CSIRO PUBLISHING

www.publish.csiro.au/journals/wr *Wildlife Research*, 2003, **30**, 179–186

Seasonal and annual variations in earthworm consumption by wild boar (*Sus scrofa scrofa* L.)

E. Baubet[A,C], *Y. Ropert-Coudert*[B] *and S. Brandt*[C]

[A]Chugoku National Agricultural Experiment Station, Department of Animal Production, Yoshinaga 60, Oda,
Shimane 694-0013, Japan. Present address: Office National de la Chasse et de la Faune Sauvage,
1 Place Exelmans, 55000 Bar le Duc, France.
[B]National Institute of Polar Research, 1-9-10 Kaga, Itabashi-ku, Tokyo 173–8515, Japan.
[C]Office National de la Chasse et de la Faune Sauvage, CNERA Cervidés-sanglier, 85 bis,
avenue de Wagram, 75017 Paris, France.

Abstract. We investigated the annual and monthly patterns of earthworm consumption by wild boar in the Maurienne valley (Alps, France). A positive correlation ($R^2 = 0.79$) was found between weather conditions and patterns of earthworm consumption. A positive correlation was also found between earthworm consumption rates and the occurence of 'worm nights', an easy and direct measure of earthworm availability.

Introduction

Earthworms represent a substantial proportion of the animal biomass in temperate ecosystems, often reaching 41.8 kg ha^{-1} and corresponding to 45% of the metazoan biomass in the soil (Bouché 1982). They play a key role in the trophic chains of a given ecosystem, where they represent a significant part of the diet of a large number of vertebrates, from small insectivores (e.g. the hedgehog, *Erinaceus europaeus*) to large carnivores (e.g. the brown bear, *Ursus arctos*) (see Granval and Muys 1995 for review). On the basis of the frequency of occurrence (FOC) of earthworms in their diet, earthworm consumers have been classified as occasional (FOC < 10%), regular (10% < FOC < 50%), or primary (FOC > 50%) predators. According to this classification, the European wild boar (*Sus scrofa scrofa*) is defined as a regular predator of earthworms (Granval and Muys 1995); this has been confirmed by dietary studies of wild boar in a variety of habitats (Table 1). Estimation of the dietary occurrence of earthworms has often been achieved by counting or weighing earthworm fragments in stomach or faecal samples; this method has been shown to underestimate the actual number of worms ingested (Baubet *et al.* 1997). The counting of earthworm setae (Bouché *et al.* 1984; Wroot 1985) in stomach or faecal samples has proved to be a more reliable estimator of earthworms consumption rates by wild boar (Baubet *et al.* 1997). Many studies have assumed that wild boar or feral pigs obtain earthworms by rooting or digging within the soil profile (Scott and Pelton 1975; Bratton 1977; Barrett 1978). Large areas of soil may be disturbed by a single feral pig, e.g. 1.4–150 m^2, as found in tropical coastal rainforests in Australia (Pavlov and Edwards 1995). Climate, especially rainfall, is known to have a strong influence on the abundance and accessibility of earthworms on ground surface favourable to earthworm predator (MacDonald 1980; Kruuk and Parish 1981; Bouché 1982). Some authors have reported an increase in earthworm activity, especially movements at the ground surface, after heavy rainfall (MacDonald 1980; Bouché 1982). Earthworm consumption may represent a substantial parameter of wild boar ecology as earthworms contain high levels of dietary protein that are important to the development of piglets and the young during their growing stage (Henry 1987; Choquenot *et al.* 1996). Earthworm consumption may influence the growth and mortality rate of piglets and influence the age of sexual maturity (Mauget 1982). In addition, earthworms are intermediate hosts of parasitic lung nematodes, and ingestion of earthworms may increase the level of parasitism, which may affect the survival rate of wild boar (Humbert and Henry 1989). The aim of this study was to assess whether weather conditions, especially those known to affect the accessibility of earthworms, influence the rates of earthworm consumption by wild boar in a mountainous area in France.

Material and Methods

Study area

The study area was located in the southern part of the Maurienne Valley, French Alps, France (45°45′N, 6°45′E). Meteorological conditions in the valley are characterised by low precipitation with the surrounding mountains creating a rain-shadow effect. A mean annual precipitation of 740 ± 190 (s.e.) mm was recorded between January 1986 and May

10.1071/WR00113 1035-3712/03/020179

1996 (data provided by a meteorological station of Météo-France, altitude 1500 m). Average temperatures in this period ranged from –0.4°C (s.e. ±2.2°C) in January to 15.0°C (s.e. ±1.2°C) in August. Vegetation shows a typical mountainous gradation (D'Andrea *et al.* 1995), with chestnut (*Castanea sativa*) and oak (*Quercus* sp.) woods in the lower part of the valley. Beech (*Fagus sylvatica*) is more abundant at higher elevation 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 1500 m. *Sorbus aucuparia* is found between 1400 and 1800 m. This upper zone ends in shrub vegetation (*Alnus viridis* and *Rhododendron* sp.) and alpine meadows, just below the rock limit. Livestock (cows, sheep and goats) graze in alpine prairies from late May to early November.

Methods

Faeces of wild boar were collected daily from March 1994 to April 1996 (Table 2), adjacent to wild boar trapping sites and on transects used during radio-tracking surveys. Faecal samples were also collected opportunistically in the various habitats within the study area. Tracks of wild boar were followed and faeces collected near signs of recent boar activity (rooting activity, fresh wallowing places, etc). Only clearly delimited faeces were collected so each faecal sample could be assumed to derive from one individual (Lynes and Campbell 2000). Stomach samples were also removed from wild boars killed during the hunting season (mid-September to mid-January), except during periods of heavy snowfall. Stomach samples from three animals accidentally killed outside of the hunting season (February and May) were also collected (Table 2). All faecal and stomach samples were collected at altitudes of 600–2400 m. Soft tissues of invertebrates are rapidly digested, so only the hard setae of earthworms can be identified in the faeces and in stomach samples (Baubet *et al.* 1997). All faecal and stomach samples were washed though a series of five sieves of different mesh-size (5 mm, 2 mm, 1 mm, 0.8 mm and 40 µm) following the method described by Fournier-Chambrillon (1996). In this study, only the fraction retained by the 40-µm sieve containing the earthworm setae was counted. Following sedimentation for 24 h in graduated test tubes, the 40-µm fraction was diluted in a 20% water solution. Sub-samples of 0.5 mL were extracted, mixed with 9.5 mL of water, placed in a cup containing a counting grid under a microscope (×40) and all setae counted. The total number of setae in the solution was defined as the mean number of setae obtained from six successive counts. The total number of ingested earthworms (M) was then estimated using the formula derived by Bouché *et al.* (1984) as:

$$M = 1077N / 8000n$$

where N is the number of setae in the sample (20% solution) and n is the average number of metameres per earthworm in the study area; in our case $n = 125$ (Baubet *et al.* 1997).

The influence of weather conditions on the rate of earthworm consumption was assessed using four different statistical approaches:

(i) First, the amount of earthworm consumption measured in stomach and faecal samples was compared between months for each year of the study. Sample data did not follow a normal distribution even

Table 1. Importance of worms in the diet of wild boar across a variety of habitats

Habitat	% earthworms in diet	Reference
Mountain forest, south Appalachian Mts, USA	<5.4% by volume	Henry and Conley (1972)
Subantarctic Auckland I.	28% on high country, 1% on the coast by dry weight	Challies (1975)
Mountains with forest area of complex vegetation pattern, GSMNP, Tennessee side, USA	<0.2% by volume	Scott and Pelton (1975)
Coastal conifer/hardwood swamp, southern California, USA	<3% of dry weight	Wood and Roak (1980)
Agricultural land/woodland, north-eastern and western Poland	<16% frequency of occurence	Genov (1981)
Lava and dry tropical woodland, Santiago I., Galapagos	20% of 81 pigs	Coblentz and Baber (1987)
Scrubland/oak forest, Algeria	26% frequency of occurence	Klaa (1992)
Subantarctic Auckland I.	26.3% by dry weight	Chimera *et al.* (1995)
Maquis scrubland/mediteranean coniferous forests, central Italy	<5% frequency of occurence	Massei *et al.* (1996)
Mountain forest/alpine meadows, Alps Mts, France	87.5% of 48 wild boar	Baubet *et al.* (1997)

Table 2. No. of faecal and stomach samples collected during each month of the study period

	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Faecal samples													
1994	–	–	1	3	5	35	12	17	28	12	29	6	148
1995	1	8	6	12	6	8	3	12	10	12	14	0	92
1996	13	19	22	10	–	–	–	–	–	–	–	–	64
Total	14	27	29	25	11	43	15	29	38	24	43	6	304
Stomach samples													
1994	–	–	–	–	–	–	–	–	6	10	5	3	24
1995	–	–	–	–	1	–	–	–	4	5	3	6	19
1996	4	1	–	–	–	–	–	–	–	–	–	–	5
Total	4	1	–	–	1	–	–	–	10	15	8	9	48
All samples	18	28	29	25	12	43	15	29	48	39	51	15	352

Table 3. Meteorological conditions required to define the two 'worm night' conditions used in this study

WN1: first case	WN2: second case
Maximum temperature reaches 8–12°C (10°C is considered the optimum temperature for earthworm activity: Kruuk and Parish 1981; MacDonald 1980)	Maximum temperature reaches 8.5–14.5°C (10°C is considered the optimum temperature for earthworm activity (Kruuk and Parish 1981; MacDonald 1980) and Abdul Rida (1995) experimentally defined 14°C as the optimal temperature for activity of *Lumbricus terrestris*)
Minimum temperature does not drop below 0°C (Kruuk and Parish 1981)	Minimum temperature does not drop below 0°C (Kruuk and Parish 1981)
Precipitation must have exceeded 2 mm during the previous 72 h (Kruuk and Parish 1981) *or* 1 mm during the previous 24 h (Kruuk and Parish 1981) *or* more than 10 mm during the night or days (arbitrary decision according to MacDonald 1980)	Precipitation must have exceeded 2 mm during the previous 72 h (Kruuk and Parish 1981) *or* 1 mm during the previous 24 h (Kruuk and Parish 1981) *or* more than 10 mm during the night or days (arbitrary decision according to MacDonald 1980)

after arcsine transformation. Monthly and annual variations in earthworm consumption were tested using Kruskal–Wallis and Mann–Whitney tests, respectively, following the procedures recommended by Sokal and Rohlf (1969).

(ii) Second, a principal component analysis (PCA) was performed on nine climatic variables in order to summarise the monthly weather characteristics into synthetic variables. Differences in earthworm consumption were tested by a one-way ANOVA with Bonferroni/Dunn *post hoc* tests (Sokal and Rohlf 1969). Simple and multiple regression analysis was then used to investigate the relationship between average earthworm consumption and the synthetic weather conditions determined by the PCA. An AIC (Akaike Information Criterion) method was used to select the regression model that offered the best compromise between robustness and accuracy (Atkinson 1980; Anderson *et al.* 2000). In order to account for the small sample size in linear regression, a corrected criterion (AIC_c) was used (see Hurvich and Tsai 1989 for details). The regression model that exhibited the lowest AIC_c value was selected (Atkinson 1980) and the difference between the AIC_c values (ΔAIC_c) of the different models are reported to facilitate interpretation following Burnham and Anderson (2001).

(iii) The monthly mean number of earthworms ingested was related to monthly earthworm accessibility, defined as the percentage of 'worm nights' during each month (Kruuk and Parish 1981). A 'worm night' is defined where specific meteorological conditions favour the presence of large nocturnal populations of earthworms at the ground surface (McDonald 1980; Kruuk and Parish 1981). For a given month, increasing rates of worm consumption are expected when the percentage of 'worm nights' is also increasing. In this study, two types of 'worm nights' were defined (WN1 and WN2) on the basis of climatic conditions (Table 3). The relationship between the mean monthly earthworm consumption and the percentage of 'worm nights' per month was tested using simple regression analysis. To account for monthly differences in the number of individuals used to calculate the average earthworm consumption, $1/\sigma^2$, where σ^2 is the variance, was used as a weighting for the regression (Burnham *et al.* 1987).

(iv) Earthworm consumption was compared at a finer temporal scale by using the data for which the exact date of faecal collection was known, i.e. faeces collected directly from the rectum of a dead animal or faeces in traps from individuals captured during the previous night-trapping session. The rate of earthworm consumption found from the faecal samples was compared using multiple regression with meteorological conditions (minimum and maximum temperature, and precipitation) observed during the day (compared with trap samples) or the day before (compared with samples from dead animals). The correlation between earthworm consumption as determined from faecal and stomach samples (obtained from dead individuals), which was considered to represent two consecutive meals, was tested with a Spearman Rank correlation test. Although transit time in the intestine is dependent on the composition of the ingested food (Loungouedi 1989), a transit time of 24 h was selected so earthworm consumption could be compared with the daily weather report.

Results

In total, 304 faecal and 48 stomach samples were collected. The frequency of occurrence of earthworms in the stomach and faecal samples was 87.5% and 93.8%, respectively. Earthworms were found in faecal samples throughout the study period (Fig. 1*a*). Rates of earthworm consumption from faecal samples varied significantly between months for

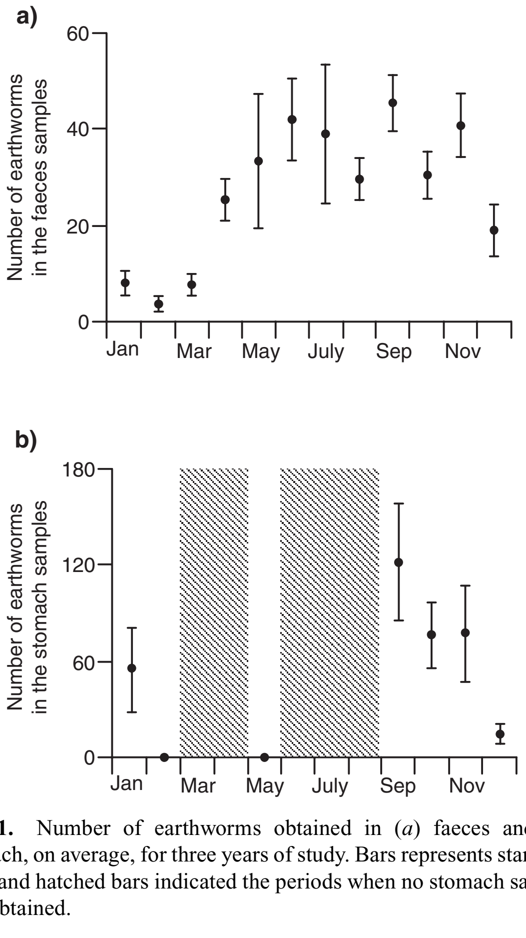

Fig. 1. Number of earthworms obtained in (*a*) faeces and (*b*) stomach, on average, for three years of study. Bars represents standard error and hatched bars indicated the periods when no stomach sample was obtained.

1994 (H = 26.65, P = 0.003), for 1995 (H = 23.71, P = 0.005), and for 1996 (H = 27.13, P = 0.0001). Overall, earthworm consumption generally increased in spring, reaching a maximum in summer and autumn, and then decreased during winter. In contrast, earthworm consumption determined from stomach samples (Fig. 1*b*) showed no significant differences in rates of earthworm consumption between months for 1994 (H = 7.09, P = 0.07) or for 1995 (H = 1.77 P = 0.62) and between the two years of the study (Z = –1.36, P = 0.17). In addition, the pattern of consumption determined from the stomach samples was generally consistent with the trend observed in the faecal

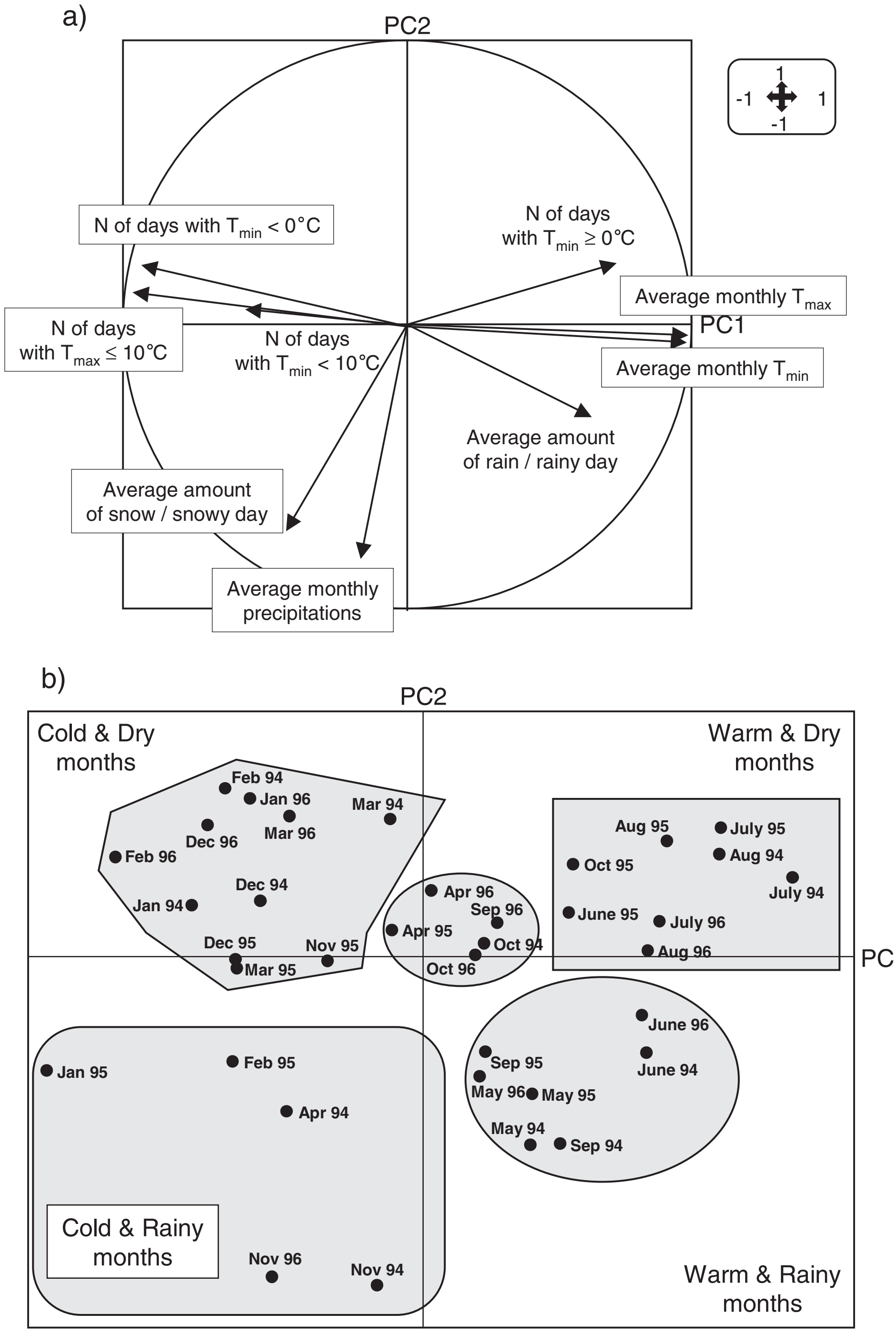

Fig. 2. (*a*) The correlation circle of PCA analysis on factorial plan 1–2. (*b*) Factorial plan 1–2 is used to define weather group conditions as follows: CD = cold and dry months, CR = cold and rainy months, WD = warm and dry months, WR = warm and rainy months. The last category, in the middle of factorial map, is defined as M = medium months.

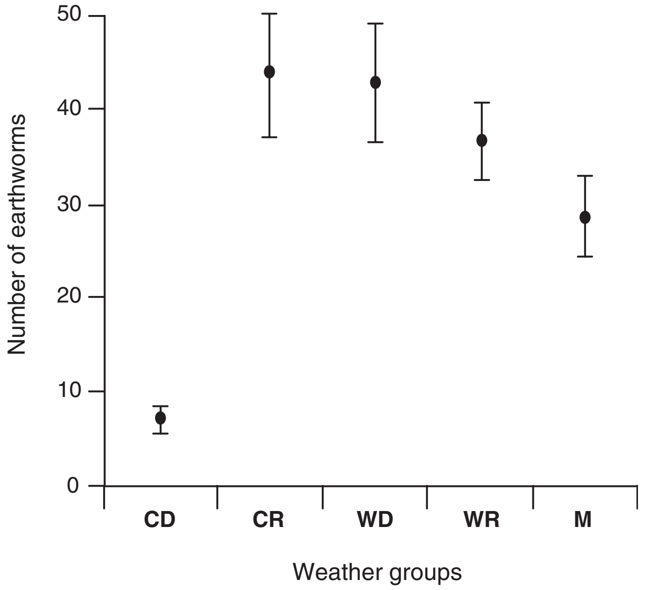

Fig. 3. Differences in earthworm consumption among the five monthly categories determined using the PCA analysis (see Fig. 2). CD = cold and dry months, CR = cold and rainy months, WD = warm and dry months, WR = warm and rainy months, M = medium months. Bars represents standard errors.

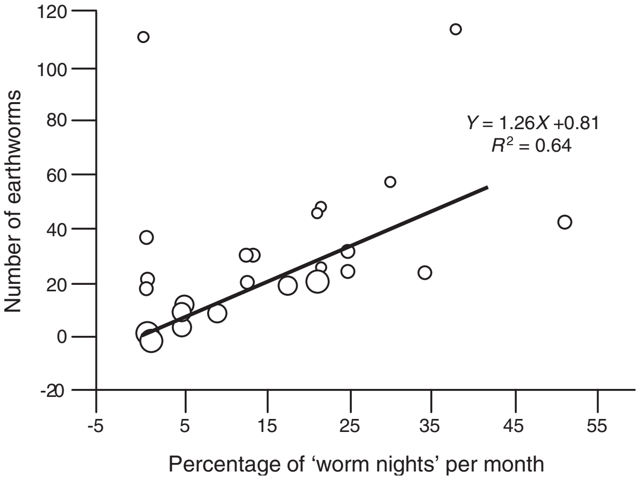

Fig. 4. The relationship between the consumption of earthworms and the percentage of 'worm nights' per month. The size of each data point indicates the influence of that point on the weighted regression (small point = small influence).

samples. The first two axes of the PCA analysis explained 75% of the total variability between monthly climatic conditions, showing a temperature gradient (PC1) along the first axis and a precipitation gradient (PC2) along the second axis (Fig. 2*a*). Thus, PC1 and PC2 were used as synthetic variables in simple and multiple regression models. On the basis of the values of the AIC_c, the multiple regression (PC1 + PC2: $AIC_c = -19.4$) was preferred to the simple regressions (ΔAIC_c (PC1 + PC2) / (PC1) = 8.6; ΔAIC_c (PC1 + PC2) / (PC2) = 21.5) since it explained ~79% of the relationship between earthworm consumption and monthly weather conditions ($Y = 3.55*PC1 - 4.60*PC2 + 19.06$, $R^2 = 0.79$, $F_{2,20} = 38.63$, $P < 0.0001$). The synthetic variables PC1 and PC2 were negatively correlated, high earthworm consumption is expected during warm and dry months and minimum worm consumption expected during cold and wet months. Heavy precipitation and cold temperatures during the winter months in mountainous areas reduce the accessibility of soil to wild boars. Following the PCA results (Fig. 2*b*), months were re-arranged into five weather groups: cold and rainy, cold and dry, warm and rainy, warm and dry, and intermediate months. A significant difference in earthworm consumption was found between these five weather groups ($F_{4,299} = 10.64$, $P < 0.0001$): earthworm consumption during cold and dry months was significantly lower than during all of the other weather categories (Fig. 3). A significant linear relationship was found between the two types of 'worm nights' and earthworm consumption ($F_{1,21} = 36.73$, $P < 0.0001$) for WN1and ($F_{1,21} = 27.75$, $P < 0.0001$) for WN2 (Fig. 4). Earthworm consumption and earthworm availability was linearly related for both WN1 ($F_{1,8} = 6.93$, $P = 0.03$) and WN2 ($F_{1,8} = 5.94$, $P = 0.04$) in 1995 and for WN1 ($F_{1,2} = 86.3$, $P = 0.01$) in 1996, but not for 1994 (WN1: $F_{1,7} = 0.01$, $P = 0.92$; WN2: $F_{1,7} = 0.33$, $P = 0.58$) and WN2 ($F_{1,2} = 2.07$, $P = 0.29$) in 1996.

None of the regression models accounted for a significant relationship between earthworm consumption and weather conditions when the exact sample collection date was known. However, within individuals, the numbers of earthworms in the stomach and in the faeces were positively and significantly correlated (Z = 2.28, $P = 0.02$).

Discussion

This study demonstrated that earthworms are consumed by wild boar in all seasons of the year. Earthworms accounted for 92% of the diet by frequency of occurrence; wild boars can therefore be categorised as primary predators of earthworms, as proposed by Granval and Muys (1995). This is further supported by recent dietary studies, carried out in France, that found the frequency of occurrence of earthworms in the diet to be greater than 50% (where earthworms were available) (Fournier-Chambrillon *et al.* 1995; Fournier-Chambrillon 1996). The pattern of consumption of earthworms in mountainous areas differed slightly from that observed in the vineyards–guarrigue habitat where no worms were consumed between June and September, possibly due to low soil moisture tending to reduce earthworm availability (Fournier-Chambrillon *et al.* 1995; Fournier-Chambrillon 1996). However, the peak in earthworm consumption in autumn that was found in this study is similar to that reported in the vineyards–guarrigue habitat. Differences in local tree composition between these two habitats may explain the differences in abundance and availability of earthworms (Bouché 1982; Granval and Muys 1992). Similarly, as meadow habitats have the highest earthworm concentration, 137 kg ha^{-1}, or 71% of the metazoan population of the soil (Bouché 1982), the proportion and type of meadows in the study area may be a crucial parameter for determining the importance of worm consumption, especially as meadows represent more than 60% of the habitat type at altitudes over 1700 m. A number of studies have assumed that invertebrates, especially earthworms, are ingested by wild boars/feral pigs during rooting activity (Challies 1975; Scott and Pelton 1975; Bratton 1977; Barrett 1978; Shaffer 1979; Pavlov and Edwards 1995; Mitchell and Mayer 1997). However, the significant relationship between earthworm consumption and the measure of earthworm availability ('worm nights') found in this study suggests that earthworm consumption may not always involve rooting activities. The positive correlation of earthworm consumption between two consecutive meals supports the suggestion that earthworm consumption is mainly opportunistic (does not involve rooting), and that wild boar forage for earthworms during weather conditions suitable for earthworms to be on the soil surface, thereby enhancing their capture rate. Wild boars may also modify their foraging behaviour to select feeding areas such as meadows or prairies where earthworm numbers are high. This suggestion is untested; no studies have been conducted to identify feeding areas used by wild boar during particular weather conditions. However, Kruuk and Parish (1981) showed that worms are more abundant at the soil surface in summer and autumn. This peak in abundance corresponds to the peak of earthworm consumption by wild boars in our study, reinforcing the idea of an opportunistic foraging behaviour.

Confounding influences in this study were, first, the 'worm night' conditions were defined for *Lumbricus terrestris* only (Kruuk and Parish 1981), and may not reflect the availability of all earthworm species found in this study site. However *L. terrestris* was often present in our samples associated with other species such as *L. rebellus*. Second, various factors that may influence earthworm consumption were not included in the definition of the 'worm night' model. Temperature changes with altitude, altitude, wind and grass height are known to modify the availability, the activity and/or the prehensility of earthworms (see MacDonald 1980; Kruuk and Parish 1981; Baubet *et al.* 1997). These parameters were not taken into account for analysis, which may reduce the value of this model in the case of mountainous areas. The seasonal vegetation growth, the period of hay production and the seasonal movement and rotation of cow pastures would modify the proportion of short-grass meadows, where prehensility of earthworms should be higher (Granval *et al.* 1993). These limitations may explain why the monthly weather conditions, calculated by the PCA, explained a higher proportion of the earthworm consumption than the 'worm night' conditions. These differences may be the expression of periods when climatic conditions are not optimum for worms to ascend to the surface, but when the soil is wet enough to allow wild boars to root (Kotanen 1994, 1995; Fournier-Chambrillon *et al.* 1995; Mitchell and Mayer 1997). For example, wild boars can forage in cattle manure piles in pastures, apparently searching for earthworms or other invertebrates (Scott and Pelton 1975), which are known to accelerate the disappearance of dung (Hirschberger and Bauer 1994*a*, 1994*b*). Similarly, wild boar diggings up to 40 cm deep have been observed in zones where epilobes (*Epilobium angustifolium*) occur. Although earthworms are not as abundant in these zones as in meadows (Baubet *et al.* 1997), earthworms may be ingested during the process of diggings for bulbs or roots.

Earthworm consumption may also have important consequences for wild boars because of such factors as parasitism and dissemination of diseases that may indirectly influence wild boar demography. Previous studies have reported on the high rate of parasitism of wild boar by lung nematodes (Humbert and Henry 1989), of which earthworms are an intermediate hosts. The high nutritional value of earthworm (see Pavlov and Edwards 1995), especially the high lysine content (an essential amino acid for body growth in pigs), suggest a difference in the rate of earthworm consumption between young and adult wild boars in order to cover the needs of growing animals (Noblet *et al.* 1987; Henry *et al.* 1992). Young wild boars are thought to ingest a higher number of earthworms than the adults and generally show a higher level of parasitism than that of adults (Humbert and Henry 1989), this being amplified by the lack of immunity in juveniles. The lack of immunity of piglets to infection by lung nematodes may influence wild boar demography, either directly through mortality (Massei *et al.* 1997) or indirectly through fecundity (age at sexual maturity, litter size and weight), which is related to body condition (Mauget 1982; Massei *et al.* 1996; Fernandez-Llario and Mateos-Quesada 1998). As wild boars act as dispersal vectors of numerous vegetables by zoochory or endochory (Lynes and Campbell 2000; Welander 2000), the ingestion of earthworms infected by lung nematodes and the subsequent excretion of a resistant form of these nematodes in the faeces may contribute to the dispersal of this parasite.

In summary, the results highlight some aspects of wild boar diet in mountainous areas. Further research is required, especially to examine the relationships between worm consumption and seasonality of rooting and damage in meadows (Howe and Bratton 1976; Baron 1982; Gallo Orsi *et al.* 1995; Kotanen 1995; Mitchell and Mayer 1997) to assess the importance of earthworm consumption due to rooting. In addition, it could be interesting to examine, by telemetry, the variation in foraging behaviour of wild boars according to 'worm night' weather conditions. Finally, knowledge of earthworm consumption patterns would be helpful in controlling dispersal of disease through wild boar populations, especially as earthworms are intermediate hosts in many disease cycles.

Acknowledgments

We are grateful to several hunters and students for help with field data collection, and to J. M. Gaillard, J. Hone, J. Mitchell, C. Pelabon, J. Vassant, E. Fromont and L. Ellison for their comments on earlier versions of the manuscript and help with our English. We thank the Office National de la Chasse, the Fédération Départementale des Chasseurs de Savoie (73), the Fédération Départementale des Chasseurs de Haute-Savoie (74), and the Conseil Général de Savoie (73) for financial support.

References

Abdul Rida, A. M. M. (1995). L'effet de la contamination des sols sur le rôle lombricien dans la disponibilité du potassium. *Revue d'Ecologie. La Terre et la Vie* **50**, 141–152.

Anderson, D. R, Burnham, K. P., and Thompson, W. L. (2000). Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**, 912–923.

Atkinson, A. C. (1980). A note on the generalized information criterion for choice of a model. *Biometrika* **67**, 413–418.

Baron, J. (1982). Effects of feral hogs (*Sus scrofa*) on the vegetation of Horn Island, Mississippi. *American Midland Naturalist* **107**, 202–204.

Barrett, R. H. (1978). The feral hog at Dye Creek ranch, California. *Hilgardia* **46**, 283–355.

Baubet, E., Touzeau, C., and Brandt, S. (1997). Les lombriciens dans le régime alimentaire du sanglier (*Sus scrofa* L.) en montagne. *Mammalia* **61**, 371–383.

Bouché, M. (1982). 'Lombriciens de France, Ecologie et Systématique.' (INRA: Paris.)

Bouché, M. B., Fayolle, L., and Richard, P. (1984). Mesure de l'importance des lombriciens dans le régime alimentaire de leurs prédateurs et en particulier de la bécasse (*Scolopax rusticola* L.). *Gibier Faune Sauvage* **1**, 57–71.

Bratton, S. P. (1977). The effect of the European wild boar on the flora of the Great Smoky Mountains National Park. In 'Research and Management of Wild Hog Populations'. (Ed. W. Wood.) pp. 47–52. (Belle W. Barush Forest Science Institute of Clemson University: Georgetown, SC.)

Burnham, K. P., and Anderson, D. R. (2001). Kullback–Leiber information as a basis for strong inference in ecological studies. *Wildlife Research* **28**, 111–119.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. (1987). Design and analysis method for fish survival experiments based on released–recapture. American Fisheries Society Monographs, Maryland, No. 5.

Challies, C. N. (1975). Feral pigs (*Sus scrofa*) on Auckland Island: status, and effects on vegetation and nesting sea birds. *New Zealand Journal of Zoology* **2**, 479–490.

Chimera, C., Coleman, M. C., and Parkes, J. P. (1995). Diet of feral goats and feral pigs on Auckland Island, New Zealand. *New Zealand Journal of Ecology* **19**, 203–207.

Choquenot, D., McIlroy, J., and Korn, T. (1996). 'Managing Vertebrate Pests: Ferals Pigs.' (Bureau of Resource Sciences & Australian Government Publishing Service: Canberra.)

Coblentz, B. E., and Baber, D. W. (1987). Biology and control of feral pigs on Isla Santiago, Galapagos, Ecuador. *Journal of Applied Ecology* **24**, 403–418.

D'Andrea, L., Durio, P., Perrone, A., and Pirone, S. (1995). Preliminary data of the wild boar (*Sus scrofa*) space use in mountain environment. *IBEX. Journal of Mountain Ecology* **3**, 117–121.

Fernndez-Llario, P., and Mateos-Quesada, P. (1998). Body size and reproductive parameters in the wild boar *Sus scrofa*. *Acta Theriologica* **43**, 439–444.

Fournier-Chambrillon, C. (1996). Etude du régime alimentaire d'une population de sangliers (*Sus scrofa* L.) en garrigue à chêne vert. B.Vet.Sc. Thesis, ENV of Nantes, France.

Fournier-Chambrillon, C., Maillard, D., and Fournier, P. (1995). Diet of wild boar (*Sus scrofa* L.) inhabiting the Montpellier garrigue. *IBEX. Journal of Mountain Ecology* **3**, 174–179.

Gallo Orsi, U., Sicuro, B., Durio, P., Canalis, L., Mazzoni, G., Serzotti, E., and Chiariglione, D. (1995). Where and when: the ecological parameters affecting wild boar choice while rooting in grasslands in an alpine valley. *IBEX. Journal of Mountain Ecology* **3**, 160–164.

Genov, P. (1981). Food composition of wild boar in north-eastern and western Poland. *Acta Theriologica* **26**, 185–205.

Granval, P., and Muys, B. (1992). Management of forest soils and earthworms to improve woodcock (*Scolopax* sp.) habitats: a literature survey. *Gibier Faune Sauvage* **9**, 243–255.

Granval, P., and Muys, B. (1995). Predation on earthworms by terrestrial vertebrates. In 'Proceedings of the International Union of Game Biologists XXII Congress'. (Eds S. Golovatch and L. Penev.) pp. 480–491. (Pensoft: Sofia, Bulgaria.)

Granval, P., Aliaga, R., and Soto, P. (1993). Effet des pratiques agricoles sur les lombriciens (Lumbricidae), les bécassines des marais (*Gallinago gallinago*) et la valeur pastorale du milieu dans les marais de la dives (Calvados). *Gibier Faune Sauvage* **10**, 59–73.

Henry, F. V. G., and Conley, R. H. (1972). Fall foods of European wild hogs in the southern Appalachians. *Journal of Wildlife Management* **36**, 854–860.

Henry, Y. (1987). Self-selection by growing pigs of diets differing in lysine contents. *Journal of Animal Science* **65**, 1257–1265.

Henry, Y., Colleaux, Y., and Seve, B. (1992). Effects of dietary level of lysine and of level and source of protein on feed intake, growth performance, and plasma amino acid pattern in the finishing pigs. *Journal of Animal Science* **70**, 188–195.

Hirschberger, P., and Bauer, T. (1994*a*). The coprophagous insect fauna in sheep dung and its influence on dung disappearance. *Pedobiologia* **38**, 375–384.

Hirschberger, P., and Bauer, T. (1994*b*). Influence of earthworms on the disappearance of sheep dung. *Pedobiologia* **38**, 475–480.

Howe, T. D., and Bratton, S. P. (1976). Winter rooting activity of European wild boar in the Great Smoky Mountains National Park. *Catanea* **41**, 256–264.

Humbert, J.-F., and Henry, C. (1989). Studies on the prevalence and the transmission of lung and stomach nematodes of the wild boar (*Sus scrofa*) in France. *Journal of Wildlife Diseases* **25**, 335–341.

Hurvich, C. M., and Tsai, C.-L. (1989). Regression and times series model selection in small samples. *Biometrika* **76**, 297–307.

Klaa, K. (1992). The diet of wild boar (*Sus scrofa* L.) in the National Park of Chrea (Algeria). In 'Ongulés/Ungulates 91'. (Eds F. Spitz, G. Janeau, G. Gonzalez, and S. Aulagnier.) pp. 403–407. (SFEPM and IRGM: Paris & Toulouse.)

Kotanen, P. (1994). Effects of feral pigs on grasslands. *Fremontia* **22**, 14–17.

Kotanen P. (1995). Responses of vegetation to changing regime of disturbance: effects of feral pigs in a Californian coastal prairie. *Ecography* **18**, 190–199.

Kruuk, H., and Parish, T. (1981). Feeding specialization of the European badger *Meles meles* in Scotland. *Journal of Animal Ecology* **50**, 773–788.

Loungouedi, C. (1989). Effets comparés du son de blé et des pulpes de betterave sur le transit intestinal, l'excrétion fécale et la digestibilité chez le porc. B.Vet.Sc. Thesis, ENV of Nantes, France.

Lynes, B. C., and Campbell, S. D. (2000). Germination and viability of mesquite (*Prosopis pallida*) seed following ingestion and excretion by feral pigs (*Sus scrofa*). *Tropical Grassland* **34**, 125–128.

MacDonald, D. W. (1980). The red fox, *Vulpes vulpes*, as a predator upon earthworms, *Lumbricus terrestris*. *Zeitschrift fr Tierpsychologie* **52**, 171–200.

Massei, G., Genov, P. V., and Staines, W. (1996). Diet, food availability and reproduction of wild boar in a mediterranean coastal area. *Acta Theriologica* **41**, 307–320.

Massei, G. Genov, P., Staines, B. W., and Gorman, M. L. (1997). Mortality of wild boar (*Sus scrofa*), in a mediterranean area in relation to sex and age. *Journal of Zoology* **242**, 394–400.

Mauget, R. (1982). Seasonality of reproduction in the wild boar. In 'Control of Pig Reproduction.' (Eds G. J. A. Colend G. R. Foxcroft.) pp. 509–526. (Butterworth Scientific: London.)

Mitchell, J., and Mayer, R. (1997). Diggings by feral pigs within the Wet Tropics World Heritage area of North Queensland. *Wildlife Research*, **24**, 591–601.

Noblet, J., Henry, Y., and Dubois, S. (1987). Effect of protein and lysine levels in the diet on body gain composition and energy utilization in growing pigs. *Journal of Animal Science* **65**, 717–726.

Pavlov, P. M., and Edwards, E. C. (1995). Feral pig ecology in Cape Tribulation National Park, North Queensland, Australia. *IBEX. Journal of Mountain Ecology* **3**, 148–151.

Scott, C. D., and Pelton, M. R. (1975). Seasonal food habits of the European wild hog in the Great Smoky Mountains National Park. In 'Proceeding of the 29th Annual Conference of the Southeastern Association of Game and Fish Commissioners.' pp. 585–593.

Shaffer, M. (1979). Behavior of the European wild boar in the Great Smoky Mountains National Parks. (In Proc. First Conf. Sci. Res. Nat Parks U.S. **5**, 357–363.)

Sokal, R. R., and Rohlf, F. J. (1969). 'Biometry.' (Freeman: San Francisco.)

Welander, J. (2000). Spatial and temporal dynamics of disturbance regime. Wild boar *Sus scrofa* rooting and its effects on plant species diversity. Ph.D. Thesis, Swedish University of Agricultural Science, Utgivningsort, Sweden.

Wood, G. W., and Roark, D. N. (1980). Food habits of feral hogs in coastal South Carolina. *Journal of Wildlife Management* **44**, 506–511.

Wroot, A. J. (1985). A quantitative method for estimating the amount of earthworm (*Lumbricus terrestris*) in animal diets. *Oikos* **44**, 239–242.

Manuscript received 5 December 2000; accepted 10 May 2002