

Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L.

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Abstract In a radiotelemetric study, we analysed space use of 24 female specimens (14 family groups and 14 nonreproductive yearling females) out of 23 wild boar groups for periods between 3 and 39 months. Generally, wild boar used relatively small areas, showed high site fidelity but also a strong individual variation of home ranges, indicating a high flexibility in space use. Although age-specific differences were not statistically significant, female yearlings tended to have larger mean annual home ranges (1,185 ha MCP) than animals ranging in family groups (771 ha). Yearlings also showed a stronger shifting from spring to summer home ranges (2,345 m) and a tendency towards larger home range sizes in summer (791 ha MCP), compared to family groups (shift 1,766 m, MCP 461 ha). Yearlings displayed a dislocation of about 1 km of the annual centre in the first year after dividing from the mother. In contrast, in adults older than 2 years, the dislocation of the annual center was only 240 m.

Keywords *Sus scrofa* · Home range · Radiotelemetry · Seasonality · Age classes

Introduction

In many parts of Europe, rapidly increasing densities of wild boar populations result in severe economical problems. Wild boar cause enormous damages notably in crop fields and forest ecosystems (Bratton 1975; Labudzki and Wlazelko 1991) and are suspected of transmitting disease to domestic livestock (Brauer et al. 2006). Consequently, farmers and animal health authorities claim for a reduction of wild boar populations by various methods (Kaden 1999; Bieber and Ruf 2005; Massei et al. 2006).

To develop an effective and biologically based wild boar management, detailed information about population structure, reproduction and space use is required. This need for knowledge is, in particular, true for family groups dominated by females, who are main subject of regulatory management measures.

Radiotelemetry was frequently used to reveal space use patterns of wild boar, but the roles of age, reproductive status, sex and seasonal changes were often neglected by using different and, thus, incomparable methods, pooling home range sizes of different ages or sexes and lack of referring to distinct and biologically relevant time periods (Mauget 1980; Gerard and Campan 1988; Fischer et al. 2004). Only a few authors estimated annual home ranges of female wild boar (Janeau and Spitz 1984; Boitani et al. 1994; Massei et al. 1997; Baubet 1998; Hahn and Eisfeld 1998), and defined periods, especially of biological importance, were rarely considered (but see Douaud 1983 in Gerard and Campan 1988; Massei et al. 1997). Several studies indicate that changes in home range sizes of wild boar depend on season, food availability and anthropogenic disturbances (Singer et al. 1981; Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002). Most authors assessed larger home ranges

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during winter and assumed food shortage and hunting influencing space use (Singer et al. 1981; Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002). In Sweden, daily home range sizes fluctuated seasonally (Lemel et al. 2003), depending on the length of the night and on weather conditions, whereas no seasonal changes seemed to occur in Italy (Russo et al. 1997). However, none of these authors considered the age and group structure of the observed animals as a factor affecting space use (but see Cousse et al. 1994, who described slightly different space use patterns of postweaning piglets and their mothers). Concerning space use, wild boar react flexibly and individually on many influencing factors as availability of resources (e.g., food, water, shelter), structural parameters of wild boar population (e.g., density, group size, age, sex ratios) and disturbances like recreation, forestry, hunting or predation (see also Boitani et al. 1994). This individuality and flexibility enables wild boar to react on changing environmental conditions, which is obvious in a high variation of seasonal home range sizes and locations within their relatively small scaled and site loyal annual and total home ranges.

The aim of our study was to investigate the roles of age, reproductive status and season for the space use of female wild boar. In total, 24 females out of 23 wild boar family, respectively, yearling groups were radio-tracked for all together more than 3 years to identify changes of annual and seasonal home range sizes and locations in consecutive years and to record potential differences between age classes.

Study area

The study area was located 60 km east of Hamburg in the federal state of Mecklenburg–Western Pomerania (north-eastern Germany, 53.28° N, 10.55° E). The landscape was formed by the Vistula glaciation and rises from 20 up to 100 m above sea level. The study area of 20,000 ha divided into a quite flat outwash plain (one-third), which enables an easy and precise work on radiotelemetry and surrounding moraines. Agriculture and forestry combined with low human settlement (20 inhabitants/km²) were the main features of the area: the study area consisted of 40% agricultural land, 34% forest stand, 23% meadows and pastures with 3% housing estates. The agricultural land was characterised by large fields of a mean size of 20 ha (up to 150 ha maximum). The core area comprised 2,400 ha unfragmented forest, which consisted of 57% pine (*Pinus sylvestris*, *Pinus strobus*), 7% spruce (*Picea abies*, *P. omorica*, *P. glauca*, *P. sitchensis*, *P. pungens*) and 7% other coniferous tree species. The most important deciduous trees were oak (*Quercus robur*, *Quercus petraea*, *Quercus rubra*: 6%), beech (*Fagus sylvatica*: 6%), elder (*Alnus glutinosa*,

A. viridis: 7%), and birch (*Betula pendula*: 7%). During the observation period there was abundant mast of acorns (2002, 2003 and 2005) and beechnuts (2004). By mapping, we found 1.9 baiting stations per 100 ha in forest, and at the border of the forest, within the agricultural fields, 0.5 baiting stations per 100 ha were located (survey of local hunters). With 3 kg at maximum regularised bait (maize, grain or mast) per day and baiting station, we guess that not more than approximately 1,000 kg supplemental food per 100 ha every year were offered.

Based on the Atlantic climate the average annual rainfall amounted to 680 mm, and the mean annual temperature was 8.2°C. The mean annual harvest of the wild boar in the study area increased continuously from 2.83 individuals per 100 ha in 1999/2000 to 5.13 Ind/100 ha in 2005/2006.

Materials and methods

Radiotelemetry

The data presented in this paper were recorded from mid-November 2002 to mid-February 2006. We captured wild boar in big cage traps of 2×5 m and fitted them with ear-tag-transmitters (Andreas Wagener Telemetrieanlagen, Cologne, Germany) with a weight of about 50 g. The transmitters had a beep-ratio of 20 beeps per minute, with a lifespan of 3 years (mean lifespan 363 days), reaching up to 3 km. In this paper, we refer to data from 24 female wild boar out of 23 different groups (family groups $N=14$, yearling groups $N=14$, five yearling groups grew up to family groups, Table 1).

We localized the wild boar once at daytime about four times a week and one to five times at night at least twice a week. Thus, we achieved a mean of 381 localisations per year and animal (total localisations: $N=9360$). To avoid disturbances, we performed the localisations with car-mounted, four-element YAGI antennas using TRX-1000S receivers (Wildlife Materials, Murphysboro, IL, USA). As recommended by Garrott et al. (1986), we used multiple triangulations with at least three bearings per localisation to eliminate reflected signal errors. Moreover, only acceptable bearings, producing error polygons with a size of less than 4 ha, were used to minimise the telemetry error (Zimmerman and Powell 1995), and the centre of the polygon was taken as the actual localisation of a particular wild boar. We mapped all localisations and recorded additional information such as activity, date and time, but also further parameters in case of sightings, such as group size and structure (including presence of offspring) or the presence of other groups nearby etc. Activity was measured by alterations of power of signal: a constant signal strength meant rest, a varying signal meant activity. Zimmerman and Powell (1995) recommended the

Table 1 Data of all female wild boar presented in this study, age at first capture, observed days and month, number of sightings

ID	Group	Age	Group structure	Total duration	Days	Months	<i>N</i> total	<i>N</i> sightings	Seasonal hr	Annual hr
B1	1	A	2A+J (AFG)	18/11/02–07/05/03	170	5.5	160	6	AFG wi02, sp03	
B2	1	A	2A+J, later 1 A+J	12/11/03–18/10/05	706	23	790	15	AFG wi03-au05	AFG12/11/03–11/11/04– 11/11/05
B17	1a	J	2Y, later 2 A+J	18/11/02–15/02/06	1,185	39	1,435	43	YG sp03-wi03, AFG sp04-wi05	YG18/11/02–17/11/03 AFG18/11/03–17/11/04– 17/11/05
B81	1b	J	YG, later AFG	12/11/03–25/11/05	744	24.5	830	13	YG sp04-wi04, AFG sp04-au05	YG12/11/03–11/11/04 AFG12/11/04–25/11/05
B77	1c	J	YG, later AFG	12/11/03–06/09/05	664	22	730	11	YG su04-wi04, AFG sp04-su05	YG12/11/03–11/11/04 AFG12/11/04–06/09/05
B18	2	J	YG	19/11/02–25/03/03	127	4	101	2	YG wi02	
B37	4	J	AFG	06/02/03–18/08/03	193	6.5	281	7	AFG sp03-su03	
B41	5	J	2Y	17/01/03–18/06/03	152	5	184	2	YG sp03-su03	
B45	6	J	6Y declining	21/01/03–26/06/03	156	5	139	5	YG sp03-su03	
B52	7	J	YG	21/01/03–08/09/03	230	7.5	308	12	YG sp03-su03	
B56	9	Y	YG	25/02/03–29/11/03	277	9	458	4	YG sp03-au03	
B59	10	J	see seasonal hr	25/08/03–13/12/05	841	27.5	1,030	19	AFG au03-wi03, YG sp04-wi04, AFG sp04-au05	YG14/12/03–13/12/04 AFG14/12/04–13/12/05
B72	11	J	2A+J	02/09/03–26/08/04	359	12	432	11	AFG au03-su04	AFG02/09/03–26/08/04
B89	12	J	7Y	20/01/04–20/12/04	335	11	310	5	YG sp04-au04	YG20/01/04–20/12/04
B91	13	J	AFG (>3A)	22/01/04–28/10/05	645	21	554	14	AFG sp04-au05	AFG29/10/04–28/10/05
B97	14	Y	Y	30/01/04–27/04/05	453	15	236	7	Y sp04-wi04, AFG sp05	Y22/04/04–22/04/05
B3	15	A	A+5J	26/02/04–03/07/04	128	4	88	3	AFG sp04	
B120	19	Y	YF+4YM, later solitary	09/02/05–22/01/05	347	11.5	412	28	YG sp04, Y su04-wi04	Y09/02/05–22/01/06
B124	20	Y	YG	23/02/05–22/04/05	58	2	80	1	YG sp05	
B128	21	Y	2YF	24/02/05–07/07/05	133	4.5	160	3	YG sp05-su05	
B4	22	A	A+6J	11/05/05–15/07/05	65	2	79	3	AFG su05	
B7	23	A	2A+14J	20/05/05–11/10/05	144	5	162	10	AFG su05-au05	
B8	24	A	A+6F	31/05/05–15/02/06	261	8.5	289	10	AFG su05-wi05	
B132	25	J	AFG	24/10/05–15/02/06	114	4	112	4	AFG wi05	
						Σ	9,360			

A Adult, *J* juvenile (less 12 month), *Y* yearling, *AFG* adult family group (family group with at least one adult female and with piglets), *YG* yearling group, *YF* female yearling, *N* number of localisations, *sp* spring, *su* summer, *au* autumn, *wi* winter, *hr* home range

use of direct measures of location errors instead of bearing angle errors as more practical. To determine the telemetry error, one person hid an ear-tag-transmitter somewhere inside the study area and noticed the exact location in a map. Another person searched for the transmitter like for a wild boar by day and night. As telemetry error, we measured the distance between assumed and real transmitter location and calculated the median distance.

We transcribed the wild boar positionings with a Calcomp® SummaSketchIII digitising tableau to Esri® ArcView 3.2 using the Movement 2.0 extension (Hooge and Eichenlaub 2001). Telemetry data were analysed with Ranges 6v1.2 (Kenward et al. 2003). Otis and White (1999) recommended defined observation periods with, at minimum, 50 local-

isations. We defined home ranges for particular periods as follows:

- 1) annual home ranges: normally exactly 1 year, in four cases at minimum 300 days observation,
- 2) seasonal home ranges, defined as biological time units of equal length: spring: February 16th to May 15th (beginning of rooting on grassland, ending with shift to fields, parturition season); summer: May 16th to August 15th (most of the groups reside inside the fields, beginning with flowering of rapeseed and grain, ending with harvest of grain, rearing and nutrition season); autumn: August 16th to November 15th (rooting in forest and grassland, mast, some in maize fields,

nutrition and fat-deposition season); winter: November 16th to February 15th (season of less food, frost, main hunting season, oestrous and mating season).

We generated incremental area analyses (KHR95 core weighted) to test whether the home ranges observed during different periods were stable. Home ranges were considered as stable when further localisations did not increase home range size. Incremental area analyses were additionally performed for total home ranges (totally observed time, lasting 2 to 39 months).

The following parameters were calculated for analyses of annual and, respectively, seasonal home ranges:

- minimum convex polygons (MCP) to describe the maximum used space (100% of localisations),
- kernel home ranges 95% core weighted (KHR95) to describe the home range (Burt 1943),
- individual core areas (CA) by determining the biggest difference between observed and expected KHR areas using cores at 5% intervals (Samuel et al. 1985), and
- range span (RS), the largest distance between two localisations of one animal.

We assessed the spatial shift of home ranges by the distance between centres of temporary kernel home ranges, calculated with Ranges6. These dislocations were identified for subsequent annual and seasonal home ranges and for home ranges of the identical season in consecutive years.

Home range estimations with the minimum convex polygon (MCP) (Mohr 1947) are not influenced by autocorrelated data (Swihart and Slade 1985). Swihart and Slade (1985) showed the importance of using independent data for home range estimates with kernel methods (Worton 1989). But as the duration of observation (Swihart and Slade 1997) and number and distribution of localisations (de Solla et al. 1999) are more important than the independence, we assumed an absolute minimum time interval of 2 h between localisations as sufficiently independent.

Statistics

We accomplished further analyses in SPSS 12.0 for annual and seasonal home ranges. Unless otherwise noted, all values are presented as mean \pm SD. We used Kruskal–Wallis H test to test for differences of annual home ranges in different years for all animals and Mann–Whitney U test to test for differences in annual and seasonal home ranges between family groups and female yearlings. Therefore, we averaged seasonal home ranges from the same animal and season in consecutive years. As the datasets include dissimilar bases of paired and independent data, we used the exact Friedman test with Monte-Carlo statistics only for

paired datasets to test for differences of home ranges in different seasons for those animals observed throughout all seasons, but presented the mean values for all observed animals. We averaged seasonal home ranges from different years for each animal. All tests were two-tailed with level of significance of $p \leq 0.05$.

Subdivision into age classes

All analyses were done for (1) family groups = adult females with piglets or female piglets within family groups with at least one adult sow leading piglets younger than 12 months; (2) yearlings = females between 12 and 24 months ranging in yearling-groups or solitary without adults, not leading piglets. We inspected the group structure, and if the observed group member was joining the group by casual or, if needed, systematic direct observation regularly at least every 2 months. Nevertheless, the exact number of group members was unknown for most of the groups. As the members of one group stayed together most of the time and did not differ significantly in size and position of their home ranges (mean overlap of KHR95 was 93%, the mean distance between centres was 39 m, Keuling et al. unpublished data), only one member of the group was observed representatively for the whole group.

Results

Due to the plain study area, the telemetry error was quite small: the median deviation between assumed and real location of transmitter was 60 m ($N=28$) at a mean bearing distance of 480 m ($N=127$).

The incremental area analyses proved only 41.7% of the total home ranges ($N=24$) as stable. The home ranges showed longer periods of stability with a sudden increase in early summer and a following period of stability; those of wild boar observed for more than 1 year showed annual steps of stability (Fig. 1a). Most of the annual (87.5%, $N=16$) and seasonal home ranges (74.4%, $N=86$) were stable (Fig. 1b). In two cases of yearlings, the annual home ranges were still increasing. At average, seasonal home range sizes ($N=64$) became independent from the number of localisations at 54 localisations, annual home range sizes ($N=14$) at 261 localisations.

Home range size

The size of annual home ranges of all females revealed no differences between consecutive years (Kruskal–Wallis H test, $N=16$, $df=2$, MCP: $\chi^2=0.315$, $p=0.854$; KHR95: $\chi^2=0.983$, $p=0.612$; CA: $\chi^2=0.315$, $p=0.854$; RS: $\chi^2=0.281$, $p=0.869$).

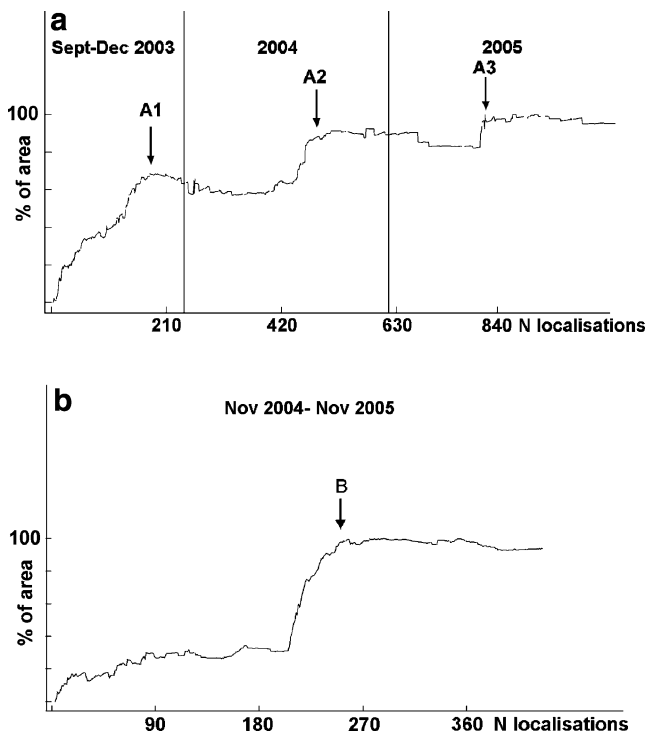


Fig. 1 Two examples for stepwise increasing home range size depending on number of localisations (incremental area analysis for kernel home ranges 95% core weighted): **a** animal A total home range (arrows A1–3 indicate stable annual home ranges 2003, 2004 and 2005), vertical lines indicate turns of years; **b** animal B annual home range 2005 reaching maximum size with begin of summer (arrow B)

The size of annual home ranges of yearlings and family groups did not differ significantly. However, the mean MCP of yearlings (1,184.9±647.2ha, N=7) tended to be slightly bigger than those of family groups (771.4±430.9 ha, N=9; Mann–Whitney U test: Z=-1.535, p=0.125); the same was true for KHR95 (yearlings 600.5±301.2 ha, N=7; family groups 400.0±230.8 ha, N=9; Mann–Whitney U test: Z=-1.641, p=0.101). Estimates of core areas (CA) and range span (RS) did not differ between yearlings and family groups (CA: yearlings 264.3±172.9 ha, N=7, family groups 157.2±85.0 ha N=9, Mann–Whitney U test: Z=-1.111, p=0.266; RS: yearlings 5,254.7±1,644.1 m, N=7, family groups 4,550.2±1014.6 m, N=9, Mann–Whitney U test: Z=-0.74, p=0.458). The mean annual KHR95 amounted to 53.0±12.5% of MCP, the mean core area represented 76.9±7.0% of localisations and was 21.6±7.5% of MCP as well as 42.4±14.9% of KHR95.

No significant differences were found between seasonal home ranges of yearlings and family groups (Fig. 2; Mann–Whitney U test, MCP: spring: Z=-1.477, p=0.140, N=24; summer: Z=-1.620, p=0.105, N=21; autumn: Z=-1.155, p=0.248, N=16; winter: Z=-0.857, p=0.391, N=13, KHR95: spring: Z=-1304, p=0.192, N=24; summer: Z=-0.775, p=0.439, N=21; autumn: Z=-1.575, p=0.155, N=16; winter: Z=-0.703, p=0.482, N=14). A tendency

towards larger MCP-home ranges of yearlings than of family groups occurred in summer (Fig. 2). The mean seasonal KHR95 of all females was 57.9%±18.3 of MCP, 70.9±11.9% of the locations described the mean seasonal core area. The CA was 21.3±11.6% of MCP and 35.9±16.0% of KHR95.

Home range sizes of family groups did not differ significantly between seasons (Friedman test, Monte-Carlo simulation for exact p: MCP: $\chi^2=2.100$, $df=3$, $p=0.654$, $N=4$; KHR95: $\chi^2=2.700$, $df=3$, $p=0.502$, $N=4$; CA: $\chi^2=2.700$, $df=3$, $p=0.504$, $N=4$; RS: $\chi^2=0.600$, $df=3$, $p=0.926$, $N=4$). Thus, the mean values of seasonal MCP, KHR95 (Fig. 2), CA and RS (Table 2) were quite similar (Fig. 2, Table 2). This was also true for yearlings (Friedman test, Monte-Carlo simulation for exact p: MCP: $\chi^2=5.700$, $df=3$, $p=0.146$, $N=4$; KHR95: $\chi^2=2.700$, $df=3$, $p=0.510$, $N=4$; CA: $\chi^2=2.100$, $df=3$, $p=0.649$, $N=4$; RS: $\chi^2=4.920$, $df=3$, $p=0.213$, $N=4$, Fig. 2, Table 2).

Centre shifting

That animals observed as yearling and in the following year (2-year-old, primiparous female) shifted their annual home range centre stronger (1,030.9±285.2 m, N=4) than older animals did (242.3±96.2 m, N=3; Mann–Whitney U test: Z=-2.121, p=0.034, N=7).

The dislocation of seasonal home range centres was significantly greater in yearlings from spring to summer and from summer to autumn than from autumn to winter and from winter to spring (Friedman test, Monte-Carlo simulation for exact p: $\chi^2=7.400$, $df=3$, $p=0.032$, $N=3$; Fig. 3).

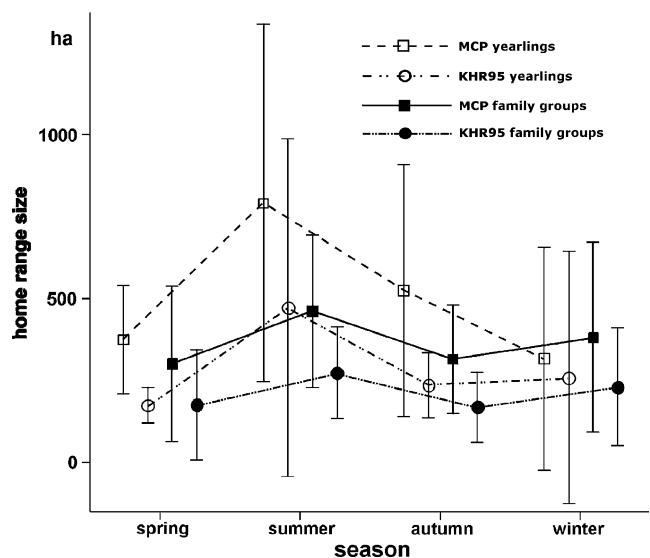


Fig. 2 Mean seasonal home range size±SD of 24 female yearling and adult wild boar during four seasons (MCP Minimum convex polygon, KHR95 kernel home range 95%, yearlings: spring N=12, summer N=10, autumn N=8, winter N=7; family groups: spring N=14, summer N=14, autumn N=11, winter N=10)

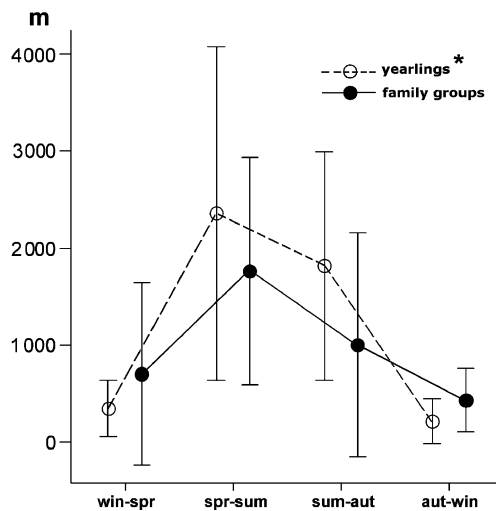


Fig. 3 Mean shifting \pm SD of seasonal home range centres of yearling and adult female wild boar (yearlings: winter–spring $N=3$, spring–summer $N=11$, summer–autumn $N=8$, autumn–winter $N=7$; family groups: winter–spring $N=11$, spring–summer $N=12$, summer–autumn $N=9$, autumn–winter $N=7$). *Friedman test, Monte-Carlo simulation for exact p : yearlings: $p=0.032$

In family groups, dislocations also tended to be greater from spring to summer than in other seasons (Fig. 3), but the differences were not statistically significant for the three tested animals (Friedman test, Monte-Carlo simulation for exact p : $\chi^2=1.000$, $df=3$, $p=0.908$, $N=3$). Consequently, yearlings showed only a bigger shift of seasonal home ranges than family groups from summer to autumn (Fig. 3, Mann–Whitney U test: winter–spring: $Z=-0.926$, $p=0.174$, $N=13$, spring–summer: $Z=-0.083$, $p=0.934$, $N=19$, summer–autumn: $Z=-2.083$, $p=0.037$, $N=15$, autumn–winter: $Z=-1.278$, $p=0.201$, $N=11$). All wild boar (pooled data of family groups and yearlings) varied the centres of the summer ($1,133.9\pm 1,146.4$ m, $N=7$) and autumn ($1,147.4\pm 1,299.7$ m, $N=6$) home ranges of consecutive years more than the spring (433.23 ± 344.90 m, $N=9$) and winter (453.25 ± 441.05 m, $N=8$) home ranges. In winter ($N=17$) and spring ($N=26$) the centres of seasonal home ranges were only situated in the forest. From spring to summer ($N=24$) 71% of wild boar groups shifted their home range centres into agricultural fields; in autumn, 21% of the seasonal home range centres were situated inside the fields

($N=19$), after the wild boar relocated back to winter/spring home ranges in forest.

Discussion

Home range sizes

The annual home range sizes estimated in our study for female wild boar in the North German lowlands were within the range of home range sizes given in literature for female wild boar in Europe and USA (Table 3). These relatively small annual home ranges of female wild boar denote strong site fidelity in all ages and reproductive classes.

Many factors may affect spatial behaviour of wild boar (Boitani et al. 1994). In our richly structured study area, the high abundance of resources like food, water or shelter may lead to small-sized space use of wild boar. The mixed forest stands and hedgerows contain lots of older oaks and beeches, offering mast nearly every year. With approximately 1,000 kg per year per 100 ha, a considerable amount of supplemental food is offered by hunters. Water is always available within less than 1 km, and as the study area is richly structured, shelter is available everywhere (34% forest annual plus another 40% agricultural fields in summer).

As annual home ranges were quite stable, it is important to observe wild boar at least for 1 year to get reliable data on annual spatial needs of this species. However, shorter defined periods may deliver detailed answers on specific questions.

Similarly to the annual home ranges, the mean seasonal home range sizes corresponded quite well to literature data (Table 3). According to published data, the mean home ranges of several wild boar groups were estimated for undefined short periods from 1 to 6 months and ranged between 175 and 470 ha with a total range between 80 and 1600 ha (Mauget 1980, Gerard and Campan 1988; Dinter 1991; Keuling et al. 2001; Fischer et al. 2004). Dinter (1991) suggested supplemental feeding and the absence of agricultural land as reasons for small home ranges in an urban forest of Berlin (Germany). Also, Fischer et al. (2004) described small home ranges as very abiding to

Table 2 Seasonal core areas (CA) and range span (RS) of adult family groups and yearling females and output from Mann–Whitney U test (Z , p)

Season	N adults/yearlings	CA (ha) adults	CA (ha) yearlings	Z	P	RS (m) adults	RS (m) yearlings	Z	p
Spring	14/12	54.7 \pm 56.1	51.1 \pm 28.0	-1.072	0.284	2,682.1 \pm 1,198.4	3,042.9 \pm 870.1	-1.449	0.147
Summer	14/10	128.3 \pm 98.7	158.7 \pm 145.1	-0.282	0.778	3,800.5 \pm 1,056.5	5,304.1 \pm 2,752.5	-1.018	0.309
Autumn	11/8	61.3 \pm 43.3	72.5 \pm 36.6	-0.735	0.462	2,555.0 \pm 710.6	3,597.8 \pm 1,217.9	-1.785	0.074
Winter	10/7	82.4 \pm 96.1	115.0 \pm 183.5	-0.0	1.0	3,137.8 \pm 1,246.3	2,893.6 \pm 2,251.7	-1.571	0.116

Table 3 Overview on literature data of female wild boar home range sizes

Author	Study area	N and sex/age	Home range		Type of home range
			ha MCP	ha KHR	
This study	NE Germany	7 YF	1,185	600	Mean annual
		9 adF	770	400	Mean annual
Massei et al. 1997	Maremma NP Italy	4 F	455		Mean annual
Hahn and Eisfeld 1998	SW Germany	4 F	760		Mean annual
Janeau and Spitz 1984	Grésigne, France	? F	4,000–6,000		Annual
Baubet 1998	French Alps	3 F	760, 940, 960		Annual
			1,380		Mean total
Boitani et al. 1994	Tuscany, Italy	3	370, 560, 2,400		Annual, total
this study	NE Germany	14 YF: 37 seasons	510	285	Mean seasonal
		16 adF: 49 seasons	370	215	Mean seasonal
Douaud 1983 (in Gerard and Campan 1988)		? F:41 seasons	300		Mean seasonal
Massei et al. 1997	MNP, Italy	10 F	245		Mean seasonal
Maillard and Fournier 1995	Hérault, S-France	2 G	205		May–Aug
			680		Sep–Dec un hunted G
			395		Jan–Apr
			255		May–Aug
Singer et al. 1981	Great Smoky Mountains, USA	4 YF	6,625		Sep–Dec hunted G
			4,510		Jan–Apr
			345		Summer
			265		Winter with mast
Baubet 1998	French Alps	23 7	1,395		Winter without mast
			1,100		Summer
Maillard and Fournier 1995	Hérault, S-France	9	415		Winter
			1,390		Summer
Baubet et al. 1998	French Alps	6	5,140		Hunt
			1,225		Summer
Calenge et al. 2002	Haute Marne, NE-France	18	1,540		Hunt
				530	Summer
Calenge et al. 2002	Hérault, S-France	9		1,350	Hunt
				380	Summer
Mauget 1980	Chizé, W-France	7 F		1,380	Hunt
					2–6 months
Gerard and Campan 1988	div. France	3 F	240–425		2, 2, 5 months
Dinter 1991	urban forest Berlin, Germany	8 F	400, 547, 1,600		2–5 months Apr–Sep
Gerard et al. 1992	Toulouse, S-France	1 adF	175		2 months
Keuling et al. 2001	N-Germany	5 F	400		1–5 months Jun–Nov
Sodeikat and Pohlmeier 2002	N-Germany	10 G	316		2–10 weeks before battue
			780		1–5 weeks after battue
Fischer et al. 2004	Geneve, Switzerland	4 G	190		4 months June–Sept

Single values give mean home ranges,

F Female, G (female) family group, Y yearling, ad adult, MCP 100% minimum convex polygon, KHR 95% kernel home range, if sex and age are not mentioned, mixed data were presented

locations reflecting favourable conditions in terms of food and shelter.

Changes in size and shift of seasonal home ranges

In our study, yearling wild boar tended to have larger home ranges in summer and showed a significant bidirectional centre shifting into agricultural fields and back. The family

groups showed no differences in the size of seasonal home ranges, but also tended to have larger centre shifting to summer home ranges. Similar findings were described by Cousse et al. (1994), when they observed piglets more often outside postnatal range than inside, which means the piglets leave or enlarge their home range from spring (postnatal range) to summer. Changing food availability influences summer home ranges as most of the animals forage on

agricultural crops (see also Briedermann 1990; Gerard et al. 1991); thus, they increase their home range by switching between resting sites in forest and feeding places in fields or even shift their complete seasonal home range into agricultural land. Some authors found smaller home ranges in summer (Singer et al. 1981; Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002), but none of them tested for shifting of home ranges between the seasons. Only in two studies, a dislocation of elevation was reported but not statistically tested: D'Andrea et al. (1995) found another seasonal change of resting places in the Italian Alps for two females (138 localisations) and seven yearlings and males (15 localisations). In winter, the wild boar rested in higher elevation; in summer, they sited their resting places near the all-year feeding places (D'Andrea et al. 1995). Singer et al. (1981) detected a shift of home ranges for 20 wild boar of both sexes in Great Smoky Mountains National Park, Tennessee, USA, which occupied areas situated at higher elevation in summer. In years with abundant mast, summer and winter home ranges of females were similar in size. In years with mast failure, more animals changed elevation between winter and summer feeding sites, as the foraging required more searching. Thus, the home ranges were bigger in those winters (mean 1,396 ha) (Singer et al. 1981). In our study, supplemental feeding (baiting) could be one reason for similar home ranges during all seasons, as there is no need to enlarge home ranges searching for food in winter as many baiting stations offer supplemental food especially in forest. We assume no reduced crop damages by supplemental feeding, as wild boar prefer food of natural and agricultural origin (Briedermann 1976, Genov 1981; Baber and Coblenz 1986; Gerard et al. 1991). In addition, supplemental food contributes to the increase of wild boar population, as food availability throughout the year appears to influence body condition and thus reproductive success (Gaillard et al. 1993; Fernández-Llario and Maetos-Quesada 1998; Bieber and Ruf 2005; Santos et al. 2006). Due to these very good nutritional conditions, we could not detect an increase of home range sizes influenced by food shortage.

In our study, total home ranges of animals tracked for more than 1 year increased stepwise from year to year; this was associated with a dislocation of home range centres. The pattern observed was probably mainly caused by foraging at different sites in consecutive summers and autumns, whereas animals showed high site fidelity in winter and spring. Foraging site choice in summer and autumn was mainly depending on the location of actual attractive crop cultivated. This is confirmed by strongest seasonal shifting of home range centres observed in summer and autumn, depending on the spatial location of fields with agricultural crops like rapeseed and wheat (in summer) or maize (in autumn). Supporting this view, Briedermann (1990) reported

that the seasonal spectrum of ingested food strongly reflected the scheme of agricultural crops. The strong variation in distances covered during shifting may reflect individual preferences (Gerard et al. 1991).

In most studies on wild boar home ranges, sample sizes are too small for statistical analyses. Also, in our study, samples allowing statistical analyses were still small. We found no differences in seasonal home range size of adult females. High standard deviations reflected high individual variations of seasonal space use of wild boar groups. This is probably responsible for the lack of significance of statistical analysis. Massei et al. (1997) estimated mean seasonal home ranges of female wild boar and mean monthly home ranges without significant differences between seasons. The monthly home ranges (MCP) of three wild boar groups and three males in a study of Boitani et al. (1994) tended to be larger from October to December. Massei et al. (1997) suggested, contrary to the main opinion (e.g., Boitani et al. 1994), that food availability is a main determinant of home range size with smaller home ranges in years with mast failure. Boitani et al. (1994) assumed food shortage, hunting pressure and bad weather as most important causes of bigger winter home ranges.

Hunting was often proposed as a main reason causing a temporary increase or shifting of home ranges or causing shifting with a decrease of home range size in winter (Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeier 2002). Maillard and Fournier (1995) estimated seasonal home ranges varying stronger under hunting pressure than in situations without hunting, but samples were small. Keuling et al. (2005) observed only small changes in home range sizes after battues and assumed seasonal factors as most important determinants of home range variations. We assume that seasonal changes recorded in this study were mainly caused by combination of differing food availability and locations with suitable shelter for rearing young piglets and assume that hunting is not a main reason for changes in home range sizes.

Dispersal and population

The tendency towards a stronger shift of annual home range centres and towards larger annual home ranges of young females found in this study may indicate a stronger dispersal of young individuals or at least a searching for new own home ranges, and perhaps, they did not have the need to be strongly small scaled, as they did not breed. Further studies reported that most wild boar stayed near their site of birth; however, in the case of dispersal, females emigrated in lower proportions and covered smaller distances when dispersing than males (Stubbe et al. 1989; Briedermann 1990; Truvé 2004).

Conclusion

A relatively small annual home range of female wild boar—like in our study—denotes strong site fidelity in all ages and reproductive classes. Thus, data of wild boar space use may be pooled for different age classes. Female wild boar show only small tendencies towards seasonal changes in home range size, but some, especially yearlings, show further shift of home range centres in summer. The fairly stable spatial behaviour in female wild boar including a philopatric dispersal pattern might be based on a reproductive strategy in which side familiarity is important to maximize reproductive success. Thus, wild boar show an optimal foraging of seasonal resources, as food and shelter. A high individual flexibility in spatial behaviour enables wild boar populations to use these resources at the best, but weakens the statistical significances.

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