

Disentangling Natural From Hunting Mortality in an Intensively Hunted Wild Boar Population

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ABSTRACT We assessed age-specific natural mortality (i.e., excluding hunting mortality) and hunting mortality of 1,175 male and 1,076 female wild boar (*Sus scrofa*) from Châteauvillain-Arc en Barrois (eastern France), using a 22-year dataset (1982–2004) and mark–recapture–recovery methods. Overall yearly mortality was >50% for all sex and age-classes. Low survival was mostly due to high hunting mortality; a wild boar had a >40% of chance of being harvested annually, and this risk was as high as 70% for adult males. Natural mortality rates of wild boar were similar for males and females (approx. 0.15). These rates were comparable to rates typical of male ungulates but high for female ungulates. Wild boar survival did not vary across sex and age-classes. Despite high hunting mortality, we did not detect evidence of compensatory mortality. Whereas natural mortality for males was constant over time, female mortality varied annually, independent of fluctuations in mast availability. Female wild boar survival patterns differed from those reported in other ungulates, with high and variable natural mortality. In other ungulates, natural mortality is typically low and stable across a wide range of environmental conditions. These differences may partly reflect high litter sizes for wild boar, which carries high energetic costs. High hunting mortality may induce a high investment of females in reproduction early in life, at the detriment to survival. Despite high hunting mortality, the study population increased. Effective population control of wild boar should target a high harvest rate of piglets and reproductive females. (JOURNAL OF WILDLIFE MANAGEMENT 72(7):1532–1539; 2008)

DOI: 10.2193/2007-378

KEY WORDS capture–mark–recapture and recovery, compensatory mortality, deciduous forest, France, hunting mortality, life-history tactic, natural mortality, *Sus scrofa*, wild boar.

Wild boar (*Sus scrofa*) are widespread in Western Europe and have been increasing in numbers for the last 3 decades, leading to increased damage to crops and forests (in Italy, Boitani et al. 1995; in Switzerland, Neet 1995; see Schley and Roper 2003 for a review in Western Europe; in France, Klein et al. 2004; in Austria, Bieber and Ruf 2005). In France the numbers of wild boar harvested annually increased 8-fold between 1974 and 2001, and wild boar currently occur throughout the country. Concurrently, damage caused to agriculture has increased, and costs of compensation to farmers have become very high (17,000,000 Euro in 2001, Klein et al. 2004).

Despite economic costs and other management problems caused by wild boar, the species remains poorly known compared to other temperate zone ungulates. Although reproductive traits such as age at primiparity, proportion of breeding females, and litter size have been well-documented (Gaillard et al. 1993, Neet 1995, Carranza 1996, Fernández-Llario and Carranza 2000, Nahlik and Sandor 2003), few studies have provided reliable estimates of age-specific survival for wild boar.

The dynamics of most European wild boar populations are strongly influenced by harvest. Disentangling natural from hunting mortality is important to understanding the dynamics of exploited populations. The functional relationship between hunting mortality and natural mortality may

range from additive to compensatory effects (Anderson and Burnham 1976, Burnham and Anderson 1984). Degrees of partial compensation can also occur. Lebreton (2005) suggested that compensation between hunting and natural mortality is expected to be very low in long-lived vertebrates such as wild boar.

In long-lived vertebrates, adult female survival consistently has the highest demographic elasticity (i.e., the highest potential effect for changing population growth rate). As a consequence, in large herbivores, annual adult survival of females is usually high (>90%) and robust to environmental variation, whereas juvenile survival is low (<70%) and highly variable over time and among populations (see Gaillard et al. 1998, 2000 for reviews). Wild boar are unusually productive for their body size, with a mean litter size as high as 5 (e.g., Boitani et al. 1995, Nahlik and Sandor 2003, Servanty et al. 2007). High productivity could lead to lower and more variable prime-age survival than usually reported in other ungulates, because of the high energetic costs of producing larger litters.

Our goal was to assess the relative contribution of age- and sex-specific hunting and natural mortality in an intensively monitored wild boar population in eastern France using capture–mark–recapture–recovery (CMRR) methods, which would allow us to combine live recaptures and hunting recoveries (see Schaub and Pradel 2004 for a similar approach) into a unified analysis. Because of the hunting

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regulations in our study area, we expected hunting mortality would be higher for males and young females than for adult females. Because of large litter sizes and current theory on life-history strategies of large vertebrates (Stearns 1992, Gaillard and Yoccoz 2003), we expected natural mortality of adult wild boar females to be high and more variable compared to females of other ungulates. Based on Lebreton (2005), we hypothesized little compensation between hunting and natural mortality.

STUDY AREA

We conducted our study in northeastern France, in the 11,000-ha forest of Châteauvillain-Arc-en-Barrois (48°02N, 4°56E). The territory was administratively divided into 2 parts: a core area that covered 8,500 ha of national forest and a surrounding area of 2,500 ha of private or communal forests. Dominant tree species were oak (*Quercus petraea*), beechnut (*Fagus sylvatica*), and hornbeam (*Carpinus betulus*). The climate was intermediate between continental (typical of eastern France's Alsace region), and oceanic (characteristic of the Parisian Basin). During the last 20 years (1983–2003), mean annual rainfall was 74.4 ± 8.6 mm, and average monthly temperatures ranged from $2.34 \pm 2.06^\circ\text{C}$ in January to $18.6 \pm 1.58^\circ\text{C}$ in August (Météo-France), which was within the norm for this climate.

Wild boar had no natural predators in the study area, except red fox (*Vulpes vulpes*) on newborns. Natural causes of mortality were mainly diseases, starvation, injuries and exhaustion linked to the rut for males, parturition complications for females, and boar–vehicle collisions.

METHODS

Since 1982, we monitored the study population by CMRR methods. Captures occurred during March to September each year in the national part of the forest using corral traps (Vassant and Brandt 1995, Sweitzer et al. 1997), box traps (Jullien et al. 1988, Choquenot et al. 1993), piglet traps (Jullien et al. 1988), and falling nets (Jullien et al. 1988); all methods were approved by the French Environment Ministry (articles L.424–11, R.411–14, and R.422–87 of the French code of environment). We marked each trapped animal with ear-tags allowing individual identification (combination of colors and no.). We determined the age of each individual captured on the basis of Matschke's (1967) procedure, validated and adjusted to our study area by Baubet et al. (1994). We distinguished 3 age-classes: piglets (aged 1–6 months at capture), yearlings (aged 13–18 months at capture) and adults (>18 months at capture). The youngest animals trapped were 1-month-olds, having survived the critical neonatal period.

Wild boar were harvested by ambush shooters each year between October and February. The number of wild boar harvested annually over the entire study area steadily increased from 200 in 1984 to 1,000 in 2004. Wild boar are sexually dimorphic; mean weights for adult sows were 72 kg (± 11 kg, $n = 379$) and for adult males were 102 kg (± 16 kg, $n = 176$) in our population (E. Baubet, Office National

de la Chasse et de la Faune Sauvage, unpublished data). Based on body size and social behavior (F live in matriarchal groups, whereas ad M are most often solitary; Kaminski et al. 2005), hunters can often target males. When harvesting larger groups hunters often avoided shooting individuals >60 kg to protect reproductive sows. Hunters randomly harvested marked and unmarked wild boar. Hunter bias relative to marked boar was unlikely because ear-tags were small, almost totally hidden by the deep autumn hair, and difficult to see on live animals.

In the National part of the forest, cooperation between hunters and the Office National de la Chasse et de la Faune Sauvage (ONCFS; the French Wildlife Agency) ensured that all wild boar harvested were checked by a government agent (from the ONCFS). We assumed that all marked animals harvested were recovered. Hunters in the surrounding areas received information about our study. However, wild boar harvested from these areas were not checked by a government agent, so there may have been some unreported harvest of marked animals. We assumed that the recovery rate was 0.9 based on field data and preliminary analysis of CMRR models.

The primary data were capture–recapture–recovery histories of marked animals. We analyzed these data using multistate models recently implemented in MSURGE 7 (Choquet et al. 2005b) to estimate overall mortality rate, mortality rate due to hunting, and natural mortality rate (i.e., excluding hunting mortality). To separate natural mortality from hunting mortality, we used a 3-state model: 1) the animal is alive, 2) the animal is harvested, and 3) the animal is dead from natural causes. The third state was not observable (see Gimenez et al. 2003 for a similar approach).

We were principally interested in capture (P) and transition (Ψ) probabilities. Survival probabilities were constrained to 1.0 for this analysis. Recapture probabilities depended on the arrival state, with $P(1)$ the probability of being captured in state 1 (i.e., alive in a trap), $P(2)$ the probability of being captured in state 2 (i.e., recovered when hunted, a probability we fixed at 0.9), and $P(3)$ the probability of being captured in the unobservable state 3 (i.e., naturally dead, a probability we fixed to 0.0).

Transition probabilities depended on departure and arrival states, with $\Psi_{1 \rightarrow 1} = P(\text{alive}) = \text{overall survival rate} = \text{OS}$; $\Psi_{1 \rightarrow 2} = P(\text{harvested}) = \text{hunting mortality rate} = \text{HM}$; and $\Psi_{1 \rightarrow 3} = P(\text{dead from natural causes}) = \text{natural mortality rate} = \text{NM}$. We defined the survival-mortality parameters as: $\text{HM} + \text{NM} = P(\text{dying}) = \text{overall mortality rate} = \text{OM}$. In addition, we invoked the following constraints: 1) The overall survival rate should be the complement of the overall mortality rate, so the models included the constraint $\text{OS} + \text{HM} + \text{NM} = 1$, and $\text{OS} = 1 - \text{OM}$. 2) Once a wild boar was dead, it could not transition to the live state, and once a wild boar had been shot, it was permanently in the dead state, so that the models implicitly included the constraints: $\Psi_{2 \rightarrow 1} = \Psi_{3 \rightarrow 1} = 0$ and $\Psi_{2 \rightarrow 3} = 1$. We conducted separate analyses for males and females.

We first tested the goodness-of-fit (GOF) of the

Arnason–Schwartz (AS) model, which is the multistate extension of the Cormack–Jolly–Seber model (Lebreton et al. 1992) with time-dependent survival and recapture probabilities (noted Ψ_t, P_t). We conducted the GOF test using U-CARE software (Choquet et al. 2005a). Starting from the AS model, we tested for time variation in recapture probability by comparing the AS model to a model with time-dependent survival and constant probability of recapture (Ψ_t, P). Then, from the best model, we tested for time and age variation in survival embodied in the following hypotheses: 1) wild boar survival is age-specific but varies annually and independently for the 3 age-classes (model $\Psi_{3a \times t}$ including interactive effects between age-class and time); 2) wild boar survival is age-specific but varies annually and similarly for the 3 age-classes (model Ψ_{3a+t} including additive effects of age-class and time); 3) wild boar survival is age-specific and is constant over time (model Ψ_{3a} including differences among the 3 age-classes); and 4) wild boar survival only differs between piglets and older animals (model Ψ_{2a} including differences between 2 age-classes).

To assess whether the total number of wild boar harvested in a given year was related to estimated annual hunting mortality, we used annual variation in harvest as a covariate (see Lebreton et al. 1992). To explore the possibility of compensatory mortality, we assessed the relationship between hunting mortality and natural mortality for each year, using the model including among-year variation in survival probabilities. If compensatory mortality occurred, natural mortality should have decreased when hunting rate increased.

Wild boar are opportunistic omnivores, but their diet is primarily composed of vegetation. When available, oak and beech mast is highly preferred to other foods, particularly compared to agricultural crops (Schley and Roper 2003 for a review). We indexed the availability of mast by analyzing the stomach contents of harvested animals since 1982 (see Bieber and Ruf 2005 for a similar approach). The index took 4 values and was related to stomach contents: 1) no mast production when maize was the preferred item, 15–55% of stomach contents, whereas acorn or beechnut represented <3%, 2) high beech-mast production when beechnut represented 65–85% of stomach contents, 3) medium oak-mast production when acorn represented 50–65% of stomach contents, and 4) high oak-mast production when acorn represented 75–90% of stomach contents. For models where natural mortality was assumed year-dependent, we tested whether mast conditions could account for observed variability over time, using an analysis of variance (because mast condition is a qualitative variable, we could not use it as an external covariate in survival models implemented in M-SURGE).

We based model selection on the corrected Akaike's Information Criterion (AIC_c ; Lebreton et al. 1992, Burnham and Anderson 2002). We calculated AIC_c weights and used these weights as evidence of statistical support among candidate models (Burnham and Anderson 2002), except for the first steps of the model selection when most models had

low AIC_c weights (<0.001), in which case we based selection on ΔAIC_c . We also compared age-specific survival probabilities using Wald tests.

RESULTS

Males

We estimated the survival rates from 1,175 males (1,065 piglets, 102 yearlings, and 8 ad; Table 1) captured and marked between 1982 and 2003. We could only test for transience effects (i.e., the difference in survival between newly marked and previously marked animals) in piglets, because the sample size of animals caught for the first time as yearlings or adults was small. We did not detect evidence of transience ($\chi^2 = 27.775$, $df = 29$, $P = 0.530$). We detected positive immediate trap-dependence (i.e., trap-happiness) in piglets ($\chi^2 = 100.215$, $df = 42$, $P < 0.001$) but not yearlings ($\chi^2 = 5.590$, $df = 9$, $P = 0.750$). Sample sizes were too small to test for immediate trap-dependence in adults. Thus recapture probability the year following the first capture of piglets was higher than recapture probability in subsequent years and recapture probability of individuals captured for the first time as yearlings or adults. To account for this, we invoked age-specific recapture probabilities.

Recapture probability was time-dependent (model Ψ_t, P_t with a lower AIC_c than model Ψ_t, P , respectively, 3,632.805 vs. 3,645.259). Recapture probability of piglets varied between 0.0 in 7 years and 0.618 (SE = 0.221) in 1999–2000. Recapture probabilities of yearlings and adults varied between 0.0 in 16 years and 0.161 (SE = 0.110) in 2000–2001.

The best model was one wherein hunting mortality was correlated with annual harvest, with a harvest \times age interaction and constant natural mortality. This model had an AIC_c weight of 0.88 and was better than the second-ranked model. We found little evidence of time-dependence in any components of survival (all models with time-dependent survival had AIC_c wt <0.001), but we did detect age-class differences among piglets, yearlings, and adults; models with all components of survival depending on 3 age-classes had lower AIC_c weights than constant models or 2 age-classes survival models (Table 1). We found evidence that probability of being harvested varied among the 3 age-classes, whereas natural mortality did not vary (i.e., the models including age-dependent hunting mortality and constant natural mortality all had lower model weights than models including age-dependence in both components).

We estimated natural mortality of wild boar males at 0.14 (corresponding to a survival rate excluding hunting mortality of 0.86) regardless of age-class (Table 2). Probability of being harvested was high and increased with age, from 0.41 for piglets to 0.70 for adults (Table 2). Accordingly, overall survival was low and decreased from piglets (0.44) to adults (0.23; Table 2).

Hunting mortality increased with total number of harvested males (i.e., models including a linear relationship between hunting mortality and the annual harvest best fit our data). For piglets and adults, the slope of the linear increase

Table 1. Number of parameters (N_p), Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c between each tested model and the best model (ΔAIC_c), and Akaike weights (w_i) for effects of year (t), age-class (noted 3a for 3 age-classes: piglets, yearlings, and ad; noted 2a for 2 age-classes: piglets and ad), and annual harvest (AH) on survival probability (ψ , including overall survival [OS] hunting mortality [HM], and natural mortality [NM]) of male and female wild boar in the Châteauxvillain-Arc en Barrois forest, France, 1983–2003. The selected model is identified with an asterisk. The probability of resighting is modeled as age- and year-dependent.

Model	Model biological meaning	N_p	ΔAIC_c	w_i
M				
$\Psi_{(HM)_{AH \times 3a}-(NM)^*}$	HM correlated to AH and 3a (interaction) – NM constant*	49	0	0.885
$\Psi_{(HM)_{AH \times 3a}-(NM)_{3a}}$	HM correlated to AH and 3a (interaction) – NM dependent on 3a	51	4.164	0.110
$\Psi_{(HM)_{3a}-(NM)}$	HM dependent on 3a – NM constant	46	10.925	0.004
Ψ_{3a}	OS, HM, and NM dependent on 3a	48	14.473	<0.001
Ψ_{2a}	OS, HM, and NM dependent on 2a	46	15.745	<0.001
Ψ_{3a+t}	OS, HM, and NM dependent on 3a and t (additivity)	68	17.294	<0.001
$\Psi_{(HM)_{AH \times 2a}-(NM)_{2a}}$	HM correlated to AH and 2a (interaction) – NM dependent on 2a	48	21.945	<0.001
$\Psi_{(HM)_{AH}-(NM)_{3a}}$	HM correlated to AH – NM dependent on 3a	47	31.921	<0.001
$\Psi_{2a \times t}$	OS, HM, and NM dependent on 2a and t (interaction)	126	46.049	<0.001
Ψ	OS, HM, and NM constant	44	63.715	<0.001
Ψ_t	OS, HM, and NM dependent on t	83	72.495	<0.001
$\Psi_{3a \times t}$	OS, HM, and NM dependent on 3a and t (interaction)	165	141.002	<0.001
F				
Ψ_{3a+t}^*	OS, HM, and NM dependent on 3a and t (additivity)*	68	0.000	0.681
Ψ_{2a+t}	OS, HM, and NM dependent on 2a and t (additivity)	66	3.929	0.096
$\Psi_{(HM)_{AH}-(NM)}$	HM correlated to AH – NM constant	45	4.132	0.086
$\Psi_{(HM)_{AH}-(NM)_{3a}}$	HM correlated to AH – NM dependent on 3a	47	4.290	0.080
$\Psi_{(HM)_{AH \times 3a}-(NM)_{3a}}$	HM correlated to AH and 3a (interaction) – NM dependent on 3a	51	5.133	0.052
$\Psi_{(HM)_{AH \times 3a}-(NM)}$	HM correlated to AH and 3a (interaction) – NM constant	49	10.048	0.004
Ψ_t	OS, HM, and NM dependent on t	83	17.413	<0.001
$\Psi_{2a \times t}$	OS, HM, and NM dependent on 2a and t (interaction)	126	18.433	<0.001
$\Psi_{(HM)_{AH}-(NM)_t}$	HM correlated to AH – NM dependent on t	65	23.833	<0.001
$\Psi_{(HM)_{3a}-(NM)_{3a}}$	HM constant – NM dependent on 3a	46	39.848	<0.001
$\Psi_{(HM)_{3a}-(NM)_{2a}}$	HM constant – NM dependent on 2a	45	40.638	<0.001
Ψ	OS, HM, and NM constant	44	40.812	<0.001
Ψ_{3a}	OS, HM, and NM dependent on 3a	48	41.086	<0.001
Ψ_{2a}	OS, HM, and NM dependent on 2a	46	42.247	<0.001
$\Psi_{(HM)_{2a}-(NM)}$	HM dependent on 2a – NM constant	45	42.908	<0.001
$\Psi_{(HM)_{3a}-(NM)}$	HM dependent on 3a – NM constant	46	45.044	<0.001
$\Psi_{(HM)_{AH}-(NM)_{3a \times t}}$	HM correlated to AH – NM dependent on 3a and t (interaction)	107	65.420	<0.001
$\Psi_{3a \times t}$	OS, HM, and NM dependent on 3a and t (interaction)	165	114.155	<0.001

in hunting mortality with increasing annual harvest was similar (0.0024 ± 0.0003 for piglets and 0.0029 ± 0.0008 for ad, on a logit scale), but the intercept was larger for adults (0.4640 ± 0.0007 vs. -0.5738 ± 0.0124), indicating that for a given annual harvest, more adults than piglets were shot (Fig. 1a). For yearlings, hunting mortality rate did not depend on total number of wild boar males shot in a given year (slope of -0.0001 ± 0.0004 on a logit scale; Fig. 1a).

Yearly natural mortality was not related to differences in mast availability for any age-class (piglets: $F = 1.463$, $df = 3, 16$, $P = 0.261$; yearlings: $F = 1.607$, $df = 3, 16$, $P = 0.227$; ad: $F = 1.655$, $df = 3, 16$, $P = 0.216$). Absence of an influence

of mast availability on age-specific survival and absence of detectable among-year variation in natural mortality both supported low variability over time ($CV = 10\%$ for ad) in natural mortality of wild boar males.

Because we did not detect any age-variability in natural mortality, we tested whether there was compensation between natural mortality and hunting mortality of all pooled age-classes. Natural mortality in a given year was not correlated to hunting mortality, in the same year ($t = 0.175$, $df = 19$, $P = 0.863$, $r^2 = 0.002$) or previous year ($t = 0.039$, $df = 18$, $P = 0.969$, $r^2 = 0$; Fig. 2a), suggesting no compensatory mortality occurred.

Table 2. Overall age-class specific survival, hunting mortality, and natural mortality (95% CI) for the wild boar population of Châteauxvillain-Arc en Barrois, France, 1983–2003. We provide estimates from the selected model.

Age-class	Overall survival			Hunting mortality			Natural mortality			
	\bar{x}	Min.	Max.	\bar{x}	Min.	Max.	\bar{x}	Min.	Max.	
M	Young (1–12 months)	0.439	0.393	0.484	0.410	0.378	0.484	0.144	0.122	0.169
	Yearling (13–24 months)	0.351	0.244	0.475	0.590	0.542	0.475			
	Ad (≥ 2 yr)	0.228	0.169	0.299	0.696	0.608	0.299			
F	Young (1–12 months)	0.426	0.381	0.472	0.392	0.358	0.472	0.182	0.143	0.230
	Ad (≥ 13 months)	0.475	0.437	0.512	0.401	0.361	0.512	0.124	0.093	0.164

Females

We estimated survival rates from 1,076 females (927 piglets, 95 yearlings, and 54 ad; Table 1) captured between 1982 and 2003. We did not detect transience for any age-class ($\chi^2 = 33.045$, $df = 40$, $P = 0.774$ for piglets; $\chi^2 = 6.331$, $df = 14$, $P = 0.957$ for yearlings; and $\chi^2 = 0.936$, $df = 3$, $P = 0.817$ for ad). We did detect a positive immediate trap-dependence in piglets ($\chi^2 = 82.081$, $df = 57$, $P = 0.016$) but not yearlings ($\chi^2 = 13.359$, $df = 20$, $P = 0.861$) or adults ($\chi^2 = 14.848$, $df = 18$, $P = 0.672$). Recapture probability the year following the first capture of piglets was higher than recapture probability the following years and also higher than recapture probability of individuals captured for the first time as yearlings or adults. As in males, such patterns suggest real age-specific differences in recapture probabilities.

Recapture probabilities varied across years (model Ψ_t, P_t with a lower AIC_c than model Ψ_t, P , respectively 3,986.676 vs. 3,993.817). We started with the model including time-dependent recapture probabilities to test for effects of year and age on survival. Recapture probability of piglets varied between 0.0 in 4 years and 0.688 (SE = 0.140) in 2000–2001. Recapture probabilities of yearlings and adults varied between 0.0 in 3 years and 0.441 (SE = 0.219) in 1992–1993.

The best model included additive effects of time and 3 age-classes on survival probabilities, and had an AIC_c weight of 0.68, which was 7 times more weight than the second-best model. However, we could not estimate natural mortality of yearlings, so we selected the model with additive effects of time and 2 age-classes: piglets and adults (hereafter for F, from ≥ 13 months at capture).

Age-dependence of both natural and hunting mortality differed from the pattern exhibited by males. Models with constant hunting mortality and age-dependent natural mortality had higher model weights than models with age-dependent hunting mortality and constant natural mortality. Probability of being harvested did not differ between piglets and adults and averaged 0.38 (Table 2). However, piglet females had a higher natural mortality rate (0.18) than adults (0.12; Table 2). Females had an overall annual survival rate of 0.43 for piglets and 0.47 for adults.

In contrast with male survival, female natural mortality varied over time, with marked among-year variation (CV = 25% for ad). In addition, constraining hunting mortality as a function of total number of females harvested in a given year did not improve model fit. For any given year, probability of a female being harvested was independent of total number of females killed that year. However, the trend was the same as for males, with a tendency of increases in annual harvest corresponding with increased hunting mortality (slope of 0.0030 ± 0.0002 ; Fig. 1b).

We did not detect any relationship between observed fluctuations in mast availability and yearly natural mortality for any age-class (piglets: $F = 1.259$, $df = 3, 16$, $P = 0.322$; ad: $F = 1.248$, $df = 3, 16$, $P = 0.325$). The among-year variation of female natural mortality we reported was not

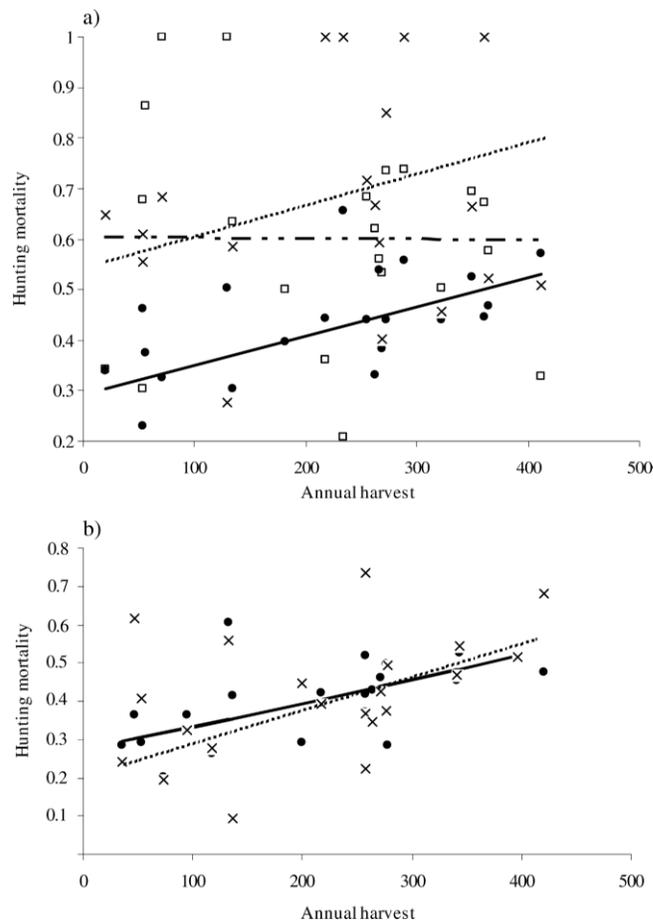


Figure 1. Relationship between the annual hunting mortality and total number of wild boar a) males and b) females hunted each year (annual harvest) in the population of Châteauvillain–Arc en Barrois, France, 1983–2003. Plain circles and plain line: piglets; open squares and dashed line: yearlings; crosses and dotted line: adults (pooled yearlings and ad for F).

accounted for by variations of oak- and beech-mast production.

We did not find any relationship between natural mortality of piglets and adults in a given year and the global hunting mortality rate for females the same year (piglets: $t = -0.660$, $df = 19$, $P = 0.517$, $r^2 = 0.022$; ad: $t = 1.475$, $df = 19$, $P = 0.157$, $r^2 = 0.103$) or previous year (piglets: $t = 0.395$, $df = 18$, $P = 0.697$, $r^2 = 0.009$; ad: $t = 1.562$, $P = 0.136$, $r^2 = 0.119$), suggesting little evidence of compensatory mortality for female wild boar, even though there was a slight positive tendency for adults (Fig. 2b).

DISCUSSION

Overall annual survival in our study population was low for both sexes, mainly due to high hunting pressure.

Natural mortality of adults was similar for males and females (approx. 0.15, $W = 0.924$, $P = 0.260$). In ungulates, annual adult survival of 0.85 is usual for males, with an average of 0.88 among 18 species in one review (Toigo and Gaillard 2003). This is low compared to average survival of females, which is commonly >0.95 in predator-free populations (Gaillard et al. 2000). After excluding hunting mortality, female wild boar survival varied substantially,

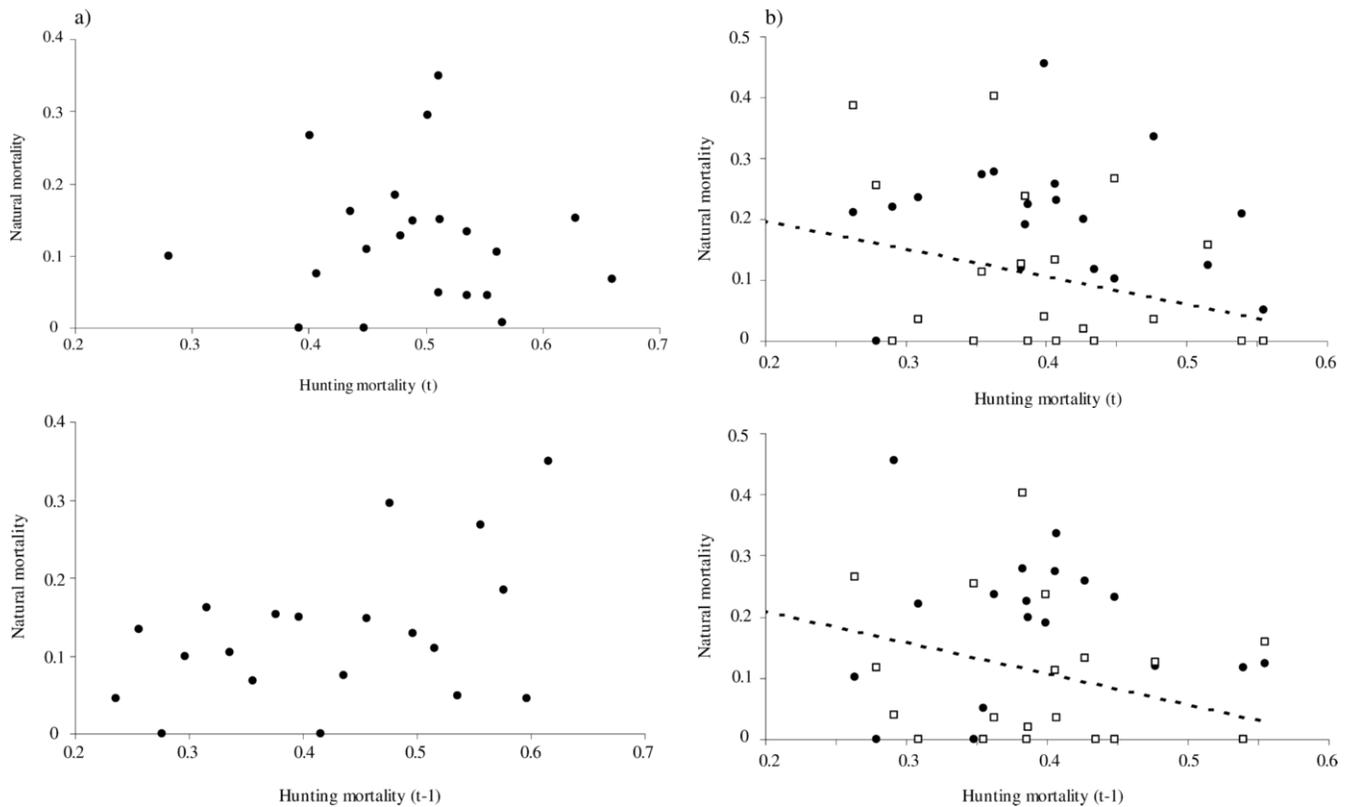


Figure 2. Relationship between wild boar natural mortality and hunting mortality the same year (t) and previous year ($t - 1$) for a) male and b) female wild boar in the population of Châteauvillain–Arc en Barrois, France, 1983–2003. For females, plain circles: piglets; open squares: yearlings and adults; all 3 age-classes pooled for males (see text).

whereas male survival did not. Such among-year variation of adult female survival ($CV = 0.25$) relative to male survival ($CV = 0.10$) is unusual for a dimorphic, polygynous ungulate. Male survival is typically more influenced by environmental variation because males expend considerable energy during mating, which can lead to exhaustion and starvation under harsh environmental conditions (see Coulson et al. 2001 for an example on Soay sheep [*Ovis aries*], Toïgo and Gaillard 2003 for a review, Toïgo et al. 2007 on Alpine ibex [*Capra ibex*]). Moreover, the observed amount of among-year variation in natural mortality of adult females ($CV = 25\%$) was almost 5 times higher than that commonly reported in other ungulates (median $CV = 5.5\%$ on 15 populations of 9 species, Gaillard and Yoccoz 2003). Energy allocated by wild boar females to reproduction early in their lifetime could account for their low and variable adult survival. In ungulate females, adult survival is generally high. When conditions are not optimal, female ungulates may sacrifice reproductive effort in a given year to enhance their own survival (Gaillard and Yoccoz 2003; see Festa-Bianchet et al. 1998 for empirical evidence on bighorn sheep [*Ovis canadensis*]). Wild boar females seem to have an unusual life-history strategy among ungulates, involving a high investment in reproduction by adult females. Wild boar females can reproduce as early as age 1 year and produce average litters as large as 5 (Taylor et al. 1998, Servanty et al. 2007). Compared to other ungulates, the population growth rate of wild boar may be less sensitive to adult survival and

more sensitive to reproductive parameters, such as breeding proportions or litter size (Bieber and Ruf 2005). Such a strategy might account for the low and variable adult survival of wild boar females.

The high natural mortality we reported in this intensively hunted population might have occurred through compensation (Schaub and Lebreton 2004, Lebreton 2005). Compensation may arise through density-dependent mortality and heterogeneity in survival across individuals (if the individuals more susceptible to hunting also have a higher risk of natural mortality). The latter mechanism may arise when hunting is selective and targets lower than average quality individuals within an age- and sex-class. Alternatively, hunting and natural mortality can be overcompensatory when hunters select higher than average quality individuals. Under this scenario, natural mortality should increase because the animals remaining in the population and, thus, subject to natural mortality have lower performance and are more susceptible to die from natural causes than animals that have been removed by hunting. Trophy hunting has been hypothesized to lead to overcompensatory mortality (Coltman et al. 2003, Garel et al. 2007). If hunters shoot individuals they encounter randomly, they should kill disproportionately the individuals easiest to harvest, presumably lower quality individuals. If so, natural mortality will be lower than in a nonhunted population because high-quality individuals will be less susceptible to die from natural causes. In our population, hunters appeared to indifferently

harvest boars, except that hunters avoided adult females, leading to little possibility of selection of individual quality within an age- and sex-class. However, even in the absence of selective harvesting, compensation between hunting and natural mortality can occur if hunting reduces population size and natural mortality decreases via release from density-dependence. We found little evidence of compensation between natural mortality and hunting mortality, despite high hunting pressure. These results support Lebreton's (2005) conclusions that compensation is expected to be rare in exploited populations of long-lived vertebrates, even under strong selectivity or high harvesting rates. Therefore, our estimates of natural mortality did not seem to have been influenced by hunting and could be expected to be close to wild boar survival in nonhunted populations with similar environmental conditions.

As expected, we found that, for a given year, hunting mortality for both sexes increased as reported harvests increased. These results would imply that hunters were able to control population increases in wild boar, whereas empirical evidence demonstrated that this did not occur. This paradox may be due to the numerical response of wild boar to hunting. According to our results (Fig. 2), a 6-fold increase in harvest led to less than a 2-fold increase of hunting mortality.

The absence of influence of mast availability on natural mortality was not surprising. The forest habitat of the study population was highly productive, and wild boar were likely on a high nutritional plane (Gaillard et al. 1993). Such a favorable environment for wild boar could also account for the absence of compensatory survival we reported here.

MANAGEMENT IMPLICATIONS

Despite high natural mortality at all ages, the hunted wild boar population we studied still increased, as evidenced by the 5-fold increase in number of wild boar harvested over the past 20 years. Efficient management of wild boar populations will likely depend on high harvest rates on all sex- and age-classes. We found that harvest focused on adult males, coincident with limited hunting pressure on adult females and piglets, reduced the effectiveness of hunting regulations designed to control growth of wild boar populations. We conclude that to achieve wild-boar management objectives across a broad agro-forested landscape highly sensitive to wild boar damage, wildlife managers should consider hunter willingness to harvest piglets and females when developing hunting regulations of wild boar.

ACKNOWLEDGMENTS

We sincerely thank all those who helped capture and mark wild boar, especially C. Thivet (Fédération Départementale des Chasseurs 52), as well as those who helped collect harvested wild boar, particularly G. Corbeau (in memory of him) and P. Van den Bulck. We are grateful to the Office National des Forêts and to F. Jehlé, who allowed us to work on the study area. The study was financed by the Office National de la Chasse et de la Faune Sauvage.

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Associate Editor: McCorquodale.