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DIET OF THE WILD BOAR IN THE FRENCH ALPS

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ABSTRACT

In France, as in many other European countries, the wild boar (*Sus scrofa*) population has increased rapidly in the last decade. Since 1990, mountainous areas have been particularly affected by the phenomenon. The growth of the wild boar population has led to an increase in the damage caused to meadows by the rooting activities of the animals. At the same time, little is known about the biology of wild boars in high elevation areas. A three-year study was undertaken to understand relationship between the diet of wild boars and damage to meadows. Diet analyses based on faecal and stomach content samples (n = 352) collected in two years (from April 1994 to April 1996). We observed strong variations in the composition of the diet throughout the year, both monthly and seasonally. All of these effects were related to food availability. Specific analyses of earthworm consumption by wild boars showed the considerable importance of those items in the wild boar diet in mountainous areas. We could not establish a relationship between earthworm consumption and belowground vegetation. Our results suggest that the rooting activities by wild boar are not directed solely toward earthworms.

Key words: annual diet, earthworm consumption, meadow damage, *Sus scrofa*, wild boar.

INTRODUCTION

Foraging behaviour plays a major role in shaping morphology, life history traits, and the ecological role of a species (Sih 1993). Feeding choices are known to affect the reproductive success of females, especially in territorial species (Clutton-Brock 1988, Newton 1989). For example, female *red deer Cervus elaphus* that selected high-quality feeding sites had a higher reproductive rate than females that did not (Iason et al. 1986). From a more practical perspective, studies of food habits are important, both for conservation (Sih 1993) by determining species requirements, and pest management by predicting the effects of animal food consumption on the environment and numerous human activities (e.g. Kruuk and Parish 1981, Low 2001).

Wild boars are ubiquitous rooting omnivores that are known to affect a variety of ecosystems throughout the world by disturbing soil, spreading weeds, preying on invertebrates and small vertebrates, competing with large vertebrates, preventing forest regeneration, and causing damage to agricultural land (Bratton 1975, Genov 1981, Alexiou 1983, Welander 1995). Knowledge of the diet of wild boars in disturbed areas is often required to understand the ecological influences of suid feeding behaviour in critical situations (Chimera et al. 1995). Diet composition based on the analysis of food use by wild boars might help in understanding how animals make relative use of woodland and several field habitats and, consequently, in determining the role of wild boars in these biocenoses and its place within the food chain.

In France, the diet of the wild boar in the hunting season (Douaud 1983, Dardaillon 1984, Sjarmidi 1992) and year-round (Fournier-Chambrillon 1996) has been studied. Most of those studies were performed in various habitats including deciduous forests (Douaud 1983, Sjarmidi et al. 1992), wetland habitats (Dardaillon 1984), and the garrigue of southern France (Fournier-Chambrillon 1996). To our knowledge, there are no reports of the diet of the wild boar in mountainous habitats. In the Italian Alps, near the French border, however, a preliminary study of the diet in autumn has been reported (Durio et al. 1995). Since the early 1990s, wild boar populations have rapidly colonized mountainous areas in parallel with a dramatic increase in the amount of damage occurring in meadows. In particular, the feeding behaviour of wild boars (e.g., rooting in prairies) might lead to economic (costs of meadow restoration, costs of hay harvesting, or visual impact) and biological problems (influences on biodiversity and soil erosion) (Baubet 1998; Hone, 2002). Thus, comprehensive studies are needed to determine the food habits of wild boar in relation to the damage observed in meadows.

The aim of this paper is to describe the temporal variations in the diet of wild boars living in mountainous habitat of the French Alps, where there is no supplemental feeding of wild boars, with an emphasis on the seasonal and elevations effects on patterns food of use. Furthermore, to determine whether earthworm consumption by wild boars is related to damage in alpine meadow (Challies 1975, Scott and Pelton 1975), we focused our attention on the role of earthworms in the diet of wild boars. For that reason, we tested to see whether there was a link between subterranean plant parts and worm consumption at the level of the individual and tested two alternative predictions: that earthworm and belowground matter consumption are mutually exclusive or that these two types of foods occur simultaneously in the diet because wild boars consume worms as they root.

STUDY AREA

The study area is located in the Maurienne Valley (45O45'N, 6O45'E) in southeastern France (Savoie Department). Trapping sites encompassed three communes in the central part of the valley (Figure 1). In the area, vegetation follows a typical mountainous gradation (D'Andrea et al. 1995). Chestnut (*Castanea sativa)* and oak (*Quercus sessiliflora, Quercus pubescens*) woodlands occur at the lower elevations of the valley. Beech (*Fagus sylvatica)* is more abundant at higher elevations and is often mixed with coniferous species (*Abies* sp., *Picea* sp., *Pinus* sp., and *Larix decidua*). Various fruit trees, such as apple (*Malus* sp.), plum (*Prunus* sp.), and cherry (*Prunus* sp.) are also present below 1500m asl. *Sorbus aucuparia* is found at elevations between 1400 m and 1800 m. That upper elevation level ends in shrub vegetation (*Alnus viridis* and *Rhododendron sp*.) and alpine meadows, just below the tree line. Wild boars encounter a typical alpine climate characterized by cool summers and cold winters with light to heavy snowfall depending on the elevation. Mean temperatures increase from January (0.4 ± 2.2 °C) to August (15.0 ± 1.2 °C) and, after a warm peak in summer, decrease steadily until December. Precipitation occurred regularly throughout most of the year, but is more common in spring and fall (mean annual precipitation at an elevation of 1500 m is 740 ± 190 mm, data provided by Météo-France). Moderate to heavy snowfall further characterizes the area in winter. The average snow depth in mid-March at 1400 m asl was 900 mm in 1995 and 210 mm in 1996. Farming practices are mainly sheep and cattle breeding, both of which are intended for meat, milk, and cheese production.

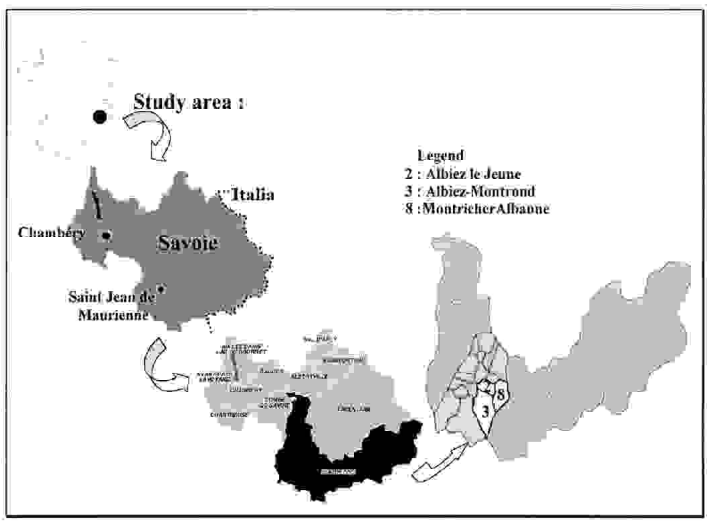

Figure 1. Location of the study area showing its central position in the French Alps.

MATERIALS AND METHODS

Description of the diet

To describe the wild boar diet, we analysed faeces and stomach contents (Putman 1984). Wild boar faeces (n = 304) were collected daily between March 1994 and April 1996, and stomachs (n = 43) were sampled in the hunting period (mid-September to mid-January) in the two years. Faeces were collected at elevations between 600 m and 2400 m asl. Faeces were preserved in a 5% formalin solution and stomachs were frozen at –20°C prior to analysis. All of the faecal and stomach samples were washed over a series of five different sizes of mesh sieves (5 mm, 2 mm, 1 mm, 0.8†mm, and 40 µm), following the procedure described by Fournier-Chambrillon (1996). The solid fraction retained by the 5-mm mesh sieves was completely analysed and dry-weighed. Each plant and animal fragment found was separated and identified to the lowest possible taxon using reference collections established prior to the study. Items were weighed after excessive water was removed using absorbent paper and dried in an incubator for 24 h at 100°C. With fractions ranging in size from 2 mm to 0.8 mm, a similar procedure was followed, but we restricted our analyses to a subsample fraction chosen randomly. Every item extracted was categorized into one of eight food classes: animal matter, corn (available only from artificial feeding, mainly through the use of corn as bait during trapping, and some provisioned by hunters), fleshy fruit, forest fruit, green matter, humus, mushrooms, and roots. The proportion of each food category was calculated using dry-weight measurements. The fraction retained by the 40†µm sieve was used to count the number of earthworm seta, only, which was used to calculate an index of the number of worms ingested (see Baubet et al. 2003).

Seasonal and elevation effects on diet

Each item in the diet is presented as a proportion, hence, they could not be considered statistically independent because the sum of all of the proportions is constrained to the sum of 1. Compositional analysis is a general methodology (see Aitchison 1986), mainly used in ecology analyses of habitat selection (e.g. Aebisher et al. 1993, Pendleton et al. 1998). Consider n proportions describing the proportion of each ingested item, $p_1, p_2, \ddot{O}, p_n$ view as n dependent variables. One can obtain n-1 linearly independent variables using the log-ratio transformation: $q_i = \ln(p_i/p_k)$ where $i\hat{I}[1,n]$, $k\pi i$; results being unrelated to the proportion chosen as the denominator (Aebisher et al. 1993). Then, the relationships between season and elevation and diet composition was explored using a MANOVA procedure, in which the n-1 independent variables (q_i) are the response. Factors introduced into the

model were season (4 modalities: spring, summer, fall and winter), elevation (4 modalities: m1, m2, m3 and m4) and the second-order interaction between both factors. Residual multivariate normality was checked using the diagnostic graphs provided by Splus software (Venables and Ripley 1994).

Earthworm consumption by wild boars

First, we tested for variations in the estimated number of earthworms eaten based on faeces samples. Counts are most often Poisson-distributed; therefore, we used a Generalized Linear Model and a log link, the number of earthworm as the response variable, and month a 12-levels factor. The effect of a factor was tested using a Likelihood Ratio Test (LRT), which corresponds to the difference in deviance between the two models being compared. LRT follows a Chi-Square distribution for which the number of degrees of freedom (df) is calculated as the between-model difference in the number of parameters. Next, to explore the relationship between the number of ingested annelids and roots intake by wild boars, we performed a Spearman rank correlation, and non-linearities were investigated using a Generalized Additive Model (GAM) and a logarithmic link (Hastie and Tibshirani 1990). GAMs rely on a local non-parametric smoothing function that describes the relationship between the number of worms counted in the faeces and the proportion of roots ingested in a more flexible way than do Generalized Linear Models. All of the statistical analyses were performed using the Splus software program (Venables and Ripley 1994). The level of significance was a=0,05 and tests were two-tailed.

RESULTS

General description of wild boar diet

An overview of this three-year study provides a general picture of the average diet composition of wild boars in the French Alps: 99% of the diet was vegetable matter and 1% was animal matter. The most commonly ingested item was the belowground part of plants, mainly roots and bulbs, which represented up to 39% of the diet (Figure 2). Next in importance were fleshy fruit (21%) and aboveground plant material (or green material) (17%). Three of the food classes represented less than 10% of the diet: humus (6%), forest fruit (7%) and corn used to bait traps (8%). The lowest proportion of ingested food was animal matter (1%) and mushrooms (1%, see Table 1).

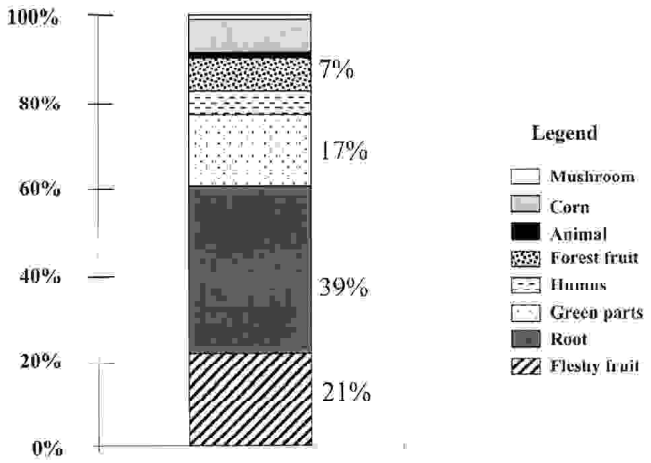

Figure 2. Average composition of wild boar diet in the French Alps as given by the 8 food categories. Diet composition is typical of mountainous suids with roots and fruits (fleshy and forest fruits) being the most represented items. Mushrooms are barely found in faecal samples for this population representing less than 1% of the diet (dry weight).

TABLE 1
Average annual diet composition of wild boar in the Alps Mountain, in the Maurienne Valley from 304 faeces samples and 43 stomachs (from April 1994 to April 1996). The percentage of occurrence shows the proportion of samples among the 352 presenting the specified food item.

	Fleshy Fruits	Roots	Green parts	Humus	Forest fruits	Animal matter	Corn	Mushrooms
% of diet composition (dry weight)	21	39	17	6	7	1	8	1
% of ocurrence	85	97	98	94	30	75	36	32

Seasonal and elevational variation in the diet

There was a significant interaction effect between season and elevation (Wilk's $l = 0,54$, $p < 0,0001$), which indicate that both factors influenced the composition of the diet. The interaction term meant that, for a given season, the diet composition varied differently depending on the elevation. On average, the changes in the diet composition focusing on the seasonal effect showed a clear distinction among all of the seasons (Figure 3). The winter diet was mainly based on roots (61%) and fleshy fruit (15%). Moreover, if we include all fruit items into a single category (fleshy fruit and forest fruit), fruit represented 84% of the overall diet. In contrast, in spring, the most important item was the green part of vegetable matter (33%). Roots (25%) and corn (21%) completed this food category. Obviously, total fruit was at the lowest level in the diet in spring (8%).

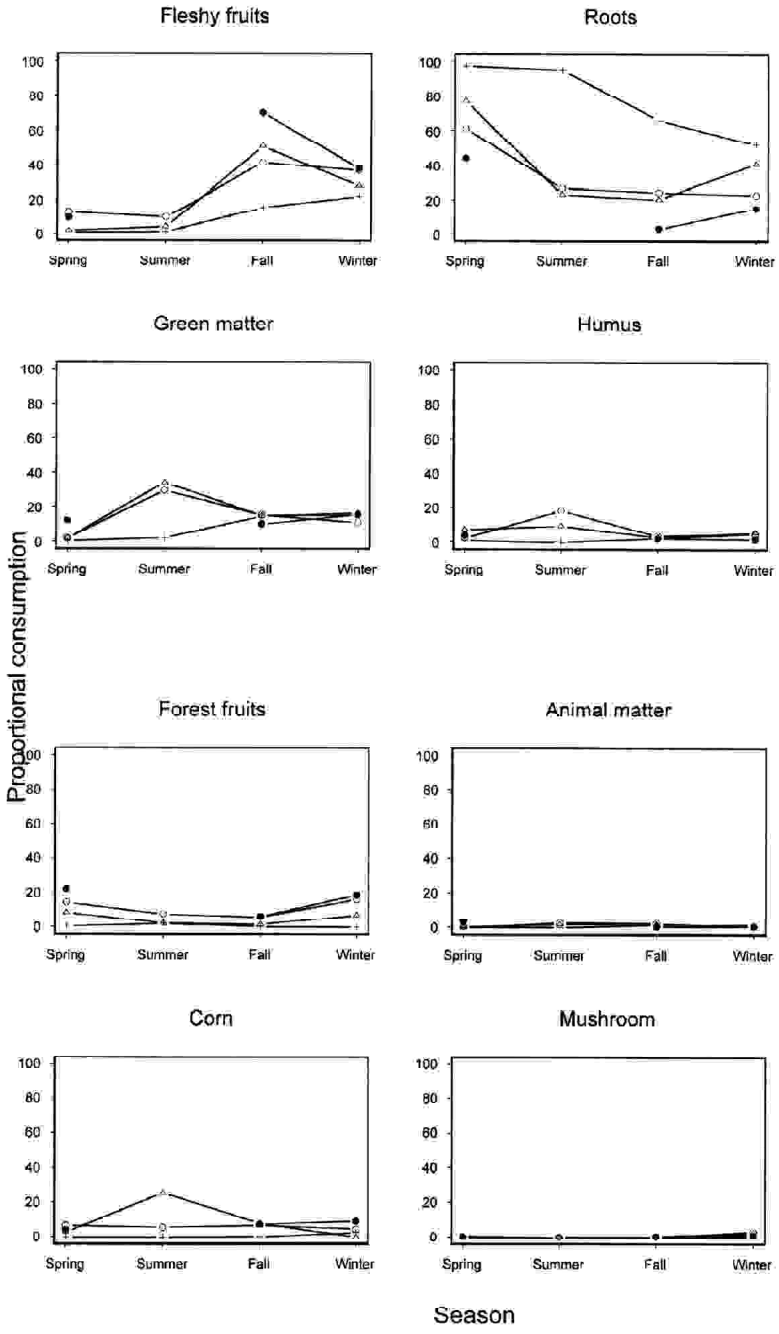

Figure 3. Elevational ([500m-850m[; [850m-1200m[; [1200m-1550m[; + [1550-1900[) and seasonal effects (spring, summer, fall and winter) on the relative use of each food items composing wild boar diet (roots, fleshy fruit, forest fruit, mushroom, corn, green matter, animal matter and humus).

During summer, the predominant items were roots (39%) and fleshy fruit (36%). We all fruit categories are pooled, fruit represented 38% of the diet. Lastly, autumn was the season in which the diet was mainly focused on fruit with, all together, up to 41% of the diet. In that season, the root portion of the diet (33%)was similar to that observed in summer. The main effect of elevation on wild boar diet (Figure 3) can be summarized as follows: root consumption varied between 16% and 38% below 1500 m and steadily increased, up to 71% of the diet above 1900 m. In contrast, the fleshy fruit component of the diet was quite constant up to 1700 m and decreased at higher elevations. Another important point is occurrence of forest fruits, mainly at the first four elevation levels, which represented, on average, 18% of the diet.

Earthworm consumption by wild boars

Earthworm were consumed throughout the year, but varied significantly among months (c_=1632,45, D.F.=11, P<0,0001). The lowest consumption of earthworms occurred in the winter months (from January to March). Those three months did not differ, but consumption in those months was significantly lower than at other times of the year (from April to December; pair-wise multiple comparison test with Fisher's Least Square Deviation method; Figure 4). There was a negative correlation between the consumption of worms and roots (r = -0,199, Z = -3,46, P = 0,005), although GAM models provided evidence for non-linearity, showing that the possible link between the two types of items might occur only when large amounts of roots are ingested (Figure 5).

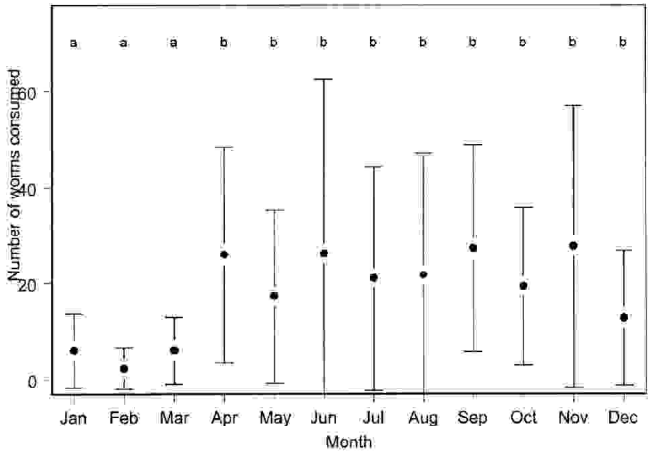

Figure 4. Monthly variations in the number of earthworm ingested by wild boar (EMBED Equation.3) from January to December in the French Alps. A significant effect of month was found (Generalized Linear Model with a log link: c_=1632,447, D.F.=11, P<0.0001). Letters indicate means that are statistically different by computing a pair-wise multiple comparison test.

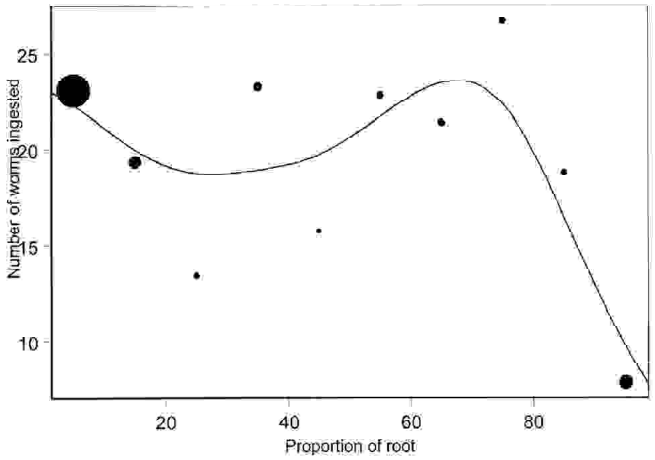

Figure 5. Relationship between the number of ingested worms and the proportion of roots composing the faeces (r = -0.199, Z = -3,463, P = 0.005). The solid line is the smoothed curve predicted by the Generalized Additive Model showing the non-linearity of the relationship. Dot size is proportional to sample size.

DISCUSSION

The wild boar diet in the French Alps shows a typical food pattern expected from an omnivorous mammal in which vegetal matter comprises about 99% of the diet. The most important items ingested were roots and bulbs, which represented 39% of the total dry weight of items. Such a diet is consistent with previous studies of wild boars in mountainous areas. Scott and Pelton (1975) reported that in the Great Smoky Mountains National Park (U.S.A.) a similar diet composed of 99.1% of vegetal matter, with roots being the major plant food consumed (44.3%). Roots are a readily available and abundant food resource that has been shown to be the major item in the diet of wild boars at high elevations (Challies 1975). Some studies, however, have shown differences in the diet of wild boar with herbaceous and aerial part of plants as the diet bulk (Howe et al. 1981), but roots were the second most commonly consumed food item (55.3% represented by aboveground parts of herbaceous plants and 40.2% by roots, n = 47). Our study confirms that roots and bulbs are staples in the wild boar diet in mountain range such as the french Alps. That contrasts sharply with Mediterranean habitats, where the diet of wild boars is mainly based on fruit (Wood and Roark 1980, Fournier-Chambrillon et al. 1995, Massei et al. 1996) and with agricultural land, where food habits essentially depend on cultivated crops, such as corn, wheat, or potatoes (Genov 1981). Nevertheless, we found that, as soon as fruit is available, and especially forest dry fruits (acorns, chestnuts, beechnuts, nuts), they are attractive to wild boars and are an important

part of the diet. Such a preference for fruit is well described and has been integrated into the food- preference scales that have been developed (Vassant 1997). Because fruits availability is seasonal, fruits contribute strongly to the marked seasonality found in the diet of the wild boar, which also depends on the availability of other food items. Such effects have been documented, especially for wild boar, in a variety of habitats (Challies 1975; Scott and Pelton, 1975; Wood and Roark, 1980; Howe et al. 1981, Fournier-Chambrillon et al. 1995; Massei et al. 1996). Moreover, with the seasonal variation in diet, we found a strong effect of elevation on the diet, as was reported in another study (Challies 1975) or from studies performed in the same field, but at different elevations (Henry and Conley 1972; Scott and Pelton 1975, Howe et al. 1981). The change in food resource use with increasing elevation indicates that wild boars adapt their diet to the vegetation succession and stratification that occurs along an elevational gradient. Our results show that the more wild boars feed at high elevations where pastures mainly occur, the more subterranean part of plants are important in the diet. It appears that the wild boar has a highly plastic diet that surely contributes to the species' wide geographic distribution and its strong ability to colonize a wide variety of habitats.

As emphasized in several studies of the food habits of the wild boar (Challies 1975; Scott and Pelton, 1975; Wood and Roark, 1980; Howe et al. 1981, Fournier-Chambrillon et al. 1995; Massei et al. 1996), earthworm consumption is a constant always reported in its diet likely because of its high protein content. In some extreme cases, annelid worms were the most important animal food eaten by wild boars (Challies 1975, Asahi 1995). In our study, wild boars consumed earthworms year-round, but with a significant decrease in the winter months, which is likely due to reduced availability. During winter, earthworms are less accessible for wild boars because of snow cover. Moreover, worms remain inactive because of cold temperatures and are probably buried more deeply in the ground. Indeed, when specific weather conditions are combined (worm-nights: temperature around 10°C and rains during previous days, see Baubet et al. 2003 for details), wild boars significantly increase consumption of worms (Baubet et al. 2003). In addition, we found a negative correlation between subterranean foods and worm consumption, which could be interpreted as a burrowing response by worms in reaction to rooting perturbations. It could also be viewed as a shorter rooting time when worms are available on the surface. Alternatively, the negative relationship between roots and worms in the diet also suggests that annelid worms might be preferred over roots or that earthworm consumption might not always involve rooting activities. Indeed, it has been established that an increase in rooting often correlates positively with an increase in the consumption of roots and bulbs, especially in winter (Scott and Pelton, 1975;

Genov 1981, Baron 1982). We observed an increase in roots and bulbs in the diet in the winter months. Rooting is the only way to obtain such food items. Simultaneously, the winter corresponds to the lowest level of worms ingestion, even rooting activities should occur. However, it should be considered that turning the ground could be a way for wild boars to get worms, but it might not be the most efficient way.

Wild boars are considered a pest in many countries because of their feeding activities, which can lead to crop damage (Choquenot et al. 1996, Schley, 2003). The wild boar is a really challenging species for landscape management decisions with regard to meadow damages that increase the likelihood of soil erosion and involve economical compensation. If we assume that the observed diet accurately reflects the wild boar foraging strategy, then two alternative interpretations have to be considered. (1) A strict correlation between diet and available food items leads to consumption by default or (2) a qualitative interest in the food resource leading to a preferential consumption. In both cases, the solution consisting in distributing preventive food supply to reduce meadow damage would need to identify mechanisms controlling food directed decisions efficiently. Indeed, food supply should be targeted in space and/or time to prevent or reduce significant pasture damage. Further experimental investigations elucidating relationships between diet and the process of meadow damage are needed to gain a better understanding of the proximate mechanisms leading to prairie rooting.

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