

## SURVIVAL OF WILD BOARS IN A VARIABLE ENVIRONMENT: UNEXPECTED LIFE-HISTORY VARIATION IN AN UNUSUAL UNGULATE

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The wild boar (*Sus scrofa*) is a large, sexually dimorphic ungulate that exhibits a life-history tactic different from what would be predicted for a mammal of its size. In particular, litter size is larger and adult survival usually lower in wild boars than in other species of comparable size. We used capture–mark–recapture methods to model survival in a Mediterranean population (*S. s. majori*) of wild boars during an 8-year period, using a large sample of individually tagged animals of known age, to investigate demographic patterns and the effects of variable environmental conditions (e.g., summer droughts), which are believed to have a strong impact on the demography of this species. Contrary to the predictions based on our current knowledge of life-history theory, survival of wild boars differed less among age classes and between sexes than has been reported in other large mammals. As predicted from current theories on sexual selection, the impact of environmental factors was stronger on males than on females. This study documents for wild boars a life-history tactic different from the accepted model for large ungulates but similar to the tactic observed in small terrestrial mammals.

Key words: capture–mark–recapture, life history, Mediterranean environments, sexual dimorphism, survival, *Sus scrofa majori*, wild boar

Comparative analyses (Harvey and Pagel 1991) of life-history variations at the interspecific level show that vertebrate species rank along a fast–slow continuum, from small, short-lived animals with high fecundity to large, long-lived animals with low fecundity (e.g., mammals [Stearns 1983], birds [Gaillard et al. 1989], reptiles [Shine and Charnov 1992], and fishes [Rochet et al. 2000]). Ungulates are large mammals, fitting the slow end of this continuum. However, among the ungulates, suids are unusual by exhibiting a high fecundity despite being relatively large. A maximum of >10 offspring per litter is often reported for wild boars (*Sus scrofa* [e.g., Servanty et al. 2007; Volokh 2002]), whereas 3 or 4 is a maximum only exceptionally reached in most polytocous ungulates of similar size (Hayssen et al. 1993). In addition, although the average litter size of wild boars is around 4–6 in

most populations (4.1 [Abaigar 1992] and 4.3 [Saez-Royuela and Telleria 1987] in Spain, 4.5 [Diong 1973] in Malaysia, 4.7 [Baber and Coblenz 1987] in the Galapagos Islands, 5 [Baber and Coblenz 1986] in the United States, 5 [Boitani et al. 1995] in Italy; 5.6 [Barrett 1978] in the United States, and 6.2 [Dzieciolowski et al. 1990] in New Zealand), all similar-sized ungulates have average litter sizes <3 (Hayssen et al. 1993). Such a high fecundity rate should prevent wild boars from showing a marked sexual size dimorphism (Carranza 1996).

However, contrary to this expectation, highly fecund wild boars also show considerable sexual size dimorphism (males are about 1.3–1.4 times larger than females—Spitz et al. 1998). Wild boars are thus very unusual ungulates, showing 2 combinations of traits that are normally opposed (i.e., large body size and high fecundity, and marked sexual size dimorphism and high fecundity). How do such unusual combinations affect the life-history strategy of wild boars? Previous studies showed that survival patterns play a crucial role for shaping mammalian life-history tactics (Gaillard and Yoccoz 2003; Pontier et al. 1993; Promislow and Harvey 1990). For example, the high, constant survival of adult

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females in conjunction with the low, variable recruitment generally reported for large herbivores (Gaillard et al. 1998, 2000) lead to marked iteroparity in these species, as would be expected from life-history theory (Stearns 1976).

Up to now, our knowledge of survival patterns in wild boars has not allowed us to assess whether wild boars fit the general life-history pattern of ungulates. Indeed, most previous studies were conducted in populations where sport hunting was a source of high mortality (e.g., Gaillard et al. 1987). Survival estimates were usually based on life tables built from hunting data (e.g., von Stubbe 1998; but see Jezierski [1977] for the only study performed in the absence of hunting). Under such conditions, strong assumptions required for reliable estimates of survival by using life tables are unlikely to be met (Eberhardt 1969). Susceptibility to hunting may vary among age and sex classes. For example, in hunted populations, survival of juveniles may be higher than survival of adults (Gaillard et al. 1987; Spitz and Valet 1991), and, in some instances, adult females are not harvested at all (von Stubbe 1998). Moreover, because accurate age determination based on tooth eruption is not possible after 3 years of age (Matschke 1967) and the effect of environmental variation cannot be assessed using life tables (Caughley 1977), these factors may strongly bias the relationships explored in comparative studies (Martin et al. 1995) conducted on this species.

Our study at Castelporziano, Italy, offered a unique opportunity for analyzing survival patterns of wild boars. The annual harvest of this population was low, and long-term (8 years) monitoring data of a large sample of individually marked animals was available from early stages of life. This population of wild boars (*S. s. majori*—De Beaux and Festa 1927) is classified as Italian wild boar type (group D4—Larson et al. 2005). The Castelporziano wild boars did not interbreed with either reintroduced wild boars or free-ranging domestic swine in the last century, and this is probably the only population to be composed of these specific genotypes (Scandura et al. 2005). Thus, the traits observed in this population represent adaptations and not the effects of uncontrolled restocking and domestication.

Before the analysis of survival patterns, we verified that the Castelporziano wild boars exhibited the life-history combinations unusual for ungulates (i.e., high fecundity relative to their size and marked sexual size dimorphism relative to their fecundity). Then, we tested the following predictions based on the current theory of life-history variation (Roff 1992; Stearns 1992). First, as expected from the strong age structure generally occurring in mammals (Caughley 1966) and in ungulates in particular (Coulson et al. 2001), and from life-history strategies exhibited by large herbivores (Gaillard et al. 2000), the survivorship of juveniles should be lower and more variable among years than that of adult females, with the survival of yearlings expected to show intermediate values and magnitudes of variation. Second, males should have lower survival than females at all ages but the between-sex difference should increase with age. Indeed, the marked sexual size dimorphism in favor of males suggests a highly polygynous mating system (Loison et al. 1999) in which males reproduce only when they

acquire dominance over conspecifics. Males should then adopt a high risk–high benefit tactic by investing more in growth and less in body reserves, leading them to be more susceptible to harsh environmental conditions than females (Clutton-Brock 1991). Thus, we expected survival of males to vary among years to a greater degree than survival of females at all ages. Juvenile and yearling males should be more susceptible to harsh environmental conditions than females of the same age because males should allocate more energy than females to growth, whereas adult males should suffer more from harsh conditions than females because of costly mating competition. Third, yearly variation in survival was not expected to be random but should be related to environmental fluctuations. In most populations of large herbivores studied so far, survival of juveniles increases with habitat quality and, at the individual level, heavier individuals survive better than others (see Gaillard et al. [2000] for a review). Some studies suggested that variable environmental conditions (mast production [Bieber and Ruf 2005; Massei et al. 1997; Okarma et al. 1995] and spring frosts [Jezierski 1977]) may influence survival via an effect on body mass or weight (von Stubbe 1998).

## MATERIALS AND METHODS

*Study area.*—Research was conducted within the fenced 60-km<sup>2</sup> preserve of Castelporziano near Rome, Italy, during 1995–2002. Wild boars, roe deer (*Capreolus capreolus italicus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*) were present within the preserve (Focardi et al. 2001, 2002), but there were no large predators in the area.

Pignatti et al. (2001) gave a detailed analysis of the vegetal communities of Castelporziano. Holly oak (*Quercus ilex*) grove represents the typical meso-Mediterranean evergreen wooded habitat of the study area (27%). Deciduous oak forest (34%) consisted of old-growth natural oak stands of *Q. cerris* and *Q. frainetto*, in most cases associated with a high coverage (80–90%) of undergrowth of *Carpinus orientalis*. Mature oaks of different species produced substantial amounts of acorns. The level of acorn production follows a periodicity of about 4 years. About 100 temporary pools (Mura and Zarattini 2001), often associated with common oak *Q. robur*, are very important for wildlife during the summer drought. In less-wet zones, this habitat is characterized by a typically Mediterranean undergrowth (*Erica arborea*, *Crataegus monogyna*, *Phyllirea latifolia*, and *Rubus*).

In depressions parallel to the shoreline, there are a few wetlands with *Fraxinus*, *Ulmus minor*, and other hygrophilous plants (2.4%). At Castelporziano, there are a few open areas characterized by arid pastures (8.3%). Commercial stands of trees (21%) are represented by pure or mixed (with *Q. ilex*) coetaneous woods of domestic pines *Pinus pinea*, concentrated in the central part of the study area, or by plantations of cork oak. There are few other plantations, urban areas, and unclassified zones.

Climate is Mediterranean with dry summers and rainfall concentrated in October–November. The presence of a summer

drought may influence important parameters of this population of wild boars; therefore, we used the following climatic covariates in the analysis of survival. Winter rainfall is the total rainfall in December, January, and February. Intensity of summer drought was described by 2 different indices. For each month we calculated the ratio between total rainfall and mean temperature (rainfall–temperature index). If the rainfall–temperature index <2, we considered the month as arid (Gausson index; see Gaillard et al. [1997], Garel et al. [2004], and Toigo et al. [2006] for applications to ungulates). Thus, each year was characterized by the number of dry or arid months. However, drought during a given month can be compensated when rainfall was abundant the previous month. Based on Rivas-Martínez et al. (1999), we calculated the compensated drought index (IOS<sub>3</sub>) as the summation of rainfall occurring in June, July, and August divided by the summation of mean temperatures in the same period. A compensated drought index <2 indicates lack of compensation in summer.

**Acorn production.**—We monitored acorn production during the study period. We used a total of 50 traps. Each trap was located under 1 oak tree at about two-thirds the distance between the trunk and the canopy margin, where acorn production is the greatest. Each trap consisted of a 1-m<sup>2</sup> iron ring enclosed by a small fence to prevent ungulate depredation of captured acorns. There was no protection against jays and rodents. Traps were distributed in groups of 5 randomly located in the preserve. Traps were checked every month (October–February) and acorns were counted and removed from the trap. For each year, the acorn production index is given by the mean number of acorns collected per group of 5 traps, per month.

**The population of wild boars.**—The preserve is completely fenced, preventing both the immigration and emigration of wild boars from the enclosure. Most juveniles were born by mid-April, making it possible to discriminate juveniles from yearlings during summer. Further, body size of yearlings was intermediate, and it was possible to differentiate yearlings from adults (Table 1). The availability of marked animals of known age permitted us to confirm that correct age discrimination in summer was attained when the animal was captured.

Management activities directed at wild boars within this population (artificial feeding, trapping, and harvests) were assigned to the preserve rangers. Wild boars were artificially fed 3–6 times/week from the end of June until late August. Corn was used as food, which was distributed among 60–80 feeding points from a moving vehicle. A count of animals present at feeding sites was conducted as follows. One or 2 observers used binoculars and a spotting telescope (Swarovski Optics CT 85 20 × 60; Swarovski Optics, Absam, Austria; and Zeiss Diascope 85TFL 20–60; Zeiss, Oberkochen, Germany) to simultaneously record the number of animals present at each of 5 feeding sites. After about 5 min, all observers moved to the next set of 5 feeding sites to count wild boars just after the vehicle distributing corn had passed. A rapid relocation between sets of feeding sites by the observers was necessary to avoid double counts of any animals shifting among the different sites. Each feeding location was observed twice on different days.

**TABLE 1.**—Mean body mass (kg, SE in parentheses) of male (M) and female (F) wild boars (*Sus scrofa*) at different ages at Castelporziano, Italy, 1995–2002. For gestation we have reported the predicted body masses on the 93rd day, which represents the largest datum recorded. ANOVA refers to the comparison between males and females within each age class and season. The category “Year” for variable “Season” indicates that the average adult body mass was calculated using both winter and summer masses.

Season	Age class	Sex	n	Body mass	ANOVA		
					F	df.	P
Gestation	Embryos	F	43	0.492 (0.14)	0.03	86	0.86
		M	45	0.527 (0.14)			
Summer	Juveniles	F	39	8.9 (0.7)	0.82	69	0.84
		M	32	8.7 (0.8)			
	Yearlings	F	18	32.3 (3.2)	0.06	38	0.8
		M	22	33.5 (3.2)			
	Adults	F	24	42.6 (1.6)	31.5	37	< 0.0001
		M	15	64.9 (4.3)			
Winter	Adults	F	52	58.5 (1.5)	4.5	75	0.036
		M	25	65.8 (3.8)			
Year	Adults	F	76	50.6 (1.7)	20.9	112	< 0.0001
		M	40	65.3 (2.2)			

Based on the approximate amount of corn used during the feeding periods, we estimated that some animals may have consumed as much as 0.41 kg of corn per day (only approximately 22% of the population was observed among the feeding sites in any given year). Assuming a requirement of 100 kcal per kilogram of live weight per day, 0.41 kg of corn represents 15% of the nutritional requirement of an adult male and 10% of that of a lactating female. After completion of the feeding site counts, we estimated the population size and a harvest plan was implemented using the model described by Focardi et al. (1996), but using deterministic parameter-assignment values. The overall objective of the harvest plan was to maintain the subadult and adult segments of the population at a constant proportion. Juveniles were captured at the age of 4–5 months. Animal handling was performed according to current regulations for animal welfare, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Because achievement of harvest plan objectives using only captures was unlikely, further animals were removed through shooting between September and March.

Size of the population in each year was estimated from data on the probability of detection of tagged animals during summer surveys. The following models were used: equal detectability, different detectability between adults and yearlings, and different detectability among age classes and sexes. The most appropriate model was selected using the Akaike information criterion (AIC). We did not fit time-dependent detectability models because there were some years in which very few tagged animals were observed at the beginning of the study. This method corrects for eventual differences of presence of the different classes on feeding sites and yielded absolute population estimates.

We used the number of juveniles counted as a proxy for density because it was strongly correlated with capture–mark–

recapture estimates of density ( $r = 0.92$ ,  $P = 0.003$ ). We did not use these latter estimates to avoid the introduction of spurious correlations between survival and density if both were estimated using the same set of tagged animals. From the end of August, wild boars were captured and removed from the area using an average of 30 traps/day. Each trap, baited with about 7 kg of corn, was a fenced enclosure  $2 \times 3$  m in area and 1.8 m high. Captures stopped when the harvest plan was accomplished or when the animals stopped entering the traps. This latter phenomenon occurred when there was enough natural food available in the preserve, usually near the end of September.

*Biometrical measures and reproductive traits.*—Adult wild boars shot in autumn–winter were aged according to Matschke (1967) and dress-weighted. In 2001 and 2002 the reproductive traits of 32 females were recorded. Fetuses were weighed, their sex was determined, and their crown–rump length was taken to compute their age according to Henry (1968). From the age of fetuses, we estimated the farrowing date assuming a gestation time of 115 days (Hayssen et al. 1993). The relationship between litter size and female body mass was assessed only on adults because too few yearling females were inspected to calculate a reliable litter size. Statistical analyses and data manipulation were performed using SAS 8.1 (SAS Institute Inc. 2000) unless specified otherwise.

*Capture–mark–recapture.*—A total of 848 wild boars (101 adults, 171 yearlings, and 576 juveniles) were marked during the 8 years of study (captures were not allowed in summer 1999). Animals were weighed, sex was determined, and age was estimated using 3 classes: juveniles or piglets (5–17 months of age), yearlings (18–30 months of age), and adults (>30 months of age). Because the growth rate of juveniles may be fast in August–September, between-year comparisons may be biased. It was not possible to trap animals exactly on the same days in different years, so a difference in mean weights of juveniles between years might reflect a difference in trapping periods. An inspection of body weights of juveniles in August–September showed that growth remained slow until approximately 19 September. After this date, growth in body mass increased quickly. We calculated 2 regressions of body weight (BW) on Julian date ( $d$ ):

$$BW = 7.55 + 0.042d \quad (1a)$$

( $F = 9.65$ ,  $d.f. = 1, 385$ ,  $P = 0.002$ ), before day 262, and

$$BW = 8.61 + 0.195d \quad (1b)$$

( $F = 29.6$ ,  $d.f. = 1, 186$ ,  $P < 0.0001$ ), at day 262 and later dates. Using the 2 equations, all values were calculated as taken on the Julian date 262 (standardized weight).

Trapped animals were individually marked with 2 plastic ear tags using a combination of numbers, colors, and tag shapes. Retrapped animals also were weighed. Ear tags allowed us to visually identify, or “recapture” a large number of animals during the summer counts.

*Survival analysis.*—We estimated survival rates from capture–mark–recapture data using recent developments of capture–mark–recapture models (Lebreton et al. 1992; Seber

and Schwarz 2002). Survival was calculated on an annual basis. Both resights on feeding places and physical recaptures were considered as “recapture events.” Marked animals that were shot were right-censored to exclude hunting from the survival analysis and to provide an estimate of natural survival. Animals included in the analysis were 1st captured as juveniles or yearlings, so that their age was always known.

We checked the goodness-of-fit of our data to the fully time-dependent model (Cormack–Jolly–Seber model—Lebreton et al. 1992) using the software U-CARE (Choquet et al. 2005). We used the Cormack–Jolly–Seber model as a starting point in the survival analysis. We tested our hypotheses by comparing the AIC among fitted models. AIC provides the best compromise between accuracy and precision (Burnham and Anderson 1998). The best model we selected had the lowest AIC when the AIC difference between models was  $>2$ , but when the difference was  $\leq 2$ , we retained the model with the lowest number of parameters as the best model (Burnham and Anderson 1998). Because we had a consistently high ratio ( $>40$  in all cases) between the information included in the data set ( $n = 496$  and  $503$  for females and males, respectively) and the number of parameters fitted (maximum of 11), we did not use the correction of AIC for small sample size. All calculations were performed in Surge 5.0 (Cooch et al. 1997).

The letters  $S$  and  $P$  were used for survival and recapture probability, respectively. Subscripts  $age$ ,  $sex$ , and  $t$  refer to factors age, sex, and year.  $Age$  can take values  $j$ ,  $y$ , and  $a$  for juveniles, yearlings, and adults, respectively;  $sex$  the values M or F, for males and females, respectively; and  $t$  values 1996 through 2002, respectively. Superscript  $e$  denotes an analysis where environmental factors were used as covariates.

When we used  $>1$  factor in the analysis we could have 2 different models. A full model included all interactions among factors, whereas an additive model used only main effects, without interactions. For instance,  $P_{sex+t}$  means that capture probability depended on sex and that time-dependence was the same for both sexes, whereas  $P_{sex*t}$  corresponds to between-sex differences in time dependence.

We tested the effect of time, age, and sex on recapture rates. To achieve this, we used a full model for survival ( $S_{age*sex*t}$ ) in order to identify the most suitable model for recapture among the following sets of a priori models:  $S_{a*sex*t}$ ,  $P_{age*sex*t}$ ,  $S_{age*sex*t}$ ,  $P_{sex*t}$ ,  $S_{age*sex*t}$ ,  $P_{age*t}$ ,  $S_{age*sex*t}$ ,  $P_t$ ,  $S_{age*sex*t}$ ,  $P$ ,  $S_{age*sex*t}$ ,  $P_{age}$ ,  $S_{age*sex*t}$ ,  $P_{age+sex+t}$ ,  $S_{age*sex*t}$ ,  $P_{sex+t}$ . In 1999 we had only “visual recaptures” because trapping was not allowed; we therefore expected lower recapture probability for 1999 than in other years. In model  $S_{age*sex*t}$   $PP_{1999}$  we assumed that recapture rates were equal among all years except 1999. The selected model for capture probability to be used in further analysis shall be denoted  $\tilde{P}$ .

We tested the variation in survival of females among the 3 age classes by comparing  $S_t \tilde{P}$  to  $S_{age*t} \tilde{P}$ . We also assessed variation of survival over time in each age class by considering  $S_{j*t} S_y S_a \tilde{P}$ ,  $S_{j*y*t} S_a \tilde{P}$ , and  $S_{j*y} S_a \tilde{P}$ . Then, we tested the effects of environmental factors on survival of juveniles of both sexes. Several of the collected parameters (number of juveniles recorded during summer counts, winter rainfall, arid months,

compensated drought index, and acorn production index) were strongly correlated, and we used principal component analysis to identify the minimal number of independent factors explaining most of the variance.

For each sex and age class we compared  $S \bar{P}$ ,  $S^e \bar{P}$ , and  $S_t \bar{P}$ , where  $e$  may be the 1st principal component, the 2nd principal component, the standardized weight, or any combination of these environmental covariates (e.g., the 1st principal component + the 2nd principal component, through the 1st principal component + the 2nd principal component + the standardized weight). To quantify the impact of environmental covariates, we used the proportion of deviance accounted for by the covariate (Schemper 1990; see Gaillard et al. [1997] for an application to large mammals).

Lastly, we tested for between-sex variation in survival by comparing  $S \bar{P}$  to  $S_{sex} \bar{P}$ , and by comparing  $S_{age} \bar{P}$  to, respectively,  $S_{j*sex} S_{y} S_a \bar{P}$ ,  $S_{j} S_{y*sex} S_a \bar{P}$  and  $S_{j} S_{y} S_a *_{sex} \bar{P}$ . In order to confirm the effect of sex, we also used a data set relative to animals that were 1st captured as adults.

### RESULTS

*Body mass and sexual size dimorphism.*—At Castelporziano, sexual size dimorphism was apparent only among adult wild boars (Table 1). Differences in body mass between sexes were very small for embryos, juveniles, and yearlings, but highly significant for adults, which had a ratio of male to female body mass as high as 1.52. Notably, however, in our study population, size dimorphism was much less in winter than in summer (Table 1). On a yearly basis, the size dimorphism between the sexes was 30%. When comparing summer and winter body masses of each sex, the body mass of males remained almost the same (analysis of variance [ANOVA],  $F = 0.02$ ,  $df = 1, 38$ ,  $P = 0.87$ ), whereas females gained significant body mass between summer and winter (ANOVA,  $F = 40.6$ ,  $df = 1, 74$ ,  $P < 0.0001$ ).

The range of farrowing dates, calculated from fetal crown–rump lengths, was 18 April–9 May ( $n = 12$ ) and 4 April–7 May ( $n = 17$ ) in 2002 and 2003, respectively. Overall mean litter size was  $4.2 \pm 0.2 SE$ , which differed between 2001 ( $3.3 \pm 0.4$ ) and 2002 ( $4.3 \pm 0.3$ ; Wilcoxon test,  $z = -2.07$ ,  $P = 0.038$ ). The number of fetuses (range 0–5) tended to increase with maternal weight (range 49–84 kg), although this relationship was not significant ( $F = 3.0$ ,  $df = 1, 27$ ,  $P = 0.09$ ).

During the study, population parameters for Castelporziano wild boars varied to a great extent. In particular, the years 1996, 1999, and 2002 were characterized by a population productivity (litter size; Table 2, section A) that ranged from 20% to 27% of the observed maximum.

*Environmental conditions.*—The first 2 principal components accounted for 70.4% of the total variance. Upon varimax rotation, the 1st principal component (36% of variance) was highly correlated with the number of juveniles ( $r = 0.656$ ), arid months ( $r = 0.778$ ), and compensated drought index ( $r = -0.750$ ), and thus it was a measure of summer conditions because it increased with drought and animal density. The 2nd principal component (34% of the variance) was highly

**TABLE 2.**—Numbers of wild boars (*Sus scrofa*) per sex and age class (sex of juveniles was not determined) at Castelporziano, Italy, 1996–2002. A) Animals counted on artificial-feeding sites. Reported values were calculated as number of animals classified in each class (during summer surveys on artificial feeding stations) to which we added the appropriate fraction of undetermined individuals. B) Yearlings and adults were estimated by dividing number from section A by the age-specific detection probability during summer surveys ( $0.325 \pm 0.023$  and  $0.205 \pm 0.01$  for yearlings and adults, respectively), whereas total juveniles were obtained by multiplying the number of juveniles per adult female (last column from section A) by the estimated number of females (from section B). Percent harvested (section D) was calculated by dividing corresponding cells in section C by those in section B. Column averages are in boldface type.

Year	Juveniles	Yearlings		Adults		Totals	Juveniles/ adult female
		Males	Females	Males	Females		
A) Counted animals							
1996	156	5 <sup>a</sup>	133	105	194	593	0.8
1997	581	57	73	89	194	994	3.0
1998	894	286	164	164	356	1,864	2.5
1999	146	84	93	132	262	717	0.6
2000	905	53	74	143	307	1,482	2.9
2001	439	185	242	163	379	1,408	1.2
2002	199	87	79	163	332	860	0.6
	<b>474</b>	<b>108</b>	<b>123</b>	<b>137</b>	<b>289</b>	<b>1,131</b>	<b>1.7</b>
B) Estimated animals							
1996	761	15	409	512	946	2,644	
1997	2,834	175	225	434	946	4,615	
1998	4,361	880	505	800	1,737	8,282	
1999	712	258	286	644	1,278	3,179	
2000	4,415	163	228	698	1,498	7,001	
2001	2,141	569	745	795	1,849	6,099	
2002	971	268	243	795	1,620	3,896	
	<b>2,314</b>	<b>333</b>	<b>377</b>	<b>668</b>	<b>1,410</b>	<b>5,102</b>	
C) Harvested animals							
1996	8	34	40	74	59	215	
1997	393	22	15	26	19	475	
1998	656	164	189	119	175	1,303	
1999	12	10	11	58	32	123	
2000	642	7	6	65	72	792	
2001	232	171	116	107	133	759	
2002	14	49	43	141	100	347	
	<b>280</b>	<b>65</b>	<b>60</b>	<b>84</b>	<b>84</b>	<b>573</b>	
D) % harvested							
1996	1.1	NA	9.8	14.5	6.2	8.1	
1997	13.9	12.5	6.7	6.0	2.0	10.3	
1998	15.0	18.6	37.5	14.9	10.1	15.7	
1999	1.7	3.9	3.8	9.0	2.5	3.9	
2000	14.5	4.3	2.6	9.3	4.8	11.3	
2001	10.8	30.0	15.6	13.5	7.2	12.4	
2002	1.4	18.3	17.7	17.7	6.2	8.9	
	<b>12.1</b>	<b>19.6</b>	<b>15.9</b>	<b>12.6</b>	<b>6.0</b>	<b>11.2</b>	

<sup>a</sup> Data collected in 1996 for this sex class were clearly underestimated and thus harvest rate of yearling males in 1996 (section D) was not calculated.

correlated with the acorn production index ( $r = 0.831$ ) and winter rainfall ( $r = 0.902$ ), and increased with favorable autumn–winter conditions. Yearly values of the 3 climatic indices are reported in Fig. 1. Interannual variability of all

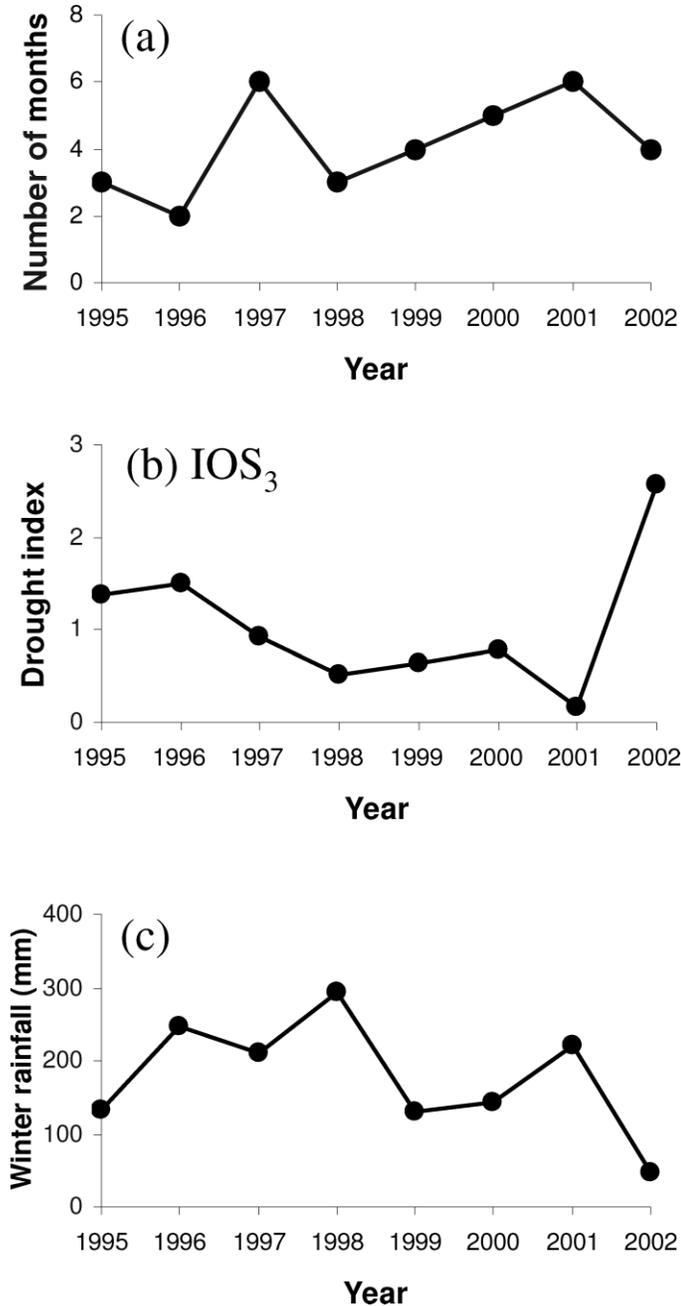


FIG. 1.—Variation in 3 climatic variables in the Preserve of Castelporziano, Italy, during the period of study. a) Number of dry months, b) summer aridity index, and c) total winter rainfall.

indices is relatively large and the drought index suggests a trend (with the exception of 2002) of increasing summer aridity in the study area.

**Population structure.**—The model of detection probability based on different detectability between yearlings and adults was selected as the best model; models based on equals detectability ( $\Delta AIC = 29$ ) or based on different detection probabilities among age and sex classes ( $\Delta AIC = 655$ ) were less parsimonious. We used estimates of the probability of detection to reconstruct the postbreeding population structure (Table 2, section B) from count data (Table 2, section A),

TABLE 3.—Model selection for recapture rates based on the most complete survival model ( $S_{age*sex*t}$ ) including interactive effects of age, time, and sex. For each model we report the Akaike information criterion (AIC) and the number of estimable parameters ( $N_{par}$ ). Models are ranked according to the difference in AIC with respect to the best model ( $\Delta AIC$ ), which has  $\Delta AIC = 0$ . Notation of capture probabilities:  $PP_{1999}$ , 2 capture rates, 1 for 1999 and the other for all other years;  $P_{s+t}$ , additive effects of sex and time;  $P_t$ , time dependence in capture probabilities;  $P_{s*t}$ , interactive effects of sex and time;  $P_{a+s+t}$ , additive effects of age, sex, and time;  $P_s$ , constant capture probability;  $P_a$ , age dependence in capture probabilities;  $P_{a*s*t}$ , interactive effects of age, sex, and time.

Model for recaptures	$N_{par}$	AIC	$\Delta AIC$
$PP_{1999}$	45	1,838.46	0.0
$P_{s+t}$	51	1,841.56	3.10
$P_t$	50	1,841.84	3.38
$P_{s*t}$	52	1,841.88	4.42
$P_{a+s+t}$	52	1,843.12	4.66
$P_s$	44	1,850.03	11.57
$P_a$	46	1,853.39	14.93
$P_{a*s*t}$	79	1,855.09	16.63

which revealed that the population was characterized by a large fraction of adults and an elevated number of juveniles during the study. The percentage of the population that was harvested each year was relatively low (Table 2, section D). Harvest rates were highest for juveniles and subadults, albeit for juveniles the proportion harvested alternated between very low ( $>2\%$ ) to moderately high (10–15%) in different years. The proportion of males harvested was always larger than the proportion of females, indicating a higher harvest probability for males.

**Goodness-of-fit.**—The capture–recapture data satisfactorily fitted the Cormack–Jolly–Seber model for both sexes. For females, we found no deviation from the Cormack–Jolly–Seber model ( $\chi^2 = 19.205$ ,  $df = 23$ ,  $P = 0.689$  and  $\chi^2 = 2.271$ ,  $df = 7$ ,  $P = 0.943$ , for wild boars released as juveniles and as yearlings, respectively), no transience ( $z = 0.262$ ,  $P = 0.793$  and  $z = -0.486$ ,  $P = 0.627$ , for wild boars released as juveniles and as yearlings, respectively), and no trap-dependence ( $z = 0.226$ ,  $P = 0.821$  and  $z = 1.016$ ,  $P = 0.310$ , for wild boars released as juveniles and as yearlings, respectively). Likewise, for males, we found no deviation from the Cormack–Jolly–Seber model ( $\chi^2 = 26.964$ ,  $df = 23$ ,  $P = 0.258$  and  $\chi^2 = 6.411$ ,  $df = 9$ ,  $P = 0.698$ , for wild boars released as juveniles and as yearlings, respectively), no transience ( $z = 0.795$ ,  $P = 0.427$  and  $z = 0.432$ ,  $P = 0.666$ , for wild boars released as juveniles and as yearlings, respectively), and no trap-dependence ( $z = -0.707$ ,  $P = 0.480$  and  $z = 1.064$ ,  $P = 0.287$ , for wild boars released as juveniles and as yearlings, respectively).

**Recapture rates.**—Model  $S_{age*sex*t}$   $PP_{1999}$  exhibited the lowest AIC value (Table 3). In general, models including time-dependent recapture probability fitted the data better than models with constant capture probability (Table 3). The selected model included 2 recapture rates: 1 for 1999 (0.194, 95% confidence interval [95% CI]: 0.116, 0.305) and 1 for the other years (0.424, 95% CI: 0.368, 0.481). Thus, we used

**TABLE 4.**—Akaike information criterion (AIC) values for comparing models including environmental effects (1st principal component, PC1; 2nd principal component, PC2; and standardized weight, SW) on survival model for each of the 6 sex and age classes considered. Survival may be constant or time-variable and model  $\hat{P}$  for recapture rates was used. The lowest AIC value within each class is indicated in boldface type. Model notation is explained in text.

Model	Covariates, $e$	$N_{par}$	Age and sex class					
			Males			Females		
			Juveniles	Yearlings	Adults	Juveniles	Yearlings	Adults
$S_t \hat{P}$		11	827.97	838.43	850.05	977.96	980.80	985.09
$S^c \hat{P}$	PC1 + PC2 + SW	8	823.54	837.94	845.64	977.25	973.71	981.00
$S^c \hat{P}$	PC1 + PC2	7	834.09	<b>836.60</b>	843.75	975.33	973.68	979.16
$S^c \hat{P}$	PC1 + SW	7	825.29	839.33	844.29	975.25	972.01	979.25
$S^c \hat{P}$	PC2 + SW	7	<b>822.35</b>	837.36	843.66	977.57	972.48	979.01
$S^{ce}$	PC1	6	832.09	837.70	842.48	<b>973.34</b>	977.27	977.40
$S^c \hat{P}$	PC2	6	842.23	838.29	841.77	977.46	977.07	977.19
$S^c \hat{P}$	SW	6	825.66	840.25	842.39	975.76	<b>970.75</b>	977.25
$S \hat{P}$		5	840.49	840.49	<b>840.49</b>	975.46	975.46	<b>975.46</b>

model  $\hat{P} = PP_{1999}$  for recapture rates when testing differences in survival.

*Test of prediction 1.*—Mean survival of females, irrespective of age, was  $0.727 \pm 0.025 SE$ . Contrary to our expectation, the model of survival that included variation in relation to age ( $S_{age} \hat{P}$ ) fit the data less well than the model without variation due to age ( $S \hat{P}$ ;  $\Delta AIC = 3.6$ ). The survival estimate for adult females ( $0.706 \pm 0.043$ ) was lower than that for both juveniles ( $0.714 \pm 0.071$ ) and yearlings ( $0.775 \pm 0.086$ ). Likewise, we detected little evidence for less variable survival of adults than of juveniles.

We did not detect evidence for marked temporal variation ( $\Delta AIC = 8.1$  for model  $S_{j^*r} S_y S_a \hat{P}$ ,  $\Delta AIC = 8.9$  for model  $S_j S_{y^*r} S_a \hat{P}$ , and  $\Delta AIC = 15.3$  for model  $S_j S_y S_{a^*t} \hat{P}$ ). Even the coefficients of variation for survival rates of the different age classes were similar (0.208, 0.167, and 0.200 for juveniles, yearlings, and adult females, respectively). The analysis of survival rates estimated from wild boars marked as adults provided similar results (mean yearly estimate of  $0.731 \pm 0.073$  and coefficient of variation of yearly estimates of 0.284).

*Test of prediction 2.*—The fitting of the different models testing for the effect of environmental variability is reported in Table 4. The 2nd principal component and the standardized weight influenced the survival of juvenile males (slopes: 0.663, 95% CI: 0.32, 1; and 0.739, 95% CI: 0.14, 1.33, respectively), which survived better when winter rainfall and standardized weight were high. Changes in the 2nd principal component and standardized weight accounted for 90.3% of the observed variation in survival over years. The pattern for juvenile females was different. The model with the lowest AIC was the one assuming an effect of the 1st principal component, although the slope was not significantly different from 0 (0.528, 95% CI:  $-0.095, 1.15$ ). Although changes in the 1st principal component accounted for 43.4% of the observed variation in survival among years, the model with constant survival was only weakly less fitted to the data ( $\Delta AIC = 2.12$ ), likely because the total variation in survival of female juveniles among years was low.

For the survival of yearling males, the best model involved an effect of both the 1st and 2nd principal components (but the

slopes were not significantly different from 0 (0.44, 95% CI:  $-0.082, 0.97$ ; 0.46, 95% CI:  $-0.064, 0.98$ , respectively). Changes in the 1st and 2nd principal components accounted for 56.1% of the observed variation in survival over years. However, the amount of temporal variation in survival of yearlings was limited (50% of the variation observed in survival of juveniles), and identifying the factors associated with the variation with certainty was not possible. Thus, 2 other models also fit the data well: 1 assuming effects of both the 2nd principal component (0.55, 95% CI: 0.059, 1.04) and the standardized weight (0.096, 95% CI:  $-0.014, 0.20$ ), and the other showing a significant effect of the 1st principal component (0.44, 95% CI: 0.15, 1.19). For yearling females, the temporal variation of survival was low, and the best model assumed a nonsignificant (0.23, 95% CI:  $-0.11, 0.48$ ) effect of standardized weight. For adults of both sexes the best model was characterized by constant survival (Table 4).

*Test of prediction 3.*—Overall, females experienced higher survival than males (0.719, 95% CI: 0.67, 0.76; and 0.637, 95% CI: 0.58, 0.69, respectively). However, when considering age structure (Table 5), survival differed between sexes only for yearlings (0.495, 95% CI: 0.38, 0.61; and 0.771, 95% CI: 0.60, 0.89 for males and females, respectively). For juveniles (0.611, 95% CI: 0.49, 0.72; and 0.740, 95% CI: 0.60, 0.84 for males and females, respectively) and adults (0.690, 95% CI: 0.58, 0.78; and 0.745, 95% CI: 0.66, 0.82 for males and females, respectively) there was only a weak tendency for a higher survival in females. For yearlings, a model that included a between-sex difference in survival with time dependence was selected over a model that did not include this interaction (Table 6). The opposite ranking of models was found for both juveniles and adults.

Contrary to our expectations, in adults, survival of males was not different from that of females, both in the case of constant or temporally variable models (Tables 5 and 6). In order to improve the reliability of this result we also considered a different set of data where wild boars were captured as adults but could not be accurately aged. In this case, we compared the model  $S_t \hat{P}$  versus the model  $S_{t^*sex} \hat{P}$ . The model

**TABLE 5.**—Comparison of models that include between-sex differences per age class for time-constant models. The model selection for survival rates adopted the model  $\hat{P}$  for recapture rates. Notation as in Table 3.

Model	$N_{\text{par}}$	AIC	$\Delta\text{AIC}$
$S_j S_y^{\text{sex}} S_a \hat{P}$	6	1,814.21	0
$S^{\text{sex}} \hat{P}$	4	1,816.20	2.08
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	8	1,817.84	3.72
$S \hat{P}$	3	1,820.74	6.62
$S_j^{\text{sex}} S_y S_a \hat{P}$	6	1,821.29	7.17
$S_j S_y S_a \hat{P}$	5	1,822.63	8.51
$S_j S_y S_a^{\text{sex}} \hat{P}$	6	1,823.90	9.78

that did not include a between-sex difference in survival of adults was considered more parsimonious ( $\Delta\text{AIC} = 9.7$ ).

### DISCUSSION

We found that for females, survival was constant in time and among age classes, survival of males differed among age classes, survival of juvenile males was correlated with variations in environmental factors and body mass, there were minimal effects of environmental factors on survival of females, and survival of males and females differed only for yearlings.

We believe that these conclusions were minimally prejudiced by the artificial feeding program at the preserve. Based on the amount of bait presented for consumption, the impact on energy requirements of adults appeared modest, and it clearly may not influence comparisons among age and sex classes. The only possible effect of baiting was to increase survival (especially for yearlings and juveniles) and to reduce between-year variability in survival. In addition, the fact that the whole preserve was sampled and that fencing prevented emigration allowed us to accurately evaluate the survival of both sexes without confounding differences in survival with differences in dispersal patterns between sexes. Biases due to capture and shooting were excluded by the analysis. Captures of juveniles were performed before juveniles were marked and thus capture may not bias our estimate of survival in the age class 5–17 months. For juveniles and adults, the limited number of animals that were shot were censored in the analysis. Because all harvesting was conducted by the preserve’s rangers, we had no problems with failure to report marks of harvested animals.

Harvest mortality (11%) was much lower than mortality determined by natural causes (32%). Comparison of these 2 values shows that the life-history traits of this population are more influenced by natural factors than by artificial selection. Further, the age distribution of losses due to harvest appeared mimetic of mortality from predation by wolves (*Canis lupus*) in Italy (Mattioli et al. 2004). Comparison of the life-history traits observed in this population with traits of nonharvested populations that are preyed on by wolves would be valuable. These populations are present in some national parks in central-south Italy, but their study on the long term would require an important cooperative effort of researchers and public authorities.

**TABLE 6.**—Model selection for survival rates using model  $\hat{P}$  for recapture rates. Within each age class, models with an equal or a different between-sex time-dependent term are compared. Notation as in Table 3.

Model	$N_{\text{par}}$	AIC	$\Delta\text{AIC}$
<b>Juveniles</b>			
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	14	1,807.53	0
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	22	1,810.16	4.63
<b>Yearlings</b>			
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	22	1,819.86	0
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	14	1,822.570	2.71
<b>Adults</b>			
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	13	1,825.26	0
$S_j^{\text{sex}} S_y^{\text{sex}} S_a^{\text{sex}} \hat{P}$	20	1,836.41	11.15

Our study has confirmed that wild boars are characterized by strong sexual dimorphism and, at the same time, by high fecundity. In the weight range of 50–80 kg, suids typically attain a litter size of 3.9, whereas bovids and cervids average approximately 1.8 young per litter (Morgan Ernest 2003).

The studied population exhibited a farrowing season similar to that of populations observed in southern France (Dardaillon 1988) and Spain (Fernández-Llario and Carranza 2000). The pattern of body growth was similar to that of other Italian populations, but markedly lower than in central and eastern European populations (Pedone et al. 1995). Further studies are hence necessary to establish whether these differences between Mediterranean and temperate populations are linked to scarce interbreeding with introduced populations or with domestic swine, a peculiar adaptation to habitats characterized by harsh conditions during the weaning period, or a reduced impact of harvest (most of studies on Mediterranean populations were performed in areas with low hunting pressure [e.g., this study; Fernández-Llario and Carranza 2000; Massei et al. 1997]). In other populations (e.g., Arc-en-Barrois, France) the strong hunting pressure may select for faster growth and early sexual maturity (Gaillard et al. 1987).

Results from this study indicate that wild boars are characterized by an unusual combination of life-history traits. In particular, at least 3 predictions derived from our current understanding of demographic tactics in ungulates are not well fit by the species. Survival of prime-aged adult females (around 0.7) appeared to be much lower than that usually reported for similar-sized ungulates (average of 0.890, minimum of 0.807, and maximum of 0.978 for 18 populations of ungulates between 40 and 80 kg [data from Gaillard et al. 2000]). Also, and despite the large variability of environmental conditions in the study area, temporal patterns of survival were not clearly evident because only juvenile males exhibited significant variation of survival among years. Although we did find evidence for differences in survival between males and females, the observed pattern was not in accordance with our theoretical framework. Specifically, the between-sex differences in survival were greater when the sexual size dimorphism was small, that is, for yearlings.

The sensitivity of survival of juvenile males to environmental conditions and their low survival as yearlings might be linked to different dispersal patterns of the sexes. Male wild boars disperse further than females (Truvé and Lemel 2003), and the disruption of family links of male yearlings during the rut is considered final (Beuerle 1975).

The theory of the evolution of mammalian life-history traits (Charnov 1991; Purvis and Harvey 1995) gives special importance to the ratio ( $\delta$ ) of the weight at independence (usually estimated at weaning) to adult weight (assuming definite growth). Species with low  $\delta$  values (such as lagomorphs) are in the fast end of the life-history continuum, whereas species with high  $\delta$  values (e.g., cetaceans or perissodactyls) fit well the low end of the continuum. It is not completely accurate to define juveniles having reached independence (i.e., weaning) at about 6 months of age (in the studied population, this would be on the median date of 20 October). We estimated an equivalent weight at independence of 14.5 kg, and therefore a  $\delta$  value of 0.34, similar to the value calculated by Purvis and Harvey (1995) for Jezierski's (1977) data. Using Morgan Ernest's (2003) data, it appears that *S. scrofa* exhibits a  $\delta$  value between those of Lagomorpha and Rodentia. The idea that the life-history tactics of wild boars are similar to that of the hare (*Lepus europaeus*) is not new (Jezierski 1977), but we demonstrated here for the 1st time that survival patterns of wild boars are indeed closer to those expected for small mammals (Gaillard and Yoccoz 2003; Price and Kelly 1994).

The question is how such a life-history strategy may be attained by such a large mammal, considering that the body mass of a wild boar is >10 times that of a hare? We can note that other mammals with litter sizes and adult body masses similar to those of wild boars are almost all carnivores (e.g., the gray wolf and the mountain lion [*Puma concolor*]). The adoption of such life-history traits may be made possible by a high-energy diet. Wild boars, in addition to feeding on plants, will use animals for food when possible. The fraction of animal food included in the diets of this species is highly variable among populations and between seasons within populations. Wild boars in temperate forests include a large frequency of occurrence of earthworm (*Lumbricus*) in their diet (Baubet et al. 2003). Such food is scarce in Mediterranean habitats, but in some cases wild boars exploit other invertebrates (Massei et al. 1996). In our study area, the diet of wild boars showed a very low percentage of animal food (1.67%—S. Focardi, in litt.). However, the analysis of the diet of these animals in summer was made from feces (Focardi et al. 2000), and this technique may overlook the presence of occasional animal food derived from scavenging. In our study area, we have often observed wild boars scavenging, as well actively preying on fawns of fallow deer. The presence of a small amount of animal food in the diet may have allowed wild boars to evolve this unusual life-history combination of large size, high fecundity, and low and variable adult survival.

The strategy of wild boars might be linked to the unpredictability of "good" years, defined as the combination of low population density and the widespread availability of high-quality foods, such as acorns. A high reproductive

potential may allow females to exploit these windows of opportunity; however, it also may cause high levels of stress when conditions are unfavorable. These selective forces may have shaped a high risk–high reward strategy in females, which results in demographic traits similar to those observed in males. This could explain the lack of sex-specific differences of survival in the adult segment of this population. We expect that such reduced differences would be more evident in Mediterranean than in temperate populations, because in the former environment, lactation overlaps with the season where resources are scarce.

## RIASSUNTO

Il cinghiale (*Sus scrofa*) è una specie massiccia e presenta un evidente dimorfismo sessuale. La storia naturale di questa specie monogastrica è caratterizzata da notevoli differenze rispetto a quella della maggior parte degli ungulati, poiché la dimensione della cucciolata è più grande e la sopravvivenza degli adulti minore di quella che caratterizza altre specie di dimensioni comparabili. In questo lavoro abbiamo studiato la popolazione della Tenuta Presidenziale di Castelporziano che probabilmente rappresenta l'ultimo resto dell'originaria popolazione di Cinghiale maremmano (*S. s. majori*). Mediante un ampio campionamento di animali di età nota, che sono stati catturati, marcati individualmente (mediante marche auricolari numerate) e ricatturati (o riavvistati) successivamente, abbiamo modellizzato la sopravvivenza delle varie classi di sesso ed età (subadulti/adulti) durante un periodo di otto anni, per studiare la demografia di questa popolazione e valutare gli effetti di condizioni ambientali variabili (in particolar modo della siccità estiva e dalla produzione di ghiande) che si ritiene possano avere un impatto significativo sui parametri demografici della specie. Contrariamente alle nostre previsioni, basate sulla conoscenza delle strategie evolutive dei mammiferi, la sopravvivenza differenziale tra classi di sesso ed età era assai meno evidente di quanto è stato documentato per altri ungulati sessualmente dimorfici di dimensioni simili, ma, come previsto dalla moderna teoria della selezione sessuale, l'impatto dei fattori ambientali era maggiore nei maschi che nelle femmine. Questo lavoro documenta una strategia vitale assai diversa da quella descritta nelle altre specie di ungulati e risulta molto più simile a quella di specie molto più piccole, come i lagomorfi. Si cerca infine di discutere le cause dello scarto tra osservazioni e predizioni teoriche in relazione alla specifica scelta di dieta del Cinghiale che include quantità variabili di cibo animale.

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