mean of 5·81 (Table 3).

Elasticity patterns of wild boar showed large between-population variation in comparison with other ungulate species, with the exception of moose *Alces alces* for which a marked difference in juvenile survival caused by heavy predation in Alaska (0·331 in Alaska vs. 0·813, 0·865 and 0·825 in Norway) accounted for most of the discrepancy in life history. However, even under optimal environmental conditions (with a record λ of 1·40 at Vega Island, Norway; population 3 in Table 3), AS was at least twice as influential on growth rate compared with juvenile survival, as expected for ungulates (Gaillard *et al.* 2008). On the other hand, AS and recruitment had similar effects on population demography in wild boar experiencing heavy hunting pressures, a demographic pattern that has not been reported for any other large mammal. Wild boar demography seems to be more similar to those reported for small mammals (Gaillard & Yoccoz 2003). Among mammals that reproduce for the first time at 1 year of age, fecundity had the highest impact on λ in only five of 18 species (Fig. 2a in Heppell, Caswell & Crowder 2000). The sum of elasticities for both reproductive and survival parameters was similar to those observed for mammals that begin reproduction at age one

(Fig. 2a in Heppell, Caswell & Crowder 2000). Changes in recruitment generally had the highest potential impact on λ in short-lived organisms (Heppell, Caswell & Crowder 2000 and Gaillard & Yoccoz 2003) and characterized species closer to the 'fast end' of the slow-fast continuum, such as small mammals (Yoccoz *et al.* 1998).

Even in the absence of strong hunting pressure, wild boar exhibit fast life-history traits (Gaillard *et al.* 2005) compared with related mammals of similar size. When applying an allometric relationship between generation time and body mass (Gaillard *et al.* 2008), the expected generation time for wild boar is 6·9 years in the French population and 6·3 years at Castelporziano. When calculating the generation time of wild boar for the three types of years defined in relation to food availability by Bieber & Ruf (2005), it varies from 3·9 years in poor years to 2·1 years in good years. Wild boar populations thus have faster turnover than expected for their size. Interestingly, when experiencing strong hunting pressure, wild boar life-history traits are even faster, because of increased reproductive output of yearling females. Under such conditions, they show a generation time of approximately 2 years, a value typically observed for rodents or passerine birds with body sizes three orders of magnitude lower. The responsiveness of a species' demographic tactic to increased hunting pressure might depend on its reproductive output. Highly polytocous species reproduce earlier (Servanty *et al.* 2009) or have larger litters (Hanson *et al.* 2009). Females of polytocous species such as wild boar (this study), black bears (*Ursus americanus*; Freedman, Portier & Sunquist 2003) and Tasmanian devils (*Sarcophilus harrisii*; Jones *et al.* 2008) seem to be able to re-allocate resources to compensate for reduced survival. On the contrary, less prolific species such as roe deer (*Capreolus capreolus*; Nilsen *et al.* 2009), bighorn sheep (*Ovis canadensis*; Festa-Bianchet *et al.* 2006) and woodland caribou (*Rangifer tarandus caribou*; Wittmer *et al.* 2005) cannot counterbalance increases in overall mortality by increasing their reproductive effort early in life, leading to declining populations with slower life histories. The inability of these large herbivores to compensate for increased adult mortality supports the theory of 'malediction of long-lived species', which predicts higher extinction rates for long-lived species (Lebreton 2006).

Our results show that wild boar population dynamics differ from those of similar-sized ungulates. Wildlife managers should therefore develop specific strategies to control wild boar populations rather than relying on methods currently applied to deer and bovids. In both the Italian and French populations, current management efforts have been ineffective in halting population growth. Our simulations of different management scenarios demonstrated that the most efficient way to stop population growth would be to increase the harvested proportion of adult females by 44% in the Italian population and to increase the proportion of hunted yearling females by 23% in the French population (Fig. 5). However, the total proportion of yearlings hunted is already so high in France (about 72% of the total number of wild boar hunted) that it would be difficult to further increase the hunting pressure on yearling females. The difficulties of halting growth in such cases are also linked to the increased recruitment associated with the shortening of generation time exhibited by wild boar in response to a high hunting pressure.

In the broader context of exploited species, our results demonstrate that any management strategy that aims to halt growth in a population facing intensive exploitation should increase the harvest in all age-classes proportionally. Appropriate management plans built on context-specific demographic models for a given species, similar to the scenario we have developed for wild boar, are relevant for other game species. In particular, an accurate assessment of the relative influence of hunting on specific age- and sex classes would help to solve any uncertainty about which individuals should be targeted in a wide range of game species.

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References

Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A. & Ryman, N. (2008) Genetic effects of harvest on wild animal populations. *Trends in Ecology and Evolution*, **23**, 327–337.

Bieber, C. & Ruf, T. (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, **42**, 1203–1213.

Brooks, E.N. & Lebreton, J.-D. (2001) Optimizing removals to control a metapopulation: application to the yellow legged herring gull (*Larus cachinnans*). *Ecological Modelling*, **136**, 269–284.

Carnevali, L., Pedrotti, L., Riga, F. & Toso, S. (2009) *Cinghiale. Banca Dati Ungulati: Status, distribuzione, consistenza, gestione e prelievo venatorio delle popolazioni di Ungulati in Italia. Rapporto 2001–2005*, pp. 37–49. *Biologia e Conservazione della Fauna*. Istituto Superiore per la Protezione e la Ricerca Ambientale, Roma, Italy, **117**.

Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer & Associates Inc., Sunderland, MA, USA.

Chevin, L.M., Lande, R. & Mace, G.M. (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *Plos Biology*, **8**, 1–8.

Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982) *Red Deer: Behavior and Ecology of Two Sexes*. University of Chicago Press, Chicago.

Clutton-Brock, T.H. & Pemberton, J.M. (2004) *Soay Sheep: Dynamics and Selection in An Island Population*. Cambridge University Press, Cambridge, UK.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.

Crampe, J.-P., Loison, A., Gaillard, J.-M., Florence, E., Caens, P. & Appolinaire, J. (2006) Patrons de reproduction des femelles d'isard (*Rupicapra pyrenaica pyrenaica*) dans une population non chassée et conséquences démographiques. *Canadian Journal of Zoology*, **84**, 1263–1268.

Dubost, G., Charron, F., Courcoul, A. & Rodier, A. (2008) Population characteristics of a semi-free-ranging polytocous cervid, *Hydropotes inermis*. *Mammalia*, **72**, 333–343.

Fernández-Llario, P. & Carranza, J. (2000) Reproductive performance of the wild boar in a Mediterranean ecosystem under drought conditions. *Ethology, Ecology & Evolution*, **12**, 335–343.

Festa-Bianchet, M. (2003) Exploitative wildlife management as a selective pressure for the life-history evolution of large mammals. *Animal Behavior and Wildlife Conservation* (eds M. Festa-Bianchet & M. Apollonio), pp. 191–207. Island Press, Washington, DC.

Festa-Bianchet, M. & Côté, S.D. (2008) *Mountain Goats: Ecology, Behavior and Conservation of an Alpine Ungulate*. Island Press, Washington DC.

Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T. & Pelletier, F. (2006) Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1537–1543.

Focardi, S., Gaillard, J.-M., Ronchi, F. & Rossi, S. (2008) Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. *Journal of Mammalogy*, **89**, 1113–1123.

Freedman, A.H., Portier, K.M. & Sunquist, M.E. (2003) Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. *Ecological Modelling*, **167**, 47–64.

Fuller, J.A., Garrott, R.A., White, P.J., Aune, K.E., Roffe, T.J. & Rhyan, J.C. (2007) Reproduction and survival of Yellowstone bison. *The Journal of Wildlife Management*, **71**, 2365–2372.

Gaillard, J.-M. & Yoccoz, N.G. (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology*, **84**, 3294–3306.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B. & Pradel, R. (1993) Roe deer survival patterns: a comparative analysis of contrasting populations. *Journal of Animal Ecology*, **62**, 778–791.

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. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gaillard, J.-M., Yoccoz, N.G., Lebreton, J.-D., Bonenfant, C., Devillard, S., Loison, A., Pontier, D. & Allainé, D. (2005) Generation time: a reliable metric to measure life-history variation among mammalian populations. *The American Naturalist*, **166**, 119–123.

Gaillard, J.-M., Duncan, P., Van Wieren, S.E., Loison, A., Klein, F. & Maillard, D. (2008) Managing large herbivores in theory and practice: is the game the same for browsing and grazing species? *The Ecology of Browsing and Grazing* (eds. I.J. Gordon & H.H.T. Prins), pp. 293–307. *Ecological Studies*, **195**, Springer Verlag, Berlin.

Gethöffer, F., Sodeikat, G. & Pohlmeyer, K. (2007) Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. *European Journal of Wildlife Research*, **53**, 287–297.

Grange, S., Duncan, P., Gaillard, J.-M., Sinclair, A.R.E., Gogan, P.J.P., Packer, C., Hofer, H. & East, M. (2004) What limits the Serengeti zebra population? *Oecologia*, **140**, 523–532.

Guibert, B. (2008) Bilan national de l'indemnisation des dégâts agricoles de sangliers. *Modalités de gestion du sanglier, Actes du colloque tenu à Reims (Marne) les 1 et 2 mars 2007* (eds. F. Klein, B. Guibert & E. Baubet), pp. 73–78. F.N.C. – O.N.C.F.S., Paris, France.

Hanson, L.B., Mitchell, M.S., Grand, J.B., Jolley, D.B., Sparklin, B.D. & Ditchkoff, S.S. (2009) Effect of experimental manipulation on survival and recruitment of feral pigs. *Wildlife Research*, **36**, 185–191.

Hayssen, V., Van Tienhoven, A. & Van Tienhoven, A. (1993) *Asdell's Patterns of Mammalian Reproduction. A Compendium of Species-specific Data*. Cornell University Press, Ithaca, NY, USA.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology*, **81**, 654–665.

Horvitz, C., Schemske, D.W. & Caswell, H. (1997) The relative 'importance' of life-history stages to population growth: prospective and retrospective analyses. *Structured Population Models in Marine, Terrestrial and Freshwater Systems* (eds S. Tuljapurkar & H. Caswell), pp. 247–271. Chapman & Hall, New York, NY, USA.

Jezierski, W. (1977) Longevity and mortality rate in a population of wild boar. *Acta Theriologica*, **22**, 337–348.

Jolles, A.E., Cooper, D.V. & Levin, S.A. (2005) Hidden effects of chronic tuberculosis in African buffalo. *Ecology*, **86**, 2258–2264.

Jones, M.E., Cockburn, A., Hamede, R., Hawkins, C., Hesterman, H., Lachish, S., Mann, D., McCallum, H. & Pemberton, D. (2008) Life-history change in disease-ravaged Tasmanian devil populations. *Proceedings of the National Academy of Sciences*, **105**, 10023–10027.

Jorgenson, J.T., Festa-Bianchet, M., Gaillard, J.-M. & Wishart, W.D. (1997) Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology*, **78**, 1019–1032.

Law, R. (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, **57**, 659–668.

Lebreton, J.-D. (1977) Maximum likelihood estimations of survival rates from bird band returns: some complements to age-dependent methods. *Biométrie-Praximétrie*, **17**, 145–161.

Lebreton, J.-D. (2006) Dynamical and statistical models of vertebrate population dynamics. *Comptes Rendus Biologies*, **329**, 804–812.

Lebreton, J.-D. & Clobert, J. (1991) Bird population dynamics, management and conservation: the role of mathematical modelling. *Bird Population Studies: Their Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 105–125. Oxford University Press, Oxford.

Massei, G. & Génov, P.V. (2004) The environmental impact of wild boar. *Wild Boar Research 2002: A Selection and Edited Paper from the 4th International Wild Boar Symposium* (eds. C. Fonseca, J. Herrero, A. Luis & A.M.V.M. Soares), pp. 53–65. Galemys 16, Málaga, Spain.

Mauget, R. (1982) Seasonality of reproduction in the wild boar. *Control of Pig Reproduction* (eds D.J.A. Cole & G.R. Foxcroft), pp. 509–526. Butterworths, London.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.

Nilsen, E.B., Gaillard, J.-M., Andersen, R., Odden, J., Delorme, D., Van Laere, G. & Linnell, J.D.C. (2009) A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. *Journal of Animal Ecology*, **78**, 585–594.

Pépin, D. & Mauget, R. (1989) The effect of planes of nutrition on growth and attainment of puberty in female wild boars raised in captivity. *Animal Reproduction Science*, **20**, 71–77.

Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences of the USA*, **95**, 213–218.

Proaktor, G., Coulson, T. & Milner-Gulland, E.J. (2007) Evolutionary responses to harvesting in ungulates. *Journal of Animal Ecology*, **76**, 669–678.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Raithel, J.D., Kauffman, M.J. & Pletscher, D.H. (2007) Impact of spatial and temporal variation in calf survival on the growth of elk populations. *The Journal of Wildlife Management*, **71**, 795–803.

Schaffer, W.M. (1974) Selection for optimal life histories: the effects of age structure. *Ecology*, **55**, 291–303.

Schley, L. & Roper, T.J. (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Review*, **33**, 43–56.

Servanty, S., Gaillard, J.-M., Toïgo, C., Lebreton, J.-D., Baubet, E. & Klein, F. (2005) Population management based on incomplete data: modelling the case of wild boar (*Sus scrofa scrofa*) in France. *Extended Abstracts of the XXVIIth Congress of the International Union of Game Biologists, Hanover 2005* (ed. K. Pohlmeyer), pp. 256–257. DSV- Verlag, Hamburg.

Servanty, S., Gaillard, J.-M., Allainé, D., Brandt, S. & Baubet, E. (2007) Litter size and fetal sex ratio adjustment in a highly polytocous species: the wild boar. *Behavioral Ecology*, **18**, 427–432.

Servanty, S., Gaillard, J.-M., Toïgo, C., Brandt, S. & Baubet, E. (2009) Pulsed resources and climate-induced variation in the reproductive traits of wild boar under high hunting pressure. *Journal of Animal Ecology*, **78**, 1278–1290.

Southwood, T.R.E. (1988) Habitat, the template for ecological strategies. *Journal of Animal Ecology*, **46**, 337–365.

Stearns, S.C. (2000) Life history evolution: successes, limitations, and prospects. *Naturwissenschaften*, **87**, 476–486.

Stubben, C.J. & Milligan, B.G. (2007) Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software*, **11**, 1–23.

Toïgo, C., Gaillard, J.-M., Festa-Bianchet, M., Largo, E., Michalet, J. & Maillard, D. (2007) Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *Journal of Animal Ecology*, **76**, 679–686.

Toïgo, C., Servanty, S., Gaillard, J.-M., Brandt, S. & Baubet, E. (2008) Survival patterns in an intensively hunted wild boar population: disentangling natural from hunting mortality. *The Journal of Wildlife Management*, **72**, 1532–1539.

Wittmer, H.U., McLellan, B.N., Seip, D.R., Young, J.A., Kinley, T.A., Watts, G.S. & Hamilton, D. (2005) Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology*, **83**, 407–418.

Yoccoz, N.G., Nakata, K., Stenseth, N.C. & Saitoh, T. (1998) The demography of *Clethrionomys rufocanus*: from mathematical and statistical models to further field studies. *Researches on Population Ecology*, **40**, 107–121.

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Supporting Information

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

Appendix S1. CMR analyses used to estimate survival rates in each wild boar population.

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