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SUMMER AND HUNTING SEASON HOME RANGES OF WILD BOAR (*SUS SCROFA*) IN TWO HABITATS IN FRANCE

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ABSTRACT

The seasonal home range of wild boar, Sus scrofa, was investigated in two study areas with different habitat types. Space occupation was studied at Puéchabon (Hérault, southern France), an area typical of the Mediterranean habitat where the wild boar is hunted by drives with big hounds, and at Arc-en-Barrois (Haute-Marne, north-eastern France), a more temperate area where the boar is hunted by drives with flushing dogs. Radio-tracking data from 40 wild boars monitored in both areas were used to estimate the dynamics of home-range size in summer (July-August) and during the hunting season (September-December). Home ranges and core areas were estimated by respectively the 95% and the 50% kernel estimator. The effects of the following factors on the home range and core area sizes, and on the ratios between these sizes during the hunting season and in summer were analysed by linear models: sex and age of the individuals, study area (site), year and interactions between the preceding factors. In summer, the wild boars monitored on both areas showed similar home ranges and core areas. These estimates varied among years, probably as a result of variations over time in food availability and population density at Puéchabon, and of an increase in wooded thickets at Arc-en-Barrois. During the hunting seasons, the wild boars of both areas increased their home range. The expansion was greater for subadult males than for the other wild boars at Puéchabon, but not at Arc-en-Barrois, where movements of the wild boars were limited by the periphery of the forest. This expansion is attributed to hunting activities, but, because core-area sizes were similar for the wild boars monitored in both sites, we believe that there was no major effect of the hunting method on wild boar distribution. The wild boar home range rarely exceeded 2,500 ha in the hunting season, except for subadult males. This is why we recommend that the size of a territory hunted by a hunter team at a time should mainly cover one home range, i.e. 3,000 ha. This will allow a female to be less disturbed than in the case where several teams of diverse smaller hunting territories are hunting in her home range.

I. INTRODUCTION

The study of the spatial organisation of the wild boar, *Sus scrofa*, is of great concern to wildlife managers and biologists. The factors influencing the wild boar home range thus have been studied in a wide range of habitats in France (e.g. in the Mediterranean garrigue, MAILLARD, 1996; in lowland forests, BRANDT *et al.*, 1998; in mountain forests, BAUBET, 1998). The most frequently considered factors were: individual characteristics, such as sex and age of the wild boars (BRANDT *et al.*, 1998), environmental characteristics, such as food availability (MASSEI *et al.*, 1997) or human disturbances (JULLIEN *et al.*, 1991), and phenological characteristics (SPITZ, 1992).

However, few studies have been carried out to compare these factors among several areas, despite the fact that a geographical variation in home-range size has already been reported (GÉRARD *et al.*, 1991). Smaller home ranges are indeed observed in northern France rather than in the south. This gradient in home-range size is maybe due to a variation in the effect of one or several of the above-described factors. Unfortunately, despite the fact that many authors are using data from the literature to compare home-range sizes among different areas (MAILLARD, 1996; BAUBET, 1998), we have no knowledge of studies specifically designed to achieve this objective. Comparing the home-range sizes estimated in different studies is extremely difficult (WHITE and GARROTT, 1990; SEAMAN *et al.*, 1999) because the home-range estimation methods used are different, the periods considered are of unequal duration and the number of relocations collected per animal varies.

Here we use radio-tracking data to compare space occupation of wild boar in two different habitats. The first data set was collected from 1989 to 1994 at Puéchabon (Hérault *département*, southern France), an area typical of the environment usually found in the French Mediterranean region. The other set was collected from 1987 to 1998 in the Arc-en-Barrois forest (Haute-Marne *département*, northern France), an area characteristic of the forests encountered in the north of France. Our aim was to identify, in both areas, the factors influencing the seasonal home ranges of wild boars in summer and during the hunting season (September-December). We also compare the changes in home range between the two seasons. Because of the high mortality rate among monitored boars in the hunting season, we had not enough data to examine home ranges during the post-hunting season (January to June).

II. MATERIAL AND METHODS

II.1. STUDY AREAS

Puéchabon study area

The central study site of the Puéchabon study area was the Puéchabon *commune* (3,000 ha), in the Hérault *département* (Figure 1). A less intensive study was conducted in an area of a total of 48,000 ha surrounding the Puéchabon *commune*. The vegetation is characteristic of the upper mesomediterranean stratum, dominated by garrigue scrublands. The domi-

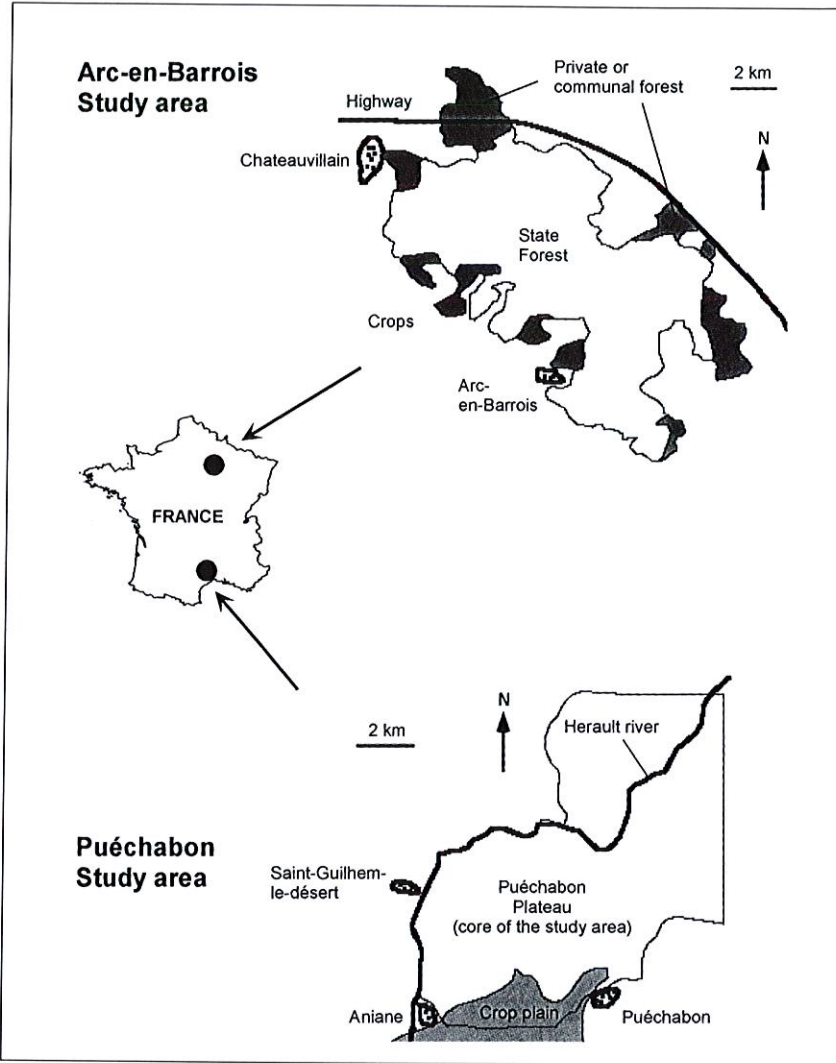


Figure 1: Location of the two study areas in France: at the bottom, the Puéchabon *commune* dominated by scrublands (Hérault), at the top, the Arc-en-Barrois State forest (Haute-Marne).

Figure 1 : Localisation des deux terrains d'étude en France : en bas, la commune de Puéchabon dominée par des terrains broussailleux (Hérault) ; en haut, la forêt domaniale d'Arc-en-Barrois (Haute-Marne).

nant tree species is holly oak, *Quercus ilex*, which represents 40% of the vegetation cover. Interspersed throughout these scrublands are: several treeless garrigue areas; conifer, *Pinus* sp. and pubescent oak, *Q. pubescent*, garrigues; holly oak coppices; and open or conifer-mixed hardwood. Reafforestations, pine groves and fallow lands cover 21% of the site.

Wild boar hunting is mostly a group sport involving pursuits with packs of

big hounds: the beaters and the pack of hounds may cover some 200 to 400 ha of ground per drive, while the hunters are posted at the strategic points of the hunted area (ridges, crossroads, etc.). When a dog flushes a wild boar, all the dogs of the pack will pursue this animal over long distances (several hundred meters) until the hunters may shoot it. Thus, the dogs must be big enough to force an adult boar to leave its lair and drive it to the posted hunters. About 20 hunters participate in each drive. Hunting is permitted three days per week (Wednesday, Saturday and Sunday) and on public holidays, from mid-September to January first. On average, one animal/km² is culled during the hunting season (mean computed for all years between 1990 and 1994; SE = 0.3). Between 1990 and 1992, the hunting bag was 0.7 animals culled/km², and the hunting bag increased to 2 animals culled/km² in 1993 and 1994.

Arc-en-Barrois study area

The Arc-en-Barrois study area is located in the Arc-en-Barrois forest (11,000 ha) in the Haute-Marne *département* (Figure 1). The forest community of the Arc-en-Barrois study area is mainly a composite wood of hornbeam, *Carpinus betulus*, durmast oak, *Quercus petraea*, and beech trees, *Fagus sylvatica*. A State forest of 8,000 ha constitutes the core of the study area. The forest administration fenced in some plots in 1991 to prevent their access by red deer, *Cervus elaphus*, and allow tree regeneration. This resulted in the development of dense woody thickets, favourable habitats for wild boar resting places (DARDAILLON, 1986). The fences, indeed, did not prevent their access by wild boars. Peripheral forests (3,000 ha) are private or communal forests. The area is surrounded by a cultivated plain, where barley, maize and rape are the most common crops. A highway is bordering the north-east side of the forest.

In this area, the wild boars are hunted by drives with flushing dogs. The beaters with 20-30 flushing dogs cover 200 to 500 ha per drive, the hunters being systematically posted around the hunted area. These dogs are rather small and they do not pursue the boars they are flushing. Hunting is allowed only two days per week (Saturday and Sunday), from mid-September to January first. The 8,000-ha State forest is hunted by one team of about 50 members. The 3,000-ha peripheral forests are hunted entirely each weekend, by 17 teams with flushing dogs. On average, 6.3 wild boars/km² are shot in this area during the hunting season (mean computed for all years between 1987 and 1997; SE = 0.76) but there are large between-year variations. The hunting bag increased from 2 wild boars shot/km² in 1987 to 9 wild boars shot/km² in 1990, then decreased to 3 wild boars/km² in 1993, and increased again to 11 wild boars shot/km² in 1996 and finally decreased to 7 wild boars shot/km² in 1998.

II.2. CAPTURE

In both study areas, wild boars were trapped in mobile box traps during spring and summer (MAILLARD *et al.*, 1994), and sedated with Zoletil® (FOURNIER *et al.*, 1995). Each individual was sexed and aged by its dentition (MATSCHKE, 1967). Although wild boars are sexually mature at 12 months,

previous studies have found that 15 to 20-month-old males are characterised by an erratic behaviour during the hunting season (BOULDOIRE and VASANT, 1989; SPITZ, 1992; MAILLARD *et al.*, 1996; MAILLARD, 1996). We therefore defined subadult boars as 15 to 20-month-old individuals, and adults as individuals older than 20 months. Captured wild boars were equipped with transmitter collars of the Pulsar 2001 (146-148 MHz) type. Radio-tracking operations were conducted with a vehicle equipped with a Yaesu (FT 290 RII) receiver linked to a directional 7-stranded Tonna antenna.

Between 1989 and 1994, 16 wild boars were caught in the Puéchabon area, and 24 in the Arc-en-Barrois site (Table I). Each wild boar was monitored for one year. Wild-boar diurnal resting sites were located every day at Puéchabon, and less frequently at Arc-en-Barrois (2-3 relocations per week). For Puéchabon wild boars, the relocations were computed with a minimum of 3 bearings, using LOCATE II program (NAMS, 1990), which led to an imprecision of about 1 ha for the relocations in Puéchabon (MAILLARD, 1996). The

TABLE I
Number of wild boars, *Sus scrofa*, fitted with radiocollars in France in 1987-1998 at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne) according to their sex and age
 (subadult: 15-20-month old; adult: > 20-month old).

TABLEAU I
Nombre de sangliers, *Sus scrofa*, équipés de colliers émetteurs en France entre 1987 et 1998 à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne) selon le sexe et l'âge (subadulte : âgé de 15 à 20 mois ; adulte : âgé de plus de 20 mois).

Study area Year of radio-tracking	Number of males		Number of females		Total
	Adult	Subadult	Adult	Subadult	
Puéchabon					
1990	1	-	1	-	2
1991	1	-	-	1	2
1992	-	1	1	1	3
1993	-	4	1	4	9
Total	2	5	3	6	16
Arc-en-Barrois					
1987	-	-	3	-	3
1989	1	2	3	-	6
1990	-	1	1	-	2
1991	-	-	2	-	2
1995	-	-	2	-	2
1997	-	1	3	1	5
1998	1	-	2	1	4
Total	2	4	16	2	24

sampling protocol was slightly different in Arc-en-Barrois. The animals were indeed located in the field, and no triangulation program was used for this area. Instead of locating the resting site of a wild boar, we rather located the forested plot where the wild boar was resting. For a given relocation, we took as many bearings as needed to ensure the identification of this plot. The forested plots covering about 1 hectare in Arc-en-Barrois, the precisions of the relocations were therefore similar in the two sites, and the results of the analyses were unlikely to be affected by this difference in protocol between the two areas.

II.3. DATA ANALYSIS

Home-range estimation

We calculated the seasonal home range with the 95% and the 50% fixed kernel estimators. Home ranges were estimated in summer (July to mid-September for both areas: piglet-rearing period) and in the hunting season (mid-September to December). To allow comparisons among boars, we took care that the duration of the monitoring period included the whole summer and the hunting seasons of the same year.

In this paper, we term "home range" the 95% home-range size estimation calculated with the diurnal resting site locations, and "core area" the 50% home-range size estimation. We took the core areas into consideration since they represent the areas of intensive use. In addition, STEPHENSON *et al.* (1996) stated that the 50% estimator illustrates long-term responses to human disturbances, which is of primary interest during the hunting season. The smoothing parameter was calculated by the reference method (WORTON, 1989). These estimates were calculated with the help of RANGES V software (KENWARD and HODDER, 1995; LAWSON and RODGERS, 1997).

Statistical analyses

We tested the main effects of sex, age, and study area as well as all interactions between these factors on the home-range and core-area sizes, for both the summer and the hunting season. Because wild boar spatial organisation may vary over time, we also looked for the effect of the year of monitoring. This factor was nested in "study area". The data were too scarce to allow the use of the test of interactions between the year and the other factors. Therefore the effect of year was considered to be additive to the effects of sex and age (SEARLE, 1971). The analyses were made with the help of general linear models (FESTA-BIANCHET *et al.*, 1998). We used backward elimination to account for the unbalanced design, *i.e.* we first tested the interactions and then the main effects (using a Type III decomposition; SEARLE, 1971). The analysis was applied to the ranks of the data instead of the data themselves. The rank transformation has been recommended by numerous authors (CONOVER and IMAN, 1981; AKRITAS, 1990), because it allows the use of parametric methods (general linear model) without any assumption with regard to the form of the distribution of the dependent variate (residual normality and homoscedasticity were thus achieved).

Then, we analysed changes in home-range size from summer to hunting season by calculating the ratio between hunting-season estimates and summer estimates (GESE *et al.*, 1989). This ratio was greater than 1 if wild boars expanded their home-range size during the hunting season, less than 1 if they reduced it and equal to 1 if the home-range size was similar between seasons. The ratios were calculated for both home-range and core-area estimates. We developed general linear models to test the effects of site, sex and age as well as the possible effects of interactions between these factors, and of year of monitoring (nested in "site", and additive to "sex" and "age"), on both the core-area ratio (CAR) and the home-range ratio (HRR). We log-transformed the HRR and CAR to achieve residual normality. We did not use the rank transformation for these analyses, because the value of the ratios was of major interest to measure the changes in space use between the two seasons (less or greater than 1). All analyses were carried out with the Statistica program (STATSOFT FRANCE, 1997).

III. RESULTS

Home ranges were calculated for 40 wild boars with a sufficient number of locations ($\bar{x} = 60$; $SD = 26.4$; Table II) for each seasonal home-range analysis. We found no relationships between the number of locations per individual and either home-range size of individuals ($R_{Spearman} = 0.167$; $t = 1.498$; $df = 78$; $p = 0.138$) or core-area size ($R_{Spearman} = 0.168$; $t = 1.502$; $df = 78$; $p = 0.137$).

III.1. SPACE USE DURING THE SUMMER

Home-range size of wild boars was influenced by the year of monitoring and the interactions between site, sex and age (Table III). But, to avoid modelling random "noise", we excluded these interactions from the model, because the p value was not much lower than 0.05 (Table III), the number of degrees of freedom ($df = 1$) and the sum of squares of the interactions were low ($SS = 398.4$) in comparison to the sum of squares of the intercept ($SS = 8907$; $df = 1$), which indicated a small amount of the explained variation, and because these interactions were not interpretable. The resulting model shows a decrease in home-range size with the year of monitoring at Arc-en-Barrois (Figure 2A). At Puéchabon, wild boars monitored in 1993 had a smaller summer home range than those monitored during previous years. No difference between sites was observed.

The study site and the year of monitoring were related to summer core-area size (Table III). The resulting model shows a pattern similar to the previous model (Figure 2B). We assumed that the significance of the predictor "study site" was a result of the large variation induced by the factor "year" (here considered to have a fixed effect). To confirm this hypothesis, F -tests were performed by considering the year as a random effect (STATSOFT FRANCE 1997). Thus, the levels of this factor are assumed to be randomly selected from an infinite population of possible levels. Variation explained by the factor "year" is therefore extracted from the variation induced by the factor "site". When "year" is considered to have a random effect, the p -values of F -tests do

TABLE II
Size (ha) of home ranges (HR) and core areas (CA) for wild boars, *Sus scrofa*, radiotracked in France at Arc-en-Barrois (Haute-Marne) and Puéchabon (Hérault) in summer and during the hunting season in 1987-1998 (France). The code gives the age (A = adult, S = subadult) and sex (M = male; F = female) of monitored animals, and *n* the number of relocations. HR and CA were estimated by the kernel method.

TABLEAU II
Taille (ha) des domaines vitaux (HR) et des zones centrales de domaine vital (CA) des sangliers, *Sus scrofa*, suivis par radiopistage en France à Arc-en-Barrois (Haute-Marne) et Puéchabon (Hérault) en été et pendant la saison de chasse entre 1987 et 1998. Le code indique l'âge (A = adulte, S = subadulte) et le sexe (M = mâle ; F = femelle) des animaux suivis, et *n* le nombre des localisations. HR et CA ont été estimés par la méthode du noyau.

Study area Wild boar code	Year	Size (ha) of home ranges and core areas in					
		Summer (July-August)			September-December (during the hunting season)		
		<i>n</i>	HR	CA	<i>n</i>	HR	CA
Arc-en-Barrois							
AF11	1995	49	275	48	50	321	108
AF15	1998	55	234	37	40	383	72
AF6	1989	38	885	78	76	453	95
AF10	1995	48	112	11	49	496	67
AF2	1987	76	615	114	48	642	151
AF12	1997	32	76	15	41	666	40
AF14	1997	49	546	14	42	667	27
AF7	1990	21	293	23	48	889	109
AF13	1997	26	186	45	35	961	104
AF1	1987	87	1,178	347	40	1,181	217
AF3	1987	107	940	220	50	1,301	293
AF5	1989	20	318	59	58	1,379	273
AF8	1991	41	1,177	43	28	1,435	218
AF16	1998	73	182	30	43	2,497	222
AF9	1991	72	433	39	31	4,437	853
AF4	1989	38	1,511	303	59	4,607	932
AM2	1998	56	213	32	44	460	55
AM1	1989	28	378	49	73	2,181	34
SF1	1997	19	247	28	27	481	75
SF2	1998	91	303	9	31	1,479	313
SM4	1997	36	74	14	37	446	46
SM1	1989	109	697	121	27	1,292	493
SM2	1989	21	1,207	33	53	1,651	90
SM3	1990	52	796	73	63	3,386	691
Puéchabon							
AF19	1993	112	137	137	71	510	205
AF18	1992	105	358	99	52	1,606	198
AF17	1990	79	358	90	60	1,987	295
AM3	1990	89	710	119	88	1,686	319
AM4	1991	45	1,144	162	93	1,823	270
SF4	1992	83	333	83	101	485	50
SF5	1993	50	509	19	94	491	53
SF8	1993	49	306	11	94	523	43
SF6	1993	50	468	16	92	550	45
SF7	1993	49	613	16	48	575	117
SF3	1991	36	344	50	108	5,659	200
SM5	1992	52	700	120	83	4,327	1,032
SM8	1993	119	91	15	88	9,053	201
SM7	1993	59	251	35	102	10,207	909
SM9	1993	56	60	7	88	18,514	423
SM6	1993	57	114	26	112	20,548	500

TABLE III

P-values of the tested effects of factors when modelling the home-range and core-area sizes of wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne). *F*-values are in parentheses. The factor "year of monitoring" was nested in "site" (from 1989 to 1993 at Puéchabon and from 1987 to 1998 at Arc-en-Barrois) and considered additive to the other factors. In bold: $P \leq 0.05$.

TABLEAU III

Valeurs de *P* pour les effets des facteurs testés (de bas en haut : âge, sexe, site, année et interactions entre ces facteurs) pour la modélisation des tailles des domaines vitaux et des zones centrales de domaine vital des sangliers, *Sus scrofa*, suivis par radiopistage en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne). Les valeurs de *F* sont entre parenthèses. Le facteur "année de suivi" a été hiérarchisé au facteur "site" (entre 1989 et 1993 à Puéchabon et de 1987 à 1998 à Arc-en-Barrois) et considéré comme additif aux autres facteurs. En gras : $P \leq 0,05$.

Effect tested	Summer		Hunting season (fall)	
	Home range size <i>P</i>	Core area size <i>P</i>	Home range size <i>P</i>	Core area size <i>P</i>
Site*sex*age	0.028 ($F_{1,23} = 5.492$)	0.712 ($F_{1,23} = 0.712$)	0.235 ($F_{1,23} = 1.488$)	0.212 ($F_{1,23} = 1.645$)
Site*sex	0.903 ($F_{1,25} = 0.015$)	0.334 ($F_{1,25} = 0.968$)	0.294 ($F_{1,24} = 1.149$)	0.069 ($F_{1,25} = 3.621$)
Site*age	0.635 ($F_{1,24} = 0.231$)	0.233 ($F_{1,26} = 1.490$)	0.025 ($F_{1,25} = 5.719$)	0.928 ($F_{1,24} = 0.008$)
Sex*age	0.218 ($F_{1,26} = 1.597$)	0.541 ($F_{1,24} = 0.385$)	< 0.001 ($F_{1,25} = 14.970$)	0.057 ($F_{1,25} = 3.840$)
Year	0.001 ($F_{9,29} = 4.266$)	< 0.001 ($F_{9,29} = 8.938$)	0.053 ($F_{9,25} = 2.24$)	0.122 ($F_{9,26} = 1.773$)
Site	0.623 ($F_{1,29} = 0.247$)	0.036 ($F_{1,29} = 4.827$)	< 0.001 ($F_{1,25} = 15.153$)	0.140 ($F_{1,35} = 2.285$)
Sex	0.605 ($F_{1,28} = 0.273$)	0.750 ($F_{1,28} = 0.104$)	0.019 ($F_{1,25} = 6.260$)	0.006 ($F_{1,25} = 8.594$)
Age	0.505 ($F_{1,27} = 0.456$)	0.691 ($F_{1,27} = 0.161$)	0.587 ($F_{1,25} = 0.304$)	0.370 ($F_{1,25} = 0.824$)

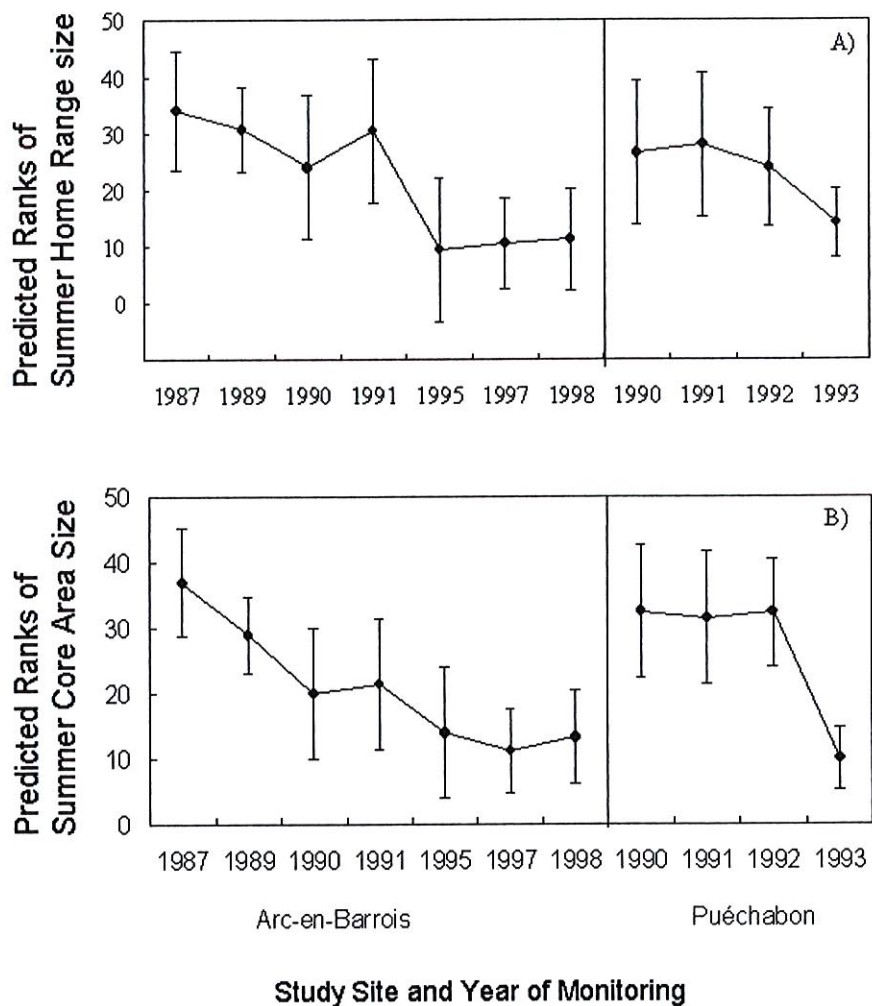


Figure 2: Model (\pm 95% confidence intervals of the estimates) developed for the summer (A) home-range size and (B) core-area size for wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne), according to the year of monitoring. A rank transformation was performed to achieve residual normality.

Figure 2 : Modèle (intervalle de confiance des estimations à \pm 95 %) développé pour la taille du domaine vital (A) et la taille de la zone centrale du domaine vital (B) des sangliers, *Sus scrofa*, suivis en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne), selon l'année de suivi. Une transformation en rangs a été effectuée pour obtenir la normalité des résidus.

not change, except for the factor "site" that is no longer significant ($F_{1,9.37} = 0.626$; $p = 0.449$).

Therefore, in summer, wild boars exhibited a similar spatial dispersion in the two study areas, for both 95% and 50% home-range size estimates. The main source of variation was induced by year.

III.2. SPACE USE DURING THE HUNTING SEASON

The interactions between study site and age, and between sex and age were significant with respect to the hunting season home-range size of boars (Table III). In addition, the effect of year was also significant. The resulting model is very difficult to interpret, because of its complexity (Figure 3). Therefore, we tested the effects of sex and age and the interactions between sex and age, as well as the effects of the year of monitoring on boar home-range size in each study area, separately. At Arc-en-Barrois, none of these factors had a significant effect (year: $F_{6,14} = 1.52$; $p = 0.24$; site*sex: $F_{1,20} = 2.19$; $p = 0.15$; sex: $F_{1,21} = 1.02$; $p = 0.32$; Age: $F_{1,22} = 0.61$; $p = 0.44$). At Puéchabon, interactions between sex and age ($F_{1,6} = 29.39$; $P < 0.001$) as well as the year ($F_{3,9} = 8.79$; $df =$; $p = 0.005$) influenced the home-range size during the hunting season: subadult males at Puéchabon showed a greater home range than other boars (Table III and Figure 3). In addition, the home range of boars monitored in 1992 and 1993 was smaller than in other years.

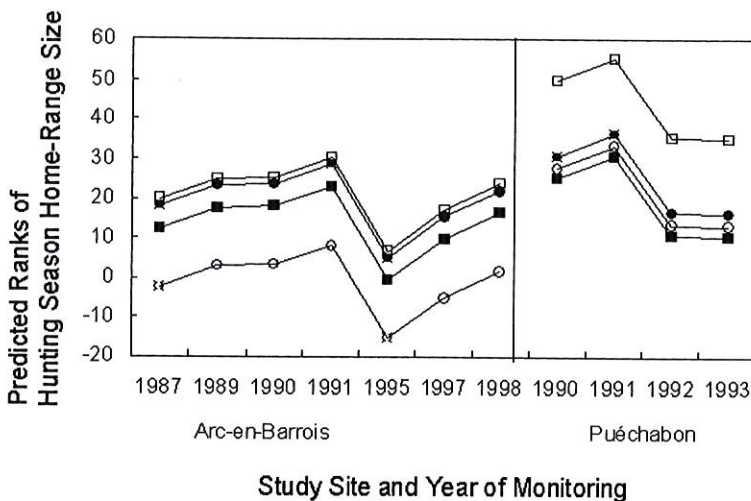


Figure 3: Model developed for home-range size of wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne) during the hunting season, according to the year of monitoring and their sex and age (black squares: Adult males, white squares: Subadult males, black dots: Adult female, and white dots: subadult female). A rank transformation was performed to achieve residual normality.

Figure 3 : Modèle développé pour la taille du domaine vital des sangliers, *Sus scrofa*, en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne) pendant la saison de chasse, selon l'année de suivi, le sexe et l'âge (carrés noirs : mâles adultes, carrés blancs : mâles subadultes, points noirs : femelles adultes, et points blancs : femelles subadultes). Une transformation en rangs a été effectuée pour obtenir la normalité des résidus.

We found a significant effect of the interactions between sex and age on the core-area size of wild boars during the hunting season (Table III). In both study sites, core areas of subadult females were smaller than those of other boars (Figure 4). Wild boars of the two study areas were showing similar core-area sizes.

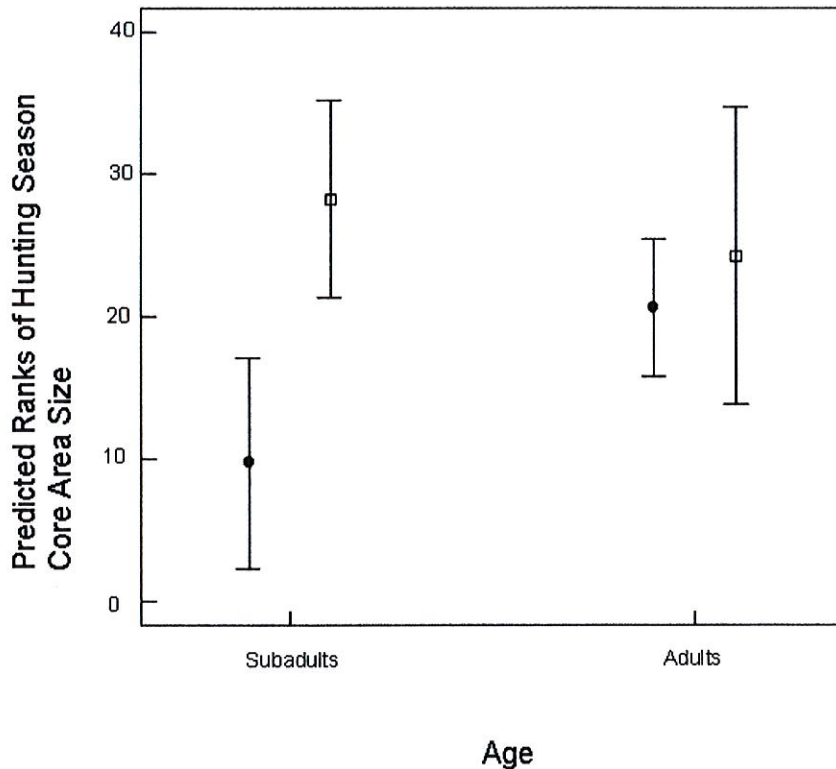


Figure 4: Model developed for core-area size (\pm 95% confidence intervals of the estimates) of wild boar, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne) during the hunting season according to their sex (squares: males, dots: females) and age. A rank transformation was performed to achieve residual normality.

Figure 4 : Modèle développé pour la taille de la zone centrale du domaine vital (intervalle de confiance des estimations à \pm 95 %) des sangliers, *Sus scrofa*, suivis en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne) pendant la saison de chasse, selon l'année de suivi, le sexe (carrés : mâles, points : femelles) et l'âge. Une transformation en rangs a été effectuée pour obtenir la normalité des résidus.

III.3. CHANGES FROM SUMMER TO HUNTING SEASON

The home-range ratio (HRR) was influenced by the full interactions between site, sex and age (Table IV). We tested the effect of site, age and interactions between these two factors separately for males and females. A significant effect of the interactions between site and age on the HRR of males was found ($F_{1,9} = 7.717$; $p = 0.022$). None of the tested factors had a significant effect on the HRR of females (site*age: $F_{1,23} = 0.24$; $p = 0.63$; age: $F_{1,24} = 1.1.93$; $p = 0.18$; site: $F_{1,25} = 0.002$; $p = 0.96$). HRR was greater for the subadult males of Puéchabon than for other wild boars (Figure 5). Only 3 boars out of 40 showed a HRR of less than 1 (7.5%; two subadult females monitored at Puéchabon and one adult female monitored at Arc-en-Barrois). In fact, there was an expansion of home range for all boars in the hunting season, that was greater for the subadult males of Puéchabon than for the others.

TABLE IV

P-values of the tested effects of factors when modelling home-range ratios (estimates of home range during the hunting season divided by estimates during summer) and core-area ratios (estimates of core areas during the hunting season divided by estimates during summer) for wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne). The F-values are shown in parentheses. The factor "year of monitoring" was nested in "site" (from 1989 to 1993 at Puéchabon and from 1987 to 1998 at Arc-en-Barrois), and considered additive to the other factors. In bold: $P \leq 0.05$.

TABLEAU IV

Valeurs de P pour les effets des facteurs testés (de bas en haut : âge, sexe, site, année et interactions entre ces facteurs) pour la modélisation des rapports de tailles de domaine vital (estimation du domaine vital pendant la saison de chasse divisée par celle en été) et des rapports de zones centrales de domaine vital (estimations de la zone centrale pendant la saison de chasse divisée par celle en été) pour les sangliers, *Sus scrofa*, suivis en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne). Les valeurs de F sont en parenthèses. Le facteur « année de suivi » a été emboîté dans « site » (de 1989 à 1993 à Puéchabon et de 1987 à 1998 à Arc-en-Barrois), et considéré comme additif aux autres facteurs. En gras : $P \leq 0,05$.

Effect tested	Home range ratio <i>P</i>	Core-area ratio <i>P</i>
Site*sex*age	0.011 ($F_{1,32} = 7.245$)	0.212 ($F_{1,23} = 1.648$)
Site*sex	0.214 ($F_{1,32} = 1.606$)	0.455 ($F_{1,24} = 0.578$)
Site*age	0.045 ($F_{1,32} = 4.364$)	0.151 ($F_{1,25} = 2.195$)
Sex*age	0.006 ($F_{1,32} = 8.597$)	0.004 ($F_{1,26} = 9.996$)
Year	0.261 ($F_{9,23} = 1.363$)	0.011 ($F_{1,26} = 3.114$)
Site	0.054 ($F_{1,32} = 3.987$)	0.548 ($F_{1,26} = 0.370$)
Sex	0.035 ($F_{1,32} = 4.878$)	0.086 ($F_{1,26} = 3.188$)
Age	0.214 ($F_{1,32} = 1.606$)	0.605 ($F_{1,26} = 0.275$)

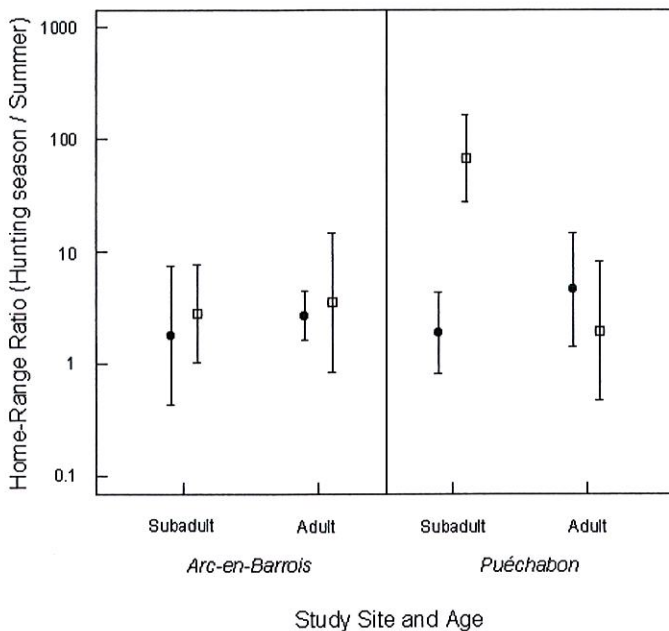


Figure 5: Predicted values (\pm 95% confidence intervals) of home-range ratio (home-range size during the hunting season divided by the summer home-range size) for male (squares) and female (dots) wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne). The Y-axis has a log scale.

Figure 5 : Valeur attendue (intervalle de confiance à \pm 95 %) du rapport des domaines vitaux (taille du domaine vital pendant la saison de chasse divisée par celle en été) pour les mâles (carrés) et les femelles (points noirs) sangliers, *Sus scrofa*, suivis par radiopistage en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne). L'axe des Y est à l'échelle logarithmique.

We found a significant effect of year and of interactions between sex and age on the core-area ratio (CAR, Table IV). No effect of study site occurred. In both areas the subadult males had a bigger core area than the subadult females, whereas adult core area sizes gave intermediate estimates (Figure 6). Only 2 boars (5% of the individuals; one subadult female monitored at Puéchabon and one adult female monitored at Arc-en-Barrois) showed a CAR lower than 1 (CAR = 0.6 in both cases). This indicates that boars generally expanded their core area during the hunting season.

IV. DISCUSSION

IV.1. SUMMER

The variation in the summer home range of wild boars according to the year of monitoring probably results from variations in food resources, habitat structure and population density. The relationship between home-range size and food availability had already been noted in previous studies (KURTZ and

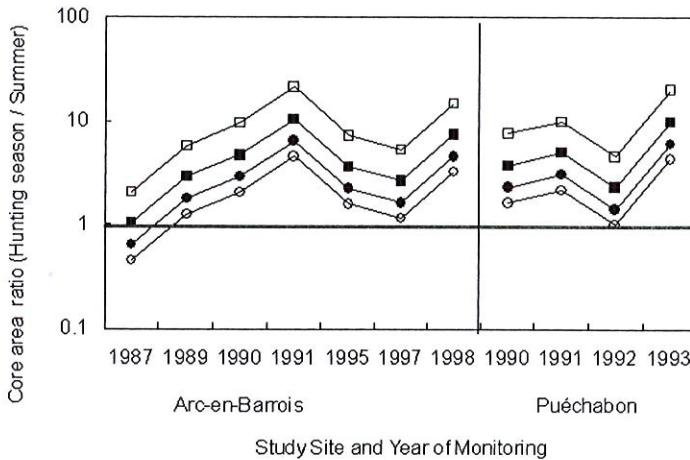


Figure 6: Predicted values of the core-area ratio (core-area size during the hunting season divided by the summer core-area size) of adult male (black squares), subadult male (white squares), adult female (black dots) and subadult female (white dots) of wild boars, *Sus scrofa*, monitored in France at Puéchabon (Hérault) and Arc-en-Barrois (Haute-Marne), according to study site and year of monitoring. The Y-axis has a log-scale.

Figure 6 : Valeur attendue (intervalle de confiance à $\pm 95\%$) du rapport des zones centrales de domaine vital (taille de la zone centrale du domaine vital pendant la saison de chasse divisée par celle en été) des sangliers, *Sus scrofa*, mâles adultes (carrés noirs), des mâles subadultes (carrés blancs), des femelles adultes (points noirs) et des femelles subadultes (points blancs), suivis par radiopistage en France à Puéchabon (Hérault) et Arc-en-Barrois (Haute-Marne) selon le territoire d'étude et l'année de suivi. L'axe des Y est à l'échelle logarithmique.

MARCHINTON, 1972; SINGER *et al.*, 1981; MASSEI *et al.*, 1997). In the absence of disturbance, increases in home-range size often result from food shortage. During summer, food availability is poor at Puéchabon. This often leads wild boars to feed on crops (MAILLARD *et al.*, 1996). In 1993, as part of a study of the efficiency of various crop-damage reduction methods (MAILLARD *et al.*, 1996), a research team distributed 4.7 tons of maize in the Puéchabon study area through the summer. The wild boars presented smaller home ranges and core areas in 1993 than during previous years, which supports this hypothesis. Moreover, the variations in population density may also have accounted for this decrease in home-range size in 1993. Indeed, the threefold increase in the hunting bag in 1993 may indicate an increase in population size at Puéchabon (0.7 animal shot/km² between 1989 and 1992, 2 animals shot/km² in 1993 and 1994, MAILLARD, 1996). This agrees with the hypothesis that higher densities lead to smaller home ranges (BABER and COBLENTZ, 1986; MASSEI *et al.*, 1997).

In the Arc-en-Barrois forest, hunters usually provide 60 tons of maize in summer to reduce crop damage. Therefore, food availability is not a limiting factor in this area. Moreover, it seems unlikely that the variations in population density accounted for the systematic decrease in wild boar home-range size during the study period. In this area, a survey of the wild boars feeding at baiting places is being carried out in the spring of each year since 1989, and this index is used as an indicator of population abundance (unpubl. data).

Between 1989 and 1998 there was no systematic increase in this index ($R_{Spearman} = 0.2$; $n = 5$; $p = 0.78$) nor in the hunting bag commonly used as an indicator of population abundance in other areas (e.g. MAILLARD, 1996; BAUBET, 1998). Therefore, the population size seemed rather stable during our study period.

On the other hand, the vegetation structure varied according to the year of monitoring. During the first years of monitoring, the red deer population was very high and damage to tree regeneration was extensive. To reduce such damage, in 1990 the forest administration fenced some regeneration plots in. This allowed woody thickets to develop (personal observation). The fences did not prevent the wild boars from finding these places, which are favourable resting habitats. Human disturbance in these plots was more frequent during the first than during the last years. The smaller home ranges of boars in the last years of the study may result from this increase in thicket areas, where the fences created calmer surroundings.

IV.2. HUNTING SEASON

Although other factors may increase the wild boars' home range between summer and the hunting season, in our opinion hunting activities would be the main source of variation. Indeed, in both areas acorns were available to the wild boars from September to March (JULLIEN *et al.*, 1991; FOURNIER-CHAMBRILLON *et al.*, 1994). Acorns are the main component of the diet of the wild boar (FOURNIER-CHAMBRILLON *et al.*, 1994). Although the importance of the mast crop varies from year to year, the food supply is always more abundant during the hunting season than in summer, and it is certainly not a limiting factor that would affect the home-range size in this season. Several authors already noted such an increased mobility of wild boar in response to hunting activities (McILROY and SAILLARD, 1989; JULLIEN *et al.*, 1991; SPITZ, 1992; MAILLARD and FOURNIER, 1995). Increase in home-range and core-area size likely is the wild boar's response to human activities.

Smaller core areas of subadult females certainly are the result of the lower hunting pressure they were subjected to. Indeed, on both study areas, the home ranges of the subadult females were situated in scarcely hunted areas, such as reserves at Puéchabon and the vicinity of a highway at Arc-en-Barrois. Only one subadult female monitored at Puéchabon, was frequently hunted. Its core-area size (200 ha) was close to those of adult boars (Table I). Previous studies indicated that females may leave their home range in response to high hunting pressure and search for quieter areas, which results in an extended home range (JULLIEN *et al.*, 1991; MAILLARD and FOURNIER, 1995). Because of their location in scarcely hunted areas, few subadult females were subjected to strong harassment from hunting.

The large home range of subadult males during the hunting season has already been noted in previous studies. Several hypotheses have been put forward to explain this, e.g. an ontogeny-linked phenomenon (SPITZ, 1992; JANEAU *et al.*, 1995), the expulsion of subadult males by adult males during the rut (BOULDOIRE and VASSANT, 1989) or a response to hunting (VASSANT, 1994; MAILLARD *et al.*, 1996). We believe that this expansion is a result of hunting activities. MAILLARD (1996) showed that the distance between a young male and its mother increased sharply at the beginning of the hunting

season. At this time the subadult males have recently quit the mother group, and their home range is not quite defined. In addition, the dogs are likely to be more frightened of subadult males because of their small size, than of bigger wild boars. Thus subadult males are usually the first ones to be flushed out by the dogs (MAILLARD, 1996). It is likely that in the hunting season harassment affects subadult males more than other boars. However, the home-range size of the radio-tracked subadult males in Arc-en-Barrois did not increase much, a phenomenon which has been stressed before (BRANDT *et al.*, 1998). Although this difference between the two sites may be explained by the difference in traditional hunting methods (flushing dogs vs big hounds), a more likely explanation is that in Arc-en-Barrois the expansion of the home range is limited by the forest edge. Several factors may act to reduce wild boar dispersion in this area: 1) the wooded mountain is surrounded by a cultivated plain, not a favourable place for resting sites, 2) a highway borders the north-east side of the forest patch and is a boundary for wild boar dispersion in this direction, and 3) the hunting pressure was greater at the periphery (3,000 ha hunted by 17 parties) than in the core of the forest (8,000 ha hunted by only one party). The hypothesis of peripheral limits is confirmed by the study of the core-area size. Core areas are not bounded by the periphery (median size in our study: 200 ha), and in the two study areas they are similar in size during the hunting season.

IV.3. EFFECT OF HUNTING METHOD

In the two study areas two different traditional hunting methods were applied (flushing dogs in Arc-en-Barrois vs big hounds in Puéchabon). The dispersion caused by the use of these two methods is a main point of concern for wildlife managers. In France, management objectives are defined for delimited areas (hunting territories). Two adjacent territories may be subjected to different management policies, so effective management implies that the spatial dispersion of wild boar toward neighbouring areas be diminished. Several authors hypothesized that drive hunting with hounds leads to a larger boar dispersion than hunting with flushing dogs (MAILLARD and FOURNIER, 1995; BRANDT *et al.*, 1998). Although this study was not designed to compare the effect of the two methods, we failed to detect a difference between the two sites with respect to the changes in home-range size from summer to the hunting season (*i.e.* no site effect on both the HRR and CAR). The small sample size may explain the lack of difference between the two sites (Table I). However, we emphasized a year effect on the changes in core-area size between the summer and the hunting season (Table IV, Figure 6). Therefore, even if the two hunting methods affect home-range size in different ways, the effect of the hunting method is low in comparison to the annual variability in home-range size. Hence, the use of flushing dogs actually does not seem to be an effective means to reduce wild boar dispersion and increase management efficiency.

Of course, this conclusion is limited by the number of sites studied. We cannot be sure that the results would have been similar if the hunting methods applied in the two areas had been inverted. Although these sites appear representative of habitats hunted by the two methods, it would be interesting to study their effect on a greater variety of habitats. In addition, the monitoring of

wild boars in a control area where they are not hunted would show the seasonal variations in their home range in the absence of hunting, and back up the assertion of this conclusion.

IV.4. HUNTING MANAGEMENT RECOMMENDATIONS

The main limitation of this work is the small sample size of the monitored animals (Table I). This is mainly due to the nature of radiotracking, a cumbersome technique in the field (high costs in terms of staff, expenses and time devoted to data collection). Few wild boar radiotracking studies involve a sufficient number of animals to allow statistical analyses (BABER and COBLENTZ, 1986; MASSEI *et al.*, 1997; BAUBET, 1998). However, we emphasized several points of concern for wildlife managers. The wild boar home range rarely exceeded 2,500 ha during the hunting season, except for subadult males. To allow effective management of the population most females should stay in the hunting territory. The hunting territory should therefore be large enough to prevent that wild boar groups be hunted by several teams during the same day. The size of the territory must be determined according to the home-range size of the hunted boar. A size of about 3,000 ha appears suitable because it allows the boars to move toward quieter areas when they are hunted, and thus prevents their "overdispersion". Hunting pressure in the whole territory should be as homogeneous as possible in space and over time, and managers should avoid harvesting the same location twice in the same week (MAILLARD and FOURNIER, 1995). Moreover, a 3,000-ha hunting territory size also prevents the boars to be submitted to more disturbance by several teams of several smaller hunting territories overlapping the home ranges. Thereby this increases management efficiency.

In the south of France, the hunt is organized following these rules (one team per *commune*), because most *communes* include more than 3,000 ha of wooded area. When smaller territories occur (as in the north of France), several sectors of a wooded mountain area (a management unit) should be grouped to establish a common management policy that would limit disturbance of the animals, and thus their dispersion.

These management rules would have no effect on subadult males, which are more affected by disturbance than females. This, however, is not a major problem and may allow a genetic exchange between adjacent populations.

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DOMAINES VITAUX DU SANGLIER (*SUS SCROFA*) EN ÉTÉ ET PENDANT LA SAISON DE CHASSE DANS DEUX HABITATS EN FRANCE

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MOTS-CLÉS : Sanglier, *Sus scrofa*, radiopistage, domaine vital, zone centrale du domaine vital, été, saison de chasse, âge, sexe, habitat, année, modèle, Hérault, Haute-Marne, France.

RÉSUMÉ

Les domaines vitaux saisonniers des sangliers, Sus scrofa, ont été étudiés dans deux terrains d'étude à habitats différents. L'occupation de l'espace par les sangliers a été étudiée à Puéchabon (Hérault, sud de la France), un terrain typique de l'habitat méditerranéen où la chasse au sanglier se pratique en battue avec des chiens courants, et à Arc-en-Barrois (Haute-Marne, nord-est de la France), un terrain au climat plus tempéré où les sangliers sont chassés à l'aide de chiens broussailleurs. Les localisations de 40 sangliers suivis par radiopistage sur les deux terrains ont été utilisées pour estimer l'évolution de la taille du domaine vital en été (juillet-août) et pendant la saison de chasse (septembre-décembre). Les tailles du domaine vital et de la zone centrale du domaine vital ont été estimées à l'aide de la méthode du noyau à 95 % et à 50 %. Les effets des facteurs (sexe et âge des individus, territoire d'étude – site -, année et interactions entre ces facteurs) sur la taille du domaine vital, sur celle de la zone centrale et sur les rapports entre les tailles pendant la saison de chasse et en été, ont été analysés à l'aide de modèles linéaires. En été, les domaines vitaux et les zones centrales de domaine vital des sangliers suivis sur les deux sites avaient des tailles semblables. Ces estimations ont varié d'année en année, probablement à cause des variations dans le temps de la disponibilité en ressources alimentaires et de la densité de la population à Puéchabon, et de l'augmentation des fourrés à Arc-en-Barrois. Pendant les saisons de chasse, les sangliers des deux sites ont agrandi leur domaine vital. Cette expansion a été plus importante chez les mâles subadultes que chez les autres sangliers à Puéchabon, mais pas à Arc-en-Barrois où les déplacements des sangliers étaient limités par la périphérie de la forêt. Cette expansion a été attri-

buée à la chasse mais, puisque les tailles des zones centrales des domaines des sangliers suivis sur les deux sites étaient semblables, nous pensons que la méthode de chasse n'a pas eu d'effet majeur sur la distribution des sangliers. La taille du domaine vital d'un sanglier n'a dépassé que rarement les 2 500 ha pendant la saison de chasse, sauf chez les mâles subadultes. C'est pourquoi nous recommandons que la taille d'un territoire de chasse, chassé par un seul groupe de chasseurs à un moment donné, fasse la taille d'un domaine vital, soit environ 3 000 ha. Ceci pour qu'une femelle soit moins soumise au dérangement que dans le cas où plusieurs groupes de chasseurs de différents territoires de chasse plus petits chassent en même temps sur son domaine vital.

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