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Diet, food availability and reproduction of wild boar in a Mediterranean coastal area

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The diet of the wild boar *Sus scrofa* Linnaeus, 1758 in a Mediterranean area, where agricultural crops were not available and supplementary food was not provided, is described. Diet was compared to the availability of the main food resources and their influence on body weight and reproduction was investigated from 1991 to 1994. Diet varied according to the availability of energy-rich foods such as acorns and olives; pine-seeds were actively consumed, even when their availability was low. When abundant, acorns and olives accounted for most of the diet, and when scarce were replaced by graminoids and juniper berries. In summer, graminoids and pine-seeds accounted for most of the diet. Acorn and olive production was likely to influence both body weight and reproduction. Following a high production of acorns and olives, wild boar exhibited higher body weight, more breeding females and a larger litter size than in years of poor production of these foods.

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Introduction

This study analyses the diet of wild boar *Sus scrofa* Linnaeus, 1758 over a three-year period, in a Mediterranean coastal area. No long-term studies have investigated the diet of the wild boar in such areas, where supplementary food was not provided and no agricultural crops were available. In addition, previous studies in Mediterranean areas (Dardaillon 1987, Sjarmidi *et al.* 1991, Valet *et al.* 1994) used stomach samples collected during the winter hunting season, thus representing only a small part of the annual diet of the wild boar.

This paper describes also how the diet of the wild boar is related to the availability of natural food resources. Previous studies showed that "non-natural" food resources such as supplementary food and crops were heavily used by boar (Belden and Pelton 1975, Lescourret and Genard 1985, Dardaillon 1987, Jullien *et al.* 1990) and their availability influenced their reproduction and body weight (Matschke 1964, Aumaitre *et al.* 1984). When crops and supplementary food were not available, energy-rich food such as acorns and nuts, represented the preferred natural diet of wild boar and feral hogs (Henry and Conley 1972, Wood and Roark 1980, Baber and Coblentz 1987, Groot Bruinderink *et al.* 1994).

Only a few studies have in fact investigated the availability and use of one or more food categories (Henry and Conley 1972, Wood and Roark 1980, Schauss *et al.* 1990, Groot Bruinderink and Hazebroek 1995). Since acorn crops are unpredictable and may vary by species and by year (Goodrum *et al.* 1971, Koenig *et al.* 1994), understanding how the diet of the wild boar changes between years of good and poor acorn crops is of particular interest.

The study aims to answer the following questions: (i) which are the food items selected by boar in a Mediterranean area where supplementary food and crops are not available? (ii) is the use of the main food items related to their availability? (iii) which foods replace the preferred ones when they are not available? (iv) is it possible to predict the diet of the wild boar in relation to the season? (v) does the composition of the diet affect the reproduction and the body weight of wild boar?

Study area

The Maremma Natural Park (MNP), from 0 to 417 m a.s.l., is located on the Tyrrhenian coast in Central Italy (42°39'N, 11°05'E) and covers 9800 hectares. The climate is Mediterranean, with minimum mean temperatures of 6°C in February and maximum mean temperatures of 23°C in July. Precipitation (500–750 mm per year) is seasonal, being mainly concentrated in spring and autumn. Seasons (winter: December–February, spring: March–May, summer: June–September, autumn: October–November) were defined according to the mean monthly temperatures and precipitation after Pigozzi (1987). Fifty-three percent of the study area was dominated by maquis scrub, characterized by *Quercus ilex, Arbutus unedo* and *Phyllirea latifolia.* The pinewood covered about 29% of the area and was dominated by *Pinus pinea* and, along the coast, by *Juniperus oxycedrus*; olive-grove (6% of the area) included *Olea europea* and was primarily grassy. Meadows (12% of the area) consisted of grassy areas (mainly *Cynodon dactilon*), and marshes characterized by *Juncus* spp. and sedges. A detailed description of the vegetation is given in Arrigoni *et al.* (1976).

Large mammals inhabiting the area include wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, fallow deer *Dama dama*, feral cattle *Bos taurus*, fox *Vulpes vulpes*, badger *Meles meles*, and porcupine *Hystrix cristata*. Hunting is not allowed in the park and large predators are absent.

Since the foundation of the Park in 1975, wild boar have been trapped every summer using Clover-type traps baited with maize. For every wild boar captured, date, sex, age and body weight were measured. Age was estimated by tooth eruption, replacement and wear after Matschke (1967). The number of wild boar in the Park was determined by the Park's wardens using vantage point counts (Ratcliffe and Mayle 1992). This method, repeated twice in March 1993, gave a minimum density of 12.8 wild boar per 100 ha. One year later, a high mortality of wild boar occurred in spring and summer 1993, death being caused by starvation (Massei 1995). In 1993 the estimated density of wild boar had dropped to 3 individuals per 100 ha (L. Tonini, pers. comm.).

Methods

Food use and availability

Wild boar faeces (n = 2487) were collected monthly between June 1991 and March 1994, stored in polythene bags and deep frozen for subsequent analysis. Faecal samples were analyzed according to the method of Kruuk and Parish (1981). The volume of each sample was measured by water displacement and samples were subsequently washed through a 1.5 mm mesh sieve. Water and fine

particles passing through the sieve during the first rinsing (microvolume) were collected in a 500 ml beaker; the solid material was allowed to settle for about 15 min and the volume of the food remains (macrovolume) retained in the sieve was measured. For those samples in which the microvolume accounted for more than 10% of the total volume, a 20 ml sample was drawn from the bottom of the beaker and examined under a binocular microscope. The food remains retained in the sieve were identified by comparison with a reference collection. The percentage of wild boar faeces in which particular food items occurred were calculated (FO = frequency of occurrence). For each sample the estimated volume of each food was scored on a seven point scale: absent, < 5%, 6–25%, 26–50%, 51–75%, 76–95%, > 96% (Kruuk and Parish 1981). Plant and animal items were identified to the lowest taxon possible. However, because of mastication, foods were placed in broad categories: (1) graminoids (grasses and sedges), (2) pine-seeds, (3) olives, (4) fruits, (5) acorns, (6) juniper berries, (7) animals, (8) other.

Preliminary observations in 1990 and 1991 showed that, throughout the year, the main food categories used by wild boar were acorns, olives, pine-seeds, grasses and sedges. Relative availabilities were therefore estimated for these foods. Acorn, olive and pine-seed production was estimated by monthly counts of their numbers in randomly placed cloth funnels fastened to 1.3 m stakes (collecting surface = 5024 cm^2, n = 26 funnels in maquis, n = 33 in pinewood and n = 10 in olive-grove). Since acorns remain on the ground long after they have fallen (McShea and Schwede 1993) their availability was also estimated by counting the number of acorns in 22 randomly selected circular plots (diameter = 60 cm) each month. This was done only in 1991–1992; subsequent acorn crop was so low that no acorns were found on the ground after the mast-fall. Since olives and pine-seeds may decompose after a few weeks on the ground (own pers. obs.), the counts in collectors were considered a good estimate of their availability. The availability of grasses was considered constant in each habitat during the whole year because most were perennial and the wild boar fed on both the stems and rhizomes.

Body weight and reproduction

The weights of adult wild boar trapped in summer 1992, 1993 and 1994 were used as an indicator of nutritional condition (Klein 1984). Only the weights of individuals older than 3 years, when growth had stopped (Pepin *et al.* 1987), were compared. Differences in the weight of wild boar trapped in different years were estimated using Kruskal-Wallis and multiple comparison tests (Zar 1984) on each sex.

Trapping allowed also to determine the percentage of lactating females out of the total number of adult trapped females. Litter size for lactating females was estimated from the number of active teats (after Barrett 1978). Reproduction was also assessed by observations, recording number of females with piglets, the number of solitary females and the litter size.

Data analyses

Correlations amongst the frequencies of occurrence and between frequency of occurrence and volumes of different food items were calculated by Spearman's rank correlation coefficient test (Siegel and Castellan 1988). This test was used also for comparing monthly use (frequency of occurrence) and availability (number of acorns, olives and pine-seeds). To investigate how much of the seasonal variation of food items in the diet was due to their seasonal availability, dummy variables (eg occurrence = 1, lack = 0) (Gilbert 1989) were entered in a correlation matrix comparing monthly diet with seasonal occurrence of the seven main food items.

The trophic niche breadth was measured by Levins' standardised index (Ba) (Hurlbert 1978) as follows:

$$Ba = (B - 1) / (n - 1)$$

where $B = 1 / \Sigma p_i^2$, n = number of resources, p_i = proportion of the ith resource. Ba ranges from 0 to 1, where 1 denotes the maximum niche breadth.

Shannon-Wiener (H1) and modified Hill's ratio (E) evenness standardised indices (Ludwig and Reynolds 1988) were used to test whether all the available resources were used equally:

$$H1 = (-\Sigma p_i \log_e p_i) / \log_e n$$

$$E = (B - 1) / (e^{H1}) - 1$$

where p_i , n and B as above. Both E and H1 range between 0 and 1, where 1 indicates that all the food items are used to an equal extent. Shannon-Wiener index is commonly used in studies on diet and Hill's index was used because it is relatively unaffected by species richness (Ludwig and Reynolds 1988).

Principal component analysis (PCA) was used to examine the overall patterns of variation, and to describe the distribution of the observed values within a cartesian system of vectors (PC) (Gilbert 1989). PCA was applied to the correlation matrix calculated on the frequency of occurrence of food items in different seasons.

Results

Food use and availability

Plants comprised an average of 86.3% of volume and 97.9% of frequency of occurrence in the annual diet of wild boar (Figs 1 and 2). Graminoids (both stems, leaves and rhizomes), acorns, olives and pine-seeds were the most common foods used, although the relative presence of these categories varied in different years. Acorns and olives accounted for more than 45% of the frequency of occurrence (FO) in 1991–1992; in subsequent years graminoids comprised more than 40% of the total diet, whilst acorns, olives and pine-seeds decreased considerably. In 1993–1994 juniper berries increased whilst all the other major foods (except for graminoids) decreased.

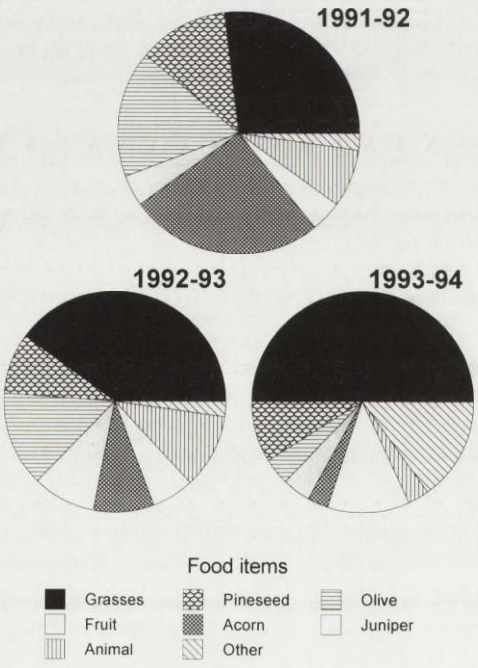

Fig. 1. Annual diet (in % frequency of occurrence) of wild boar in the MNP, derived from dropping analysis.

Graminoids sometimes accounted for up to 98% (in FO) of the total diet (April 1993), were a staple food in all months (Fig. 2a, b, c) and were dominated by *Cynodon* sp. and *Carex* sp.; *Ampelodesmos mauritanica, Ammophila arenaria, Erianthus ravennae* and *Phragmites communis* were eaten less. Acorns, olives and juniper berries were mainly consumption in autumn and winter, with the exception of spring and summer 1992 . The consumption of pine-seeds and fruits was highest in summer and autumn. "Fruits" were composed of fruits of *Pistacia lentiscus,* blackberries, figs, and wild apples. The "other" class was represented by forbs: among these, liquorice *Glycyrrhiza glabra* roots, *Eryngium* sp. and *Veronica* spp. were the most common. Animal food accounted for an average of 2.1% of the volume and 13.7% of the frequency of occurrence in the annual wild boar diet.

Vertebrates were found only in ten faeces: mammals (microrodents and porcupine; $n = 4$), birds ($n = 1$) and reptiles (lizards and tortoises; $n = 5$). Invertebrates accounted for the great majority of animal food and showed a peak of occurrence between May and July. The main categories of invertebrate found in all the droppings were Cicada (*Cicada orni,* Homoptera) larvae (FO = 5%), Coleoptera larvae (FO = 1%) and Chilopoda (FO = 3%). Bibionidae and Tipulidae (Diptera) larvae, caterpillars (Lepidoptera), Orthoptera, earthworms (Lumbricidae) and snails (Mollusca) contributed 5% of the frequency of occurrence in total diet. In each dropping, the percent composition of volume accounted for by all the invertebrates, apart from cicada larvae, rarely exceeded 1.0. Cicada larvae were found in late spring and summer and, when present, ranged from 12.7% (in 1992) to 47.89% (in 1993) of the faeces volume.

Monthly frequency of occurrence and percentage volume of each food category were highly correlated. Thus, only frequency of occurrence was used in subsequent analyses as it was considered a more objective measure. Spearman rank correlation analyses on frequency of occurrence of seven food items suggested that the use of acorns, olives and, to a lesser extent juniper berries, greatly altered the use of staple foods such as graminoids. Graminoids were negatively correlated with olives ($r = -0.75$, $p < 0.01$), acorns ($r = -0.54$, $p < 0.01$), and juniper berries ($r = -0.39$, $p < 0.05$). This suggested that graminoids were discarded when other food categories were available. Acorns and olives were positively correlated ($r = 0.63$, $p < 0.01$); pine-seeds and fruits, both eaten mainly in summer, were positively correlated ($r = 0.45$, $p < 0.05$). Since most food categories were seasonally available, monthly data were pooled in seasons for subsequent analyses (Table 1).

Spearman rank correlation analyses on frequency of occurrence of seven food items in months and seasons showed that the use of graminoids was related to their seasonal availability in summer and autumn: explained variance (r^2) ranged from 18 to 26% respectively. Pine-seeds, olives, juniper berries and fruits did not show a seasonal pattern in availability that could account for their use. Similarly, the frequency of occurrence of acorns and animals in wild boar diet was not predictable from seasonal availability.

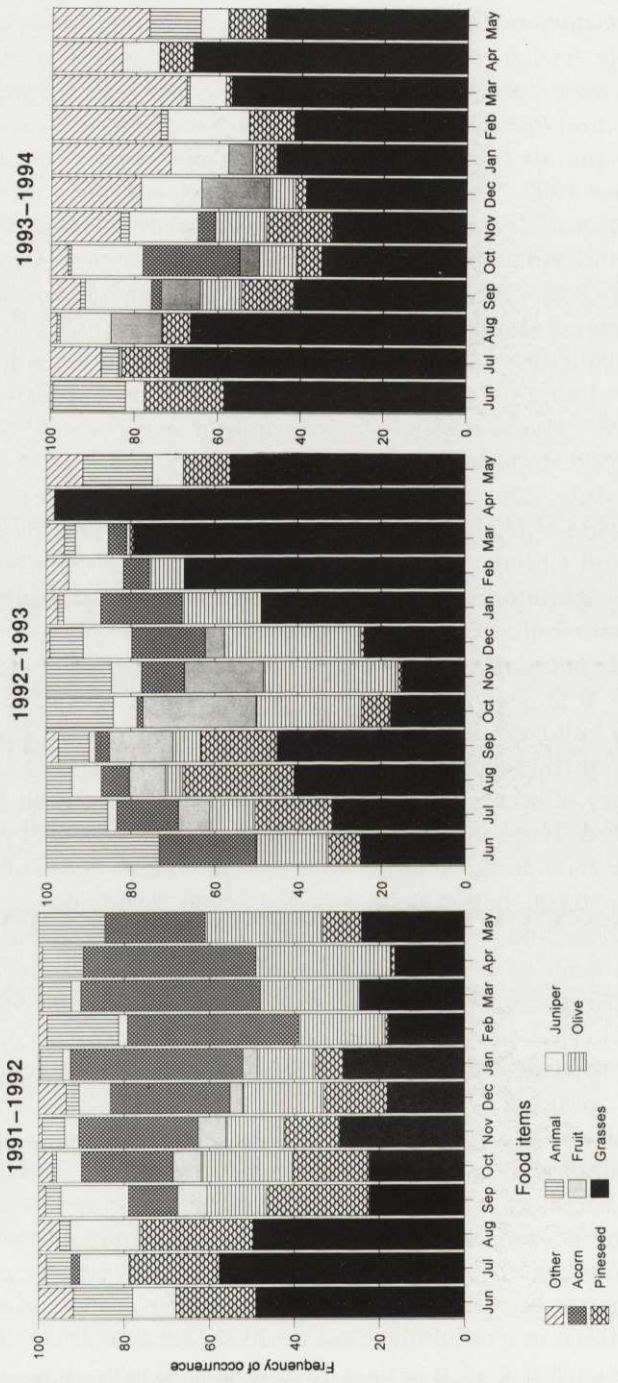

Fig. 2. Monthly percentage frequency of occurrence of food items in wild boar droppings in the MNP in three succeeding years.

Table 1. Seasonal variation of the diet of wild boar in the MNP. Data are expressed as frequency of occurrence.

	Grasses	Pine-seed	Olive	Fruits	Acorn	Juniper	Animal	Other
Summer 1991	0.73	0.41	0.08	0.14	0.07	0.14	0.11	0.07
Autumn 1991	0.55	0.32	0.31	0.14	0.53	0.09	0.06	0.04
Winter 1992	0.51	0.20	0.39	0.06	0.82	0.09	0.16	0.07
Spring 1992	0.50	0.08	0.63	0.00	0.80	0.01	0.25	0.01
Summer 1992	0.78	0.40	0.21	0.17	0.26	0.10	0.30	0.01
Autumn 1992	0.36	0.07	0.65	0.50	0.13	0.14	0.36	0.34
Winter 1993	0.72	0.01	0.33	0.02	0.24	0.17	0.05	0.01
Spring 1993	0.91	0.07	0.01	0.00	0.01	0.08	0.11	0.07
Summer 1993	0.84	0.19	0.05	0.09	0.01	0.13	0.08	0.07
Autumn 1993	0.50	0.15	0.15	0.04	0.22	0.25	0.02	0.14
Winter 1994	0.57	0.08	0.03	0.10	0.00	0.22	0.01	0.34
Spring 1994	0.80	0.09	0.00	0.00	0.00	0.11	0.07	0.35

Acorn use and availability are compared in Fig. 3. Acorn crops varied substantially between years: availability was very high in 1991–1992 (when acorns remained on the ground until May), poor in 1992–1993 and very poor in 1993–1994, when virtually no acorns were found on the ground. Use and availability of acorns were significantly correlated ($r = 0.59$, $p < 0.01$).

Olive availability followed an annual pattern similar to that of acorns, with a large crop in the first year of study and a very poor crop in the last (Fig. 4). Olive use and availability were correlated ($r = 0.53$, $p < 0.01$).

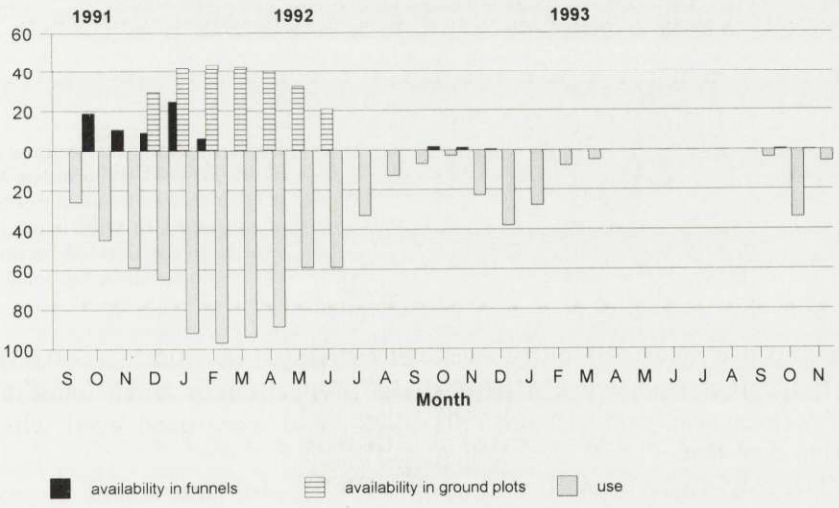

Fig. 3. Monthly acorn use and availability in 1991–1993 in the MNP. Use is estimated as the frequency of occurrence in wild boar droppings, availability is derived by mean number of acorns in funnels and ground plots.

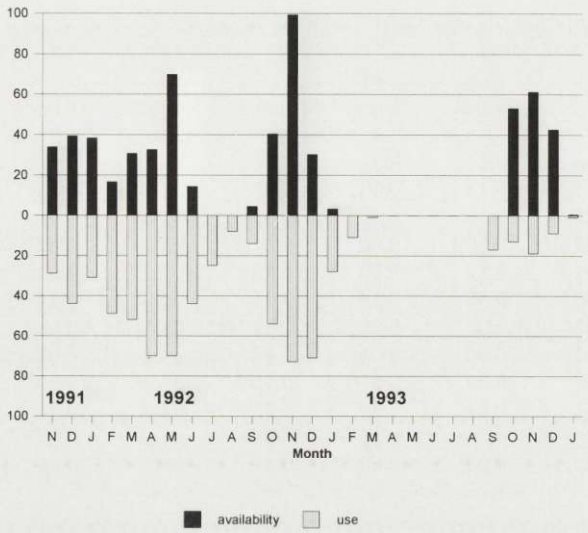

Fig. 4. Monthly olive use and availability in 1991–1993 in the MNP. Use is estimated as frequency of occurrence of olive in wild boar droppings, availability is derived by mean number of olives per funnel.

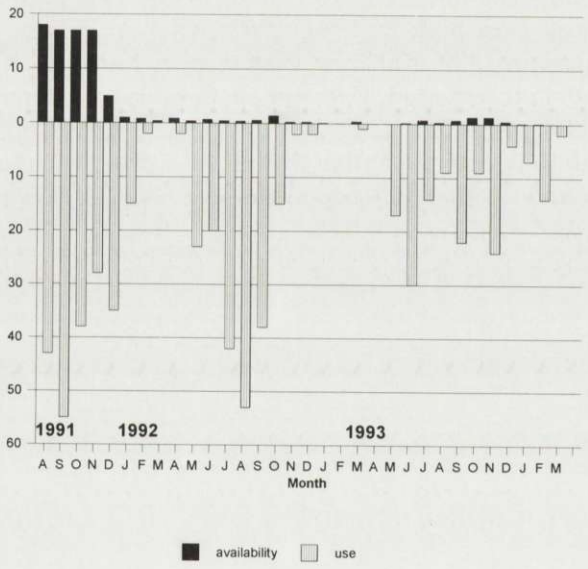

Fig. 5. Monthly pine-seed use and availability in 1991–1993 in the MNP. Use is estimated as frequency of occurrence of pine-seed in wild boar droppings, availability is derived by mean number of pine-seed in funnels.

Pine-seed use and availability were not correlated ($r = 0.21$, $p > 0.05$). Fig. 5 shows that pine-seeds were consumed in proportion to their availability in favourable pine-seed-years (ie in 1991–1992), and were used even when their production was low.

The monthly niche breadth as measured by Levins' index and the evenness measured by Shannon's standardised and Hill's indices are summarised in Fig. 6. Both niche breadth and evenness reached a peak in autumn, showing that the number of food items used was maximum in autumn and that each food category

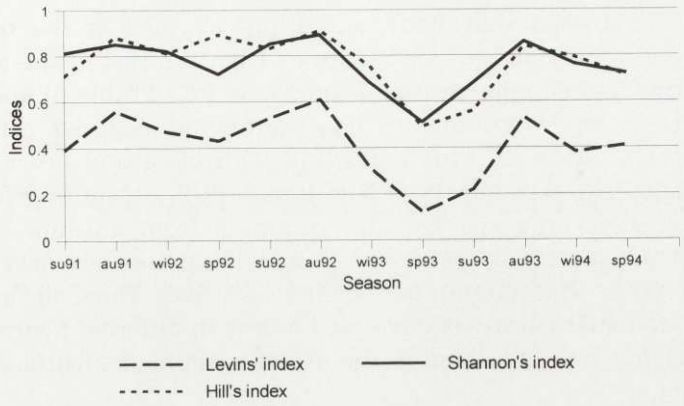

Fig. 6. Niche breadth and evenness indices calculated for the seasonal diet of wild boar in the MNP. Values range from 0 (minimum breadth and evenness) to 1 (maximum breadth: all available resources used to an equal degree). sp – spring, su – summer, au – autumn, wi – winter.

was used to an approximately equal degree. The minimum values for the three indices in spring 1993 reflected the fact that graminoids dominated in the diet of wild boar.

Results from PCA summarized the variation among seasons characterized by different amounts of the food items, and showed that the three principal components accounted for 80.2% of the total variation (Table 2). The scatterplot of the first two principal com-

Table 2. Loadings of food variables on the first three principal components.

	PC1	PC2	PC3
Grasses	−0.44	0.45	0.21
Pine-seed	−0.01	0.21	0.35
Olive	0.57	−0.09	−0.11
Fruit	0.28	−0.44	0.55
Acorn	0.44	0.26	−0.44
Juniper	−0.31	−0.64	−0.08
Animal	0.31	0.23	0.55
% variance	39.1	22.4	18.5
Cumulative %	39.1	61.6	80.2

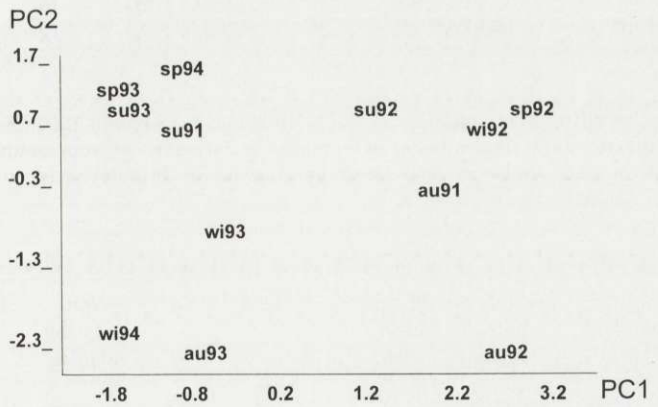

Fig. 7. Scatterplot, on the first two principal components (PC1 and PC2), of the seasonal diet of the wild boar in the MNP in 1991–1994. sp – spring, su – summer, au – autumn, wi – winter.

ponents (Fig. 7) showed that PC1, accounting for 39.1 of the total variance, separated autumn 1991 and all 1992 seasons from the rest of the other seasons. Olive and acorns had similar positive loadings on PC1 (Table 2) and were highly correlated with it, whilst graminoids had the highest negative correlation with PC1. The opposite signs of graminoids and both olive and acorns indicated a negative correlation be- tween these food items. PC2, accounting for 22.4 of the total variance, separated springs and summers from autumns and winters, irrespective of the year. PC2 contrasted graminoids, pine-seeds, acorn and animal (positive) with olive, fruit and juniper berries (negative). Thus, an "annual" factor, mainly due to the different use of olives and acorns in different years, domi- nated a "seasonal" factor mainly related to the use of graminoids, fruits and juniper in different seasons.

Body weight and reproduction

During the three years of study, body weights fluctuated greatly (Table 3). The Kruskal-Wallis test showed significant differences ($p < 0.001$) within male and within female weights in different years. The multiple comparison test showed that males and females in 1992 were heavier than in 1993 and 1994 ($p < 0.05$). Females in 1993 were significantly heavier ($p < 0.05$) than females in 1994. In 1993, during peak mortality (Massei 1995) male and female boar had lost 36% and 17% of the body weight of the previous year respectively. In 1994 males gained 12%, but females lost another 12% of their body weight.

Table 3. Body weight (kg) of adult wild boar trapped in the MNP during summer. Standard error shown in brackets.

Year	Male	*n*	Female	*n*
1992	78.7 (± 1.88)	15	48.0 (± 3.22)	11
1993	53.9 (± 5.04)	10	39.8 (± 1.84)	16
1994	56.8 (± 2.94)	24	35.2 (± 1.80)	12

Table 4. Reproductive patterns of wild boar in the MNP between 1992 and 1994. Numbers in brackets show the percentage out of the total number of females. (a) Data derived from summer trapping. Mean litter size derived from the number of active teats per female. (b) Data derived from field observations between June and August.

(a)					(b)				
Year	*n*	Solitary females	Females with piglets	Mean litter size	Year	*n*	Non lactating females	Lactating females	Mean litter size
1992	154	4 (3%)	150 (97%)	4.4	1992	12	1 (9%)	11 (91%)	4.5
1993	274	223 (82%)	51 (18%)	2.3	1993	22	17 (78%)	5 (22%)	2.4
1994	127	72 (56%)	55 (44%)	3.0	1994	15	10 (67%)	5 (33%)	2.8

Data on reproductive patterns derived by trapping in 1992 and 1994 were in close agreement with those derived from field observations (Table 4). The number of lactating females, as well as the litter size, changed considerably within the three years of study. In 1992, about 90% of the females were lactating and had a mean litter size of 4.5 piglets. In 1993, after a considerable loss body weight (Table 3), only about 20% of the females had piglets, with a mean litter size of 2.4 piglets. In 1994, although the body weight of adult females showed a further decrease, about 35% of the females were lactating, with a mean litter size of 2.8–3.0 piglets.

Discussion

The results of this study showed that, in the MNP, the wild boar use energy-rich foods such as acorns, olives and pine-seeds in relation to their availability. Pine-seeds were consumed even when their production was low possibly because they represented the only energy-rich resource in periods when acorns and olives were absent. When acorns and olives were scarce, an increase in graminoids, forbs and juniper berries was observed: these latter were thus regarded as alternative, less preferred foods. This was in agreement with previous studies (Baber and Coblentz 1987, Groot Bruinderink *et al.* 1994) indicating that in winters with low availability, acorns were replaced by grasses.

When acorns are available a tendency to monophagy would be expected if they could meet the energetic requirements of the wild boar. Acorns are high in carbohydrates and fats (Henry and Conley 1972) that are essential for reproduction and maintenance of good physical condition (Matschke 1964). Moreover, acorns are also highly digestible (McCullogh 1985), but contain little crude protein (Barrett 1978). According to Torrent *et al.* (1962 in cited Barrett 1978), when hogs are feeding heavily on acorns, protein is a major factor limiting efficient body weight gains; this could explain why, as found in this study, they have to counterbalance their diet with animal food or graminoids that are richer in crude protein (Barrett 1978). Olives, rich in lipid content (Pigozzi 1992), could represent an alternative to acorns. In winter 1993–1994, when the availability of olives and acorns was low, these foods were replaced by juniper berries, rich in fats and carbohydrates, though poor in crude protein (Cavani 1989).

The results of this study are in agreement with previous ones indicating that wild boar and feral hogs (also *Sus scrofa*) feed mainly on seasonally available plants, seeds and fruits (eg Wood and Roark 1980, Genov 1981a, b, Briedermann 1986, Dardaillon 1987, Groot Bruinderik *et al.* 1994). In these studies, acorns, beech nuts and chestnuts, as well as cultivated plants (maize, wheat, sunflower, and rice), are indicated as preferred foods by wild boar. This study confirmed the dependence on energy-rich food as being a general characteristic of wild boar throughout their range, irrespective of the habitat and latitude.

Animal food seemed to play a minor role in the diet of boar in the MNP. Cicada larvae and pine-seeds, both rich in proteins and lipids (Clark 1992), might have

provided the protein that in other areas would come from wild boar using higher proportions of animal food. In agreement with this study, Schauss *et al.* (1990), in an area with Mediterranean climate (California), found only traces of insects and no vertebrates in the diet of the local boar.

The heavy use of acorns, olives and pine-seeds, by wild boar, even after these foods become scarce, suggested the potential for this species to reduce their availability for other vertebrates. Acorn crops have a regulatory influence on reproductive success, survival, and body conditions of other mammals, such as squirrels and deer (Goodrum *et al.* 1971, McShea and Schwede 1993). In the MNP fallow deer feed on both olives and acorns (own pers. obs.), and juniper berries represent a staple winter resources for foxes and badgers (Ciampalini and Lovari 1985, Cavallini and Lovari 1991, Pigozzi 1991). Depending on the quantity and quality of food resources for a given year, competition of wild boar with other species such as deer, foxes and badgers could occur in the MNP.

This study found that the diet of boar depends on food items whose availability is not necessarily related to seasons. Consistent differences found in annual diet during the three years of the study suggested that seasons could not be used to predict the diet of boar.

The production of acorns and olives in the MNP was likely to be a major factor influencing the body conditions of wild boar, as well as the number of breeding females and the litter size. This was consistent with previous studies showing food-related differences in natality and mortality and indicating that body weight and reproduction in wild boar are directly related to high energy food (Matschke 1964, Aumaitre *et al.* 1984, Mauget *et al.* 1984, Pepin *et al.* 1987, Gerard and Campan 1988). In the MNP, the lack of high-energy food in winter 1992–1993 could explain the decrease of body weight recorded in 1993 and 1994 and the crash in the boar population which occurred in 1993 (Massei 1995). The low number of females breeding and the relatively small litter size in 1992–1993 possibly reflected low food availability. Similarly, Matschke (1964) and Okarma *et al.* (1995) reported that in poor acorn years pig mortality due to starvation is high and reproduction was low in the following year. In the MNP, acorn, pine-seed and olive production fluctuates considerably between years (Bencini 1992, this study). Since in this area natality and mortality seemed related to the production of these resources it follows that the population dynamics of wild boar is also unpredictable (Massei and Genov 1996, Genov *et al.* 1996). The density of boar, relatively high in 1992 and low in 1993, might also have played an important role, for instance increasing intraspecific competition. The data collected in this study did not allow to separate the effect of density from that of food availability on population dynamics of boar. Long-term studies, where both factors are measured, would be necessary to investigate the relative roles of these two factors.

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