Managing wild boar - Considerations for wild boar management based on game biology data

Grouping patterns, space use, dispersal, hunting impact, and hunting efficiency

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Erklärung des Promovenden

Die Übereinstimmung dieses Exemplars mit dem Original der Dissertation zum Thema:

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MANAGING WILD BOAR

Considerations for wild boar management based on game biology data

Grouping patterns, space use, dispersal, hunting impact, and hunting efficiency

Doctoral thesis
Doctor rerum naturalium (Dr. rer. nat.)

Dipl.-Biol. Oliver Keuling

Abstract

Keuling O (2009) Managing wild boar - Considerations for wild boar management based on game biology data. Doctoral dissertation.

Objectives

To prevent economic problems by high wild boar populations, an effective and biologically based wild boar management has to be established. A lot of wild boar research has been done in the last decades. However, game managers were not able to incorporate this knowledge into the development of effective management strategies. Thus, furthermore studies have to be accomplished to expand wild boar science and management.

This thesis, based on a radiotelemetric study in southwestern Mecklenburg–Western Pomerania, presents research results on wild boar space use patterns, dispersal, grouping patterns and divisions. For all these measures I examined the influence of age classes and environmental factors affecting behavioural patterns (e.g. hunting, seasonal resources, seasonal requirements). Finally, I discussed efficiency and amount of hunting pressure of different hunting methods.

Results

The wild boar groups divided temporarily in 12.3 % of all observed localisations. We defined four types of divisions: short-term local, short-term extensive, long-term extensive and final division. The small home range sizes did not differ between age classes or group types with a slight tendency for larger home ranges of yearlings, especially in summer. The shift of summer home ranges was stronger in yearlings than in adults. Three space use patterns occurred in summer: field sows, commuters and forest sows. Only 15 % of all shot animals were shot outside their mothers' home range, only one fourth of these "dispersed" animals were females. Males were shot at larger distances than females. Diurnal activity was positively influenced by daytime length, nutritional needs and fewer disturbances. Due to this reasons an impact of hunting was not clearly detectable. Hunting did influence activity and space use only in moderate intensities. Single hunt from hides is the dominating and an efficient hunting method. The sustainable harvest rate was not exhausted.

Conclusions

The small home ranges and low, male biased, dispersal rates denote strong site fidelity in all age and reproductive classes within female wild boar. The short distances and low dispersal rates, even within males, might be affected by all year round equally distributed high abundance of resources. Changed space use patterns in summer are mainly influenced by changed food availability. Although hunting was often presumed to be responsible for behavioural changes, little direct influences were observed in this study. The results reflect an interaction between habitat types, season, and nutritional needs on most behavioural patterns. Sound nutritional conditions and year-round low hunting pressure might be responsible for similar seasonal home ranges. Group fluctuations, occurrence of sub-groups as well as temporary and final divisions seem to be common behavioural patterns within wild boar groups, depending on age classes, reproduction, and seasonal nutritional supplies. Wild boar groups react flexible on several seasonal internal and extrinsic factors. The omnivore wild boar is enabled easily to adapt to various environments. Its wide eco-ethological plasticity enables the species to colonize new habitats and enlarge its distribution.

All over Europe hunting rates seem to be lower than reproduction of wild boar. To reduce populations and thus, damages, supplemental feeding should be reduced and hunting rates have to be increased especially for females, as all age classes of females are highly reproductive. Hunting management is the most important tool for disease and damage control. As all hunting methods caused similar and negligible disturbances in this study, efficiency should get top priority. The combination of different hunting methods is necessary for reduction on comprehensive areas.

Keywords: wild boar, *Sus scrofa*, game management, radiotelemetry, spatial utilisation, home range, dispersal, hunting impact, seasonality, age class differences, grouping pattern

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Deutsche Zusammenfassung

Keuling O (2009) Schwarzwildbewirtschaftung – Überlegungen zur Schwarzwildbewirtschaftung begründet auf wildbiologischen Daten. Doktorarbeit

Ziele

Um ökonomische Probleme durch Schwarzwild zu vermeiden, muss eine effektive und biologisch fundierte Schwarzwildbewirtschaftung etabliert werden. Die Schwarzwildforschung hat sich in den letzten Jahrzehnten stark entwickelt. Trotzdem konnten viele Erkenntnisse nicht in eine effektive Bewirtschaftung umgesetzt werden. Daher sind Untersuchungen zur Erweiterung des Wissens um das Schwarzwild weiterhin wichtig.

Diese These, basierend auf einer radiotelemetrischen Studie im südwestlichen Mecklenburg-Vorpommern, präsentiert Ergebnisse zu Raumnutzung, Ausbreitung, Rottenverhalten und –teilungen. Für all diese Verhaltensmuster wurden Einflüsse der Altersklassen und anderer Faktoren wie Bejagung, saisonale Ressourcen und Bedürfnisse untersucht. Abschließend werden Effektivität und Störungseinfluss verschiedener Bejagungsmethoden diskutiert.

Ergebnisse

In 12,3 % der Lokalisationen waren die Rotten vorübergehend getrennt. Wir haben vier Trennungstypen definiert: kurzzeitig-lokal, kurzzeitig-extensiv, langzeitig-extensiv und final. Die kleinen Streifgebietsgrößen unterschieden sich kaum zwischen Altersklassen und Rottentypen. Überläuferbachen zeigten eine leichte Tendenz zu größeren Sommerstreifgebieten und verlagerten die Sommerstreifgebiete stärker als Familienrotten. Drei Raumnutzungsmuster waren im Sommer offensichtlich: Feldsauen, Pendler und Waldsauen. Lediglich 15 % aller erlegten Tiere wurden außerhalb ihres Mutterstreifgebietes geschossen, nur ein Viertel dieser „abgewanderten" Tiere waren weiblich. Keiler wurden in größeren Distanzen als Bachen erlegt. Tagaktivität wurde positiv von der Tageslichtlänge, Nahrungsbedarf und geringer Störung beeinflusst. Aufgrund dieser Faktoren war ein Einfluss durch Bejagung nicht klar erkennbar. Bejagung beeinflusste Aktivität und Raumnutzung nur moderat. Die dominierende Jagdart „Einzeljagd auf dem Ansitz" war durchaus effektiv, dennoch wurde die nachhaltige Zuwachsrate nicht abgeschöpft.

Schlüsse

Die kleinen Streifgebiete und niedrigen, keilerdominierten Abwanderungsraten deuten eine starke Standorttreue weiblichen Schwarzwildes in allen Altersklassen an. Die niedrige Abwanderung mit gleichzeitig geringen Distanzen, auch bei Keilern, dürfte durch ganzjährig gleichmäßig verteilte besonders günstige Ernährungsbedingungen beeinflusst sein. Unterschiedliche geänderte Raumnutzungsmuster werden vor allem durch unterschiedliche Nahrungsverfügbarkeiten beeinflusst. Obwohl oft Jagddruck als Hauptursache für Verhaltensänderungen angesehen wird, konnten in dieser Untersuchung nur ein geringer Einfluss der Jagd nachgewiesen werden. Die Ergebnisse reflektieren eine Interaktion zwischen Habitattypen, Jahreszeiten und Nahrungsbedarf auf die meisten Verhaltensmuster. Günstige Ernährungsbedingungen und ganzjährig gleichmäßig niedriger Jagddruck könnten für gleich bleibende saisonale Streifgebiete verantwortlich sein. Änderungen in der Rottenstruktur, Auftreten von Teilrotten sowie temporäre und finale Teilungen scheinen normale Verhaltensmuster beim Schwarzwild zu sein, abhängig von Altersklassen, Reproduktion und saisonalem Nahrungsangebot. Schwarzwildrotten reagieren flexibel auf diverse saisonale interne und externe Faktoren. Das omnivoren Schwarzwild ist befähigt, sich schnell an verschiedenste Umwelten anzupassen. Die große öko-ethologische Plastizität ermöglicht es dieser Art neue Lebensräume zu erschließen und sein Verbreitungsgebiet auszudehnen.

In ganz Europa scheinen die Jagdstrecken unter der Zuwachsrate des Schwarzwildes zu liegen. Um die Populationen, und damit die Schäden zu reduzieren, müssen Fütterungen reduziert und die Bejagung intensiviert werden. Dieses gilt insbesondere für die Bejagung von weiblichem Schwarzwild, da alle Altersklassen hohe Reproduktionsraten aufweisen. Jagdliche Bewirtschaftung ist das wichtigste Werkzeug zur Bekämpfung von Krankheiten und Wildschäden. Da alle Jagdmethoden in der vorliegenden Studie ähnlich geringe Störungen hervorrufen, sollte die Effektivität in den Vordergrund treten. Die Kombination verschiedener Jagdmethoden und Zusammenarbeit der Jäger ist zwingend erforderlich zur Reduktion der Schwarzwildpopulationen.

Schlüsselworte: Wildschwein; *Sus scrofa*; Jagdwirtschaft; Radiotelemetrie; Raumnutzung; Streifgebiet; Ausbreitung; Bejagungseinflüsse; Saisonalität; Altersklassenunterschiede; soziale Gruppierungsmuster

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Contents

List of papers (Appendix)

I based my thesis on the following papers, which will be referred to in the text by their corresponding Roman numerals.

I.   Keuling O, Ihde J, Stier N, Roth M (in prep.) Temporary divisions of wild boar groups *Sus scrofa* L. and within-group relationships. manuscript

II. Keuling O, Stier N, Roth M (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur J Wildl Res 54:403-412

III. Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Wild boar *Sus scrofa* L. space use patterns in summer. Mamm Biol 74:145-152

IV. Keuling O, Stier N, Roth M (2008) How does hunting influence activity and space use in wild boar *Sus scrofa*. Eur J Wildl Res 54:729-737

V.   Keuling O, Lauterbach K, Stier N, Roth M (2009) Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. Eur J Wildl Res online first: DOI 10.1007/s10344-009-0296-x

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Introduction

The wild boar *Sus scrofa* is a common species native in Europe, Asia and northern Africa (BRIEDERMANN 1990). Regionally endangered or extinct in previous centuries wild boar recovered main parts of its native habitat and nowadays is increasing in population density (GOULDING 2003, TRUVÉ 2004, FERREIRA et al. 2006, WILDAUER & REIMOSER 2007), whereby it was introduced or savaged to America and Australia as well as to several Islands (amongst many others BRATTON 1975, MCILROY 1989, COWLED et al. 2006a).

Wild boar populations may positively or negatively affect diverse ecosystems (WELANDER 2000, MASSEI & GENOV 2004, SCHMIDT et al. 2004, KAPLAN 2005). However, recently rapidly increasing densities (SÁEZ-ROYUELA & TELLERIA 1986, GETHÖFFER et al. 2007, CELLINA 2008) of dispersing wild boar populations result in severe economical problems in many parts of Europe. Wild boar cause enormous damages notably in crop fields (LABUDZKI & WLAZELKO 1991, GEISSER & REYER 2004, SANTOS et al. 2004, CELLINA 2008, SCHLEY et al. 2008) and forest ecosystems, especially as alien species (BRATTON 1975, SINGER et al. 1981, GROOT BRUINDERINK & HAZEBROEK 1996, GÓMEZ et al. 2003, GOULDING 2003, ICKES et al. 2003), and are suspected of transmitting disease to domestic livestock (e.g. DEXTER 2003, CALEY & HONE 2004, BRAUER et al. 2006, GORTÁZAR et al. 2007). Especially classical swine fever caused enormous economic damages in pig farming, whereas wild boar populations often provided a reservoir (KERN et al. 1999, ACEVEDO et al. 2007, KRAMER-SCHADT et al. 2007). Consequently, farmers and animal health authorities claim for a stringent reduction of wild boar populations (KADEN 1999, BIEBER & RUF 2005, MASSEI et al. 2008).

Within their behaviour patterns like grouping, space use, dispersal or activity wild boar react flexible and individually on several factors like seasonal resource availability and disturbances like hunting, human activities or predation (SINGER et al. 1981, BOITANI et al. 1994, MAILLARD & FOURNIER 1995, BAUBET et al. 1998, CALENGE et al. 2002, LEMEL et al. 2003). However, internal factors like age and group structure were rarely regarded (BOITANI et al. 1994, MASSEI et al. 1997a).

Managing big game populations, especially ungulates, is conducted to produce meat of high quality (WILKE et al. 2000, DOBROWOLSKA & MELOSIK 2008), but also to regulate populations to control damages (ANDRZEJEWSKI & JEZIERSKI 1978, BOUTIN 1990, GEISSER & REYER 2004, PUTMAN & STAINES 2004, ZIEGLTRUM 2004), diseases and zoonoses (KADEN 1999, CALEY & HONE 2004, ACEVEDO et al. 2007, GORTÁZAR et al. 2007), and vehicle-collisions (DOERR et al. 2001). Game management is also necessary to avoid contingent anthropogenic genetic changes within hunted populations (ALLENDORF et al. 2008) as well as to foster other species (e.g. predation, competition, BAINES 1996) or complete ecosystems (BRATTON 1975, SINGER et al. 1984, WELANDER 1995, ICKES et al. 2003).

Many economic and ecologic factors give reasons for wild boar management, as this species is an important component of the indigenous European fauna and an economically important

game species (CELLINA 2008). For at least 30 years the discussion on wild boar management is ongoing (BRIEDERMANN 1977). However, only few efforts were done, mainly as hunters do often misinterpret game biological findings.

The results of my study offered wide insights in wild boar biology but also some opportunities for wild boar management to be discussed in the following.

To develop an effective and biologically based wild boar management, detailed information about the biology of this species and the influencing factors is required. This need for knowledge is in particular true for family groups dominated by females, who are main subject of regulatory management measures. For understanding mechanisms of epidemics and damages it is essential to gain knowledge about space use and dispersal functions. Answering the following questions may help to investigate management implications, improve hunting methods and thus help to reduce high population levels causing severe economic problems.

1) As a basis for space use first the group stability was studied.
How stable are wild boar groups? Does group stability vary under different conditions?
To assess occurrence and extent of temporal and final group divisions, I analysed the bonds within groups, frequencies of divisions, and group structures of different group types during distinct seasons.
2) Do female wild boar groups differ in home range sizes during different seasons? Do age or sex determine dispersal rates and distances?
To evaluate the roles of age, reproductive status and seasonal effects on spatial patterns, I investigated size and location of wild boar home ranges as well as rates, distances and sex bias of dispersal.
3) Is hunting the main factor influencing activity cycles and space use? Which hunting method causes fewer disturbances? Which hunting method is most efficient?
To weigh up the capability of different hunting methods, I studied the impact of different hunting methods as well as the influence of seasonal environmental factors on activity and spatial patterns of wild boar. Furthermore, I calculated the efficiency of hunting and proportions of hunting methods having a share in the hunting bags within my study area.
Finally I discuss my findings in comparison to literature data under the aspect of hunting management.

Methods

Study area

This thesis is based on data of a study conducted in south-western Mecklenburg–Western Pomerania, 60 km east of Hamburg (north-eastern Germany, 53.28° N, 10.55° E) (see Figure 1 in V). The landscape was formed by the Vistula glaciation and rises from 20 m up to 100 m above sea level. The study area of about 20,000 ha was divided into a quite flat outwash plain (one third of the area), which enabled an easy and precise work on radiotelemetry, and into surrounding moraines. The landscape was richly structured. Agriculture with large fields and grassland took 40 % and 23 % of the area, respectively. The 34 % forest with 2,400 ha un-fragmented forest was mainly mixed with 74 % coniferous, and 26 % deciduous predominant tree species. Solely 3 % human settlement with all in all comparatively low human density of 20 inhabitants per km² means low anthropogenic disturbances. The nutritional conditions were optimal for wild boar (compare HERRERO et al. 2006, TOÏGO et al. 2008) as every year a mast of oak or beech occurred and supplemental food was offered in high amounts by baiting (I-V). Based on the Atlantic climate the average annual rainfall amounted to 680 mm and the mean annual temperature was 8.2° C. Other ungulate species, also hunted by single and drive hunts, within the study area were red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and mainly fallow deer (*Dama dama*).

The mean annual harvest of 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 2005/06.

Capture techniques

We captured wild boar in big cage traps of 5 x 2 x 2 m by video-observation and manual (electromagnetic) release from mid November 2002 to end of March 2006. After separating them in small handling cages 152 wild boar were marked with ear-tags printed with address and phone number of our institute. Additionally, 68 females and 11 males of 30 different groups were fitted with ear tag radiotransmitters (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.

Data collection

The data presented in this thesis were recorded from mid November 2002 to July 2007. The data were collected by triangulation with car mounted antennas (I-V). All localisations were transcribed to ArcView 3.2 and analysed with Ranges6 and Movement 2.0 extension for ArcView.

Summarising chapters

Social grouping patterns (I-IV)

"Mammalian societies are complex socio-ecological systems controlled by the interactions of numerous internal constraints and external factors" (CROOK et al. 1976). Within-group associations are kinships and "friendships" (REINHARDT & REINHARDT 1981).

In polygynous ungulates social groups are usually formed by closely related philopatric females (GREENWOOD 1980, KAMINSKI et al. 2005). Seasonal changes in group size and composition depend on reproductive behavioural patterns in ungulates, and separation for parturition is common in females (PRUITT 1960, GEIST 1971, REINHARDT & REINHARDT 1981, BON et al. 1986, BRIEDERMANN 1990, KLÖS & FRÄDRICH 1991, ALBON et al. 1992, SCHWEDE et al. 1993, LAZO 1994, LE PENDU et al. 1995, SOMERS et al. 1995).

The wild boar *Sus scrofa* is a social species with a strong post weaning association between mothers and daughters lasting several years with some fluctuations throughout the year (KAMINSKI et al. 2005). They usually live in maternal family groups with close kinship whilst males are solitary (BRIEDERMANN 1990, BARRETT & SPITZ 1991, KLÖS & FRÄDRICH 1991, TSAREV 1991). Wild boar groups are assumed to be stable with only seasonal changes, depending mainly on reproduction and mortality (DARDAILLON 1988, GERARD & CAMPAN 1988, BRIEDERMANN 1990, MEYNHARDT 1990, BOITANI et al. 1994, ROSELL et al. 2004). Divisions are suggested to occur after disturbances, especially hunting (SODEIKAT & POHLMEYER 2002, 2003, 2004, SODEIKAT et al. 2005a, SODEIKAT & POHLMEYER 2007), and are suspected to spread wild boar populations and thus disease. In our observations only 4.6 % of the divisions occurred after disturbances.

Wild boar can be separated in three main categories: subadult groups, family groups and solitary males (IV). The space use patterns of different female group types were similar (II).

Group fluctuations, occurrence of sub-groups as well as temporary and final divisions within wild boar groups seem to be common behavioural patterns independent from disturbances, hunting, and death of the alpha sow (I, II, DARDAILLON 1988, NAKATANI & ONO 1995, ROSELL et al. 2004, KAMINSKI et al. 2005), avoiding intra-family competition. This is indicated by all year round group divisions and by different types of divisions (I). Every possible constellation of different animals within one sounder might occur, when these sounders divide. However, some animals are closer associated and stay together more often. One observed final division reflected these within-group associations, as closest associated animals formed the new groups after the final division (I). Home range sizes and location of different group members of a divided group were similar (II).

Although divisions of wild boar groups are common, one animal was considered as representative for its group, as the members of one group spend most of the time together and have similar space use patterns (I, II).

Temporary and final divisions increase frequently with increasing group sizes above the carrying capacity (I, II, BRIEDERMANN 1990, MEYNHARDT 1990, HIGASHI & YAMAMURA 1993).

This is also reflected in higher division rates of family groups than yearling groups. Temporary longer separations of yearling females from their mothers are described as a normal pattern (I, DARDAILLON 1988, NAKATANI & ONO 1995, ROSELL et al. 2004). Seasonal changes of group structure and stability depend on reproduction and also on competition for food (DARDAILLON 1988, GERARD & CAMPAN 1988, BRIEDERMANN 1990, MEYNHARDT 1990, TSAREV 1991, BOITANI et al. 1994, FERNÁNDEZ-LLARIO et al. 1996, ROSELL et al. 2004). However, different needs of family groups and yearling groups (for example in summer, when family groups are more site loyal than not leading yearling females) may lead to long lasting or even final separations of yearling groups and also to different proportions of divisions within different group types (I, II, IV). Adult females have higher requirements for food and shelter for rearing (I-IV, COUSSE et al. 1994), whereas yearlings explore their habitat and potential new home ranges (II).

In summer the wild boar groups were mostly stable, as piglets were mother dependent (COUSSE et al. 1994). This corresponds to several observations of high proportions of very large (family groups) and quite small (yearling groups) groups in summer (BRIEDERMANN 1990, FERNÁNDEZ-LLARIO et al. 1996). An increasing degree of independence of post-weaning piglets from late summer on leads to diurnal activity and small scaled temporary divisions (I, IV, COUSSE et al. 1994). Additionally, the decrease of nutritional resources in winter may be another reason for division to avoid direct competition within family groups. The highest proportion of divisions occurred in spring when adult sows separate for parturition (e.g. DARDAILLON 1988, BRIEDERMANN 1990, MEYNHARDT 1990, TSAREV 1991, FERNÁNDEZ-LLARIO et al. 1996) and one year old animals become more and more independent, respectively. Yearlings remaining within a very large group may separate very often (I).

Feral pig populations are described as one single open population with a high level of social contact (SPENCER et al. 2005). Dispersal did occur only within but not between those populations (HAMPTON et al. 2004b). However, not only the meta groups or sounders of feral pigs (sensu GABOR et al. 1999) seem to be fission-fusion societies (GABOR et al. 1999) but also family groups of wild boar in our study. Similarity of behavioural dendrograms to genetic dendrograms indicated that genetic relationships of feral pigs played a role in observed population structure (GABOR et al. 1999). However, these authors also observed dispersing to adjacent sounders by telemetry and fission of sounders by genetic analyses. Similar results of "unrelated" animals were found by BRÜN & KEULING (2008) and IACOLINA et al. (2009).

The role of the alpha sow seems not as incontrovertible as assumed, nevertheless, is still unanswered regarding reproductive and dispersal processes.

Spatial utilisation and dispersal (II-V)

Space use of wild boar depends on season, food availability and anthropogenic disturbances (SINGER et al. 1981, BOITANI et al. 1994, MAILLARD & FOURNIER 1995, BAUBET et al. 1998, CALENGE et al. 2002, LEMEL et al. 2003). However, few authors considered age and group

structure of the observed animals as a factor affecting space use. Concerning space use, wild boar react flexible and individually on these influencing factors (see also BOITANI et al. 1994). The few, sometimes sketchy, literature on dispersal of wild boar (ANDRZEJEWSKI & JEZIERSKI 1978, STUBBE et al. 1989, TRUVÉ 2004) indicates low dispersal rates (STUBBE et al. 1989, BRIEDERMANN 1990, TRUVÉ 2004). However, high dispersal distances in male wild boar were recorded (ANDRZEJEWSKI & JEZIERSKI 1978, STUBBE et al. 1989). In wild boar, like in most polygynous ungulates, dispersal is male biased (GREENWOOD 1980, KAMINSKI et al. 2005). The direction and intensity of dispersal (of individuals) is influenced by landscape, environment, habitat, and population density (DARDAILLON & BEUGNON 1987, SPITZ 1989, STUBBE et al. 1989, CARGNELUTTI et al. 1992, GERARD et al. 1992, GABOR et al. 1999, TRUVÉ 2004), but also by climate and sex (GABOR et al. 1999).

In my study wild boar home ranges were small scaled and site loyal. This was true even for seasonal, annual and total home ranges (II). A slight tendency for larger summer home ranges (II), especially in yearling groups, was caused by larger centre shifts in this age class (II). Yearlings were predominantly commuters and thus used fields as well as forest in summer (III). Most of the family groups appeared as field groups with small but shifted field use home ranges or as forest groups staying within their small forest home ranges during summer (III). In total most summer home range centres were situated within fields in summer (II).

Males older than 14 months showed higher dispersal rates and distances (V). However, many males also stayed near their natal home range (see also BRIEDERMANN 1990, TRUVÉ 2004) and only a fraction of all surviving first year animals dispersed (V: 50% males, 16.7% females). Nevertheless, male yearlings might have been shot on beginning dispersal and thus, the dispersal distances and rates might even be higher under unhunted conditions.

Many factors influence size and location of wild boar home ranges like resources (e.g. food, water, CARGNELUTTI et al. 1992, GERARD et al. 1992, BOITANI et al. 1994, MASSEI et al. 1997a), reproduction (KURZ & MARCHINTON 1972, JANEAU & SPITZ 1984, BABER & COBLENTZ 1986, DEXTER 1999) and disturbances (e.g. hunting pressure, MAILLARD & FOURNIER 1995, BAUBET et al. 1998, CALENGE et al. 2002, SODEIKAT & POHLMEYER 2002).

Small home ranges result from high food abundance and quality, when wild boar stayed on optimal feeding sites (III, SINGER et al. 1981, BOUTIN 1990, BOITANI et al. 1994, MASSEI et al. 1997a). Home ranges seem to be larger under poor conditions, as wild boar need to roam in search of food and water (BABER & COBLENTZ 1986, CALEY 1997, MASSEI et al. 1997a). In exceptional situations, very small home ranges with less activity are caused by extremely poor conditions (nearly no food and water, e.g. during frost and snow or during drought) and the associated need to save energy (CALEY 1997, MASSEI et al. 1997b, a). The small and seasonal constant home ranges estimated in this study for female wild boar in the North German lowlands correspond to literature data (II-IV). These relatively small home ranges and low dispersal rates of female wild boar denote strong site fidelity in all age and reproductive classes, which might be affected by year-round equably distributed high abundance of resources like food, water or shelter in the richly structured study area (II-V, see also DINTER 1991, BOITANI et al. 1994, FISCHER et al. 2004).

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Varying space use patterns in summer are mainly influenced by changing food availability (II, III, SINGER et al. 1981, BRIEDERMANN 1990, D'ANDREA et al. 1995). Natural habitats are of very big importance within agroecosystems (DARDAILLON & BEUGNON 1987, GERARD et al. 1991), where most of the bedding sites are located during this season. During summer wild boar spent most nights in adjacent arable land (GERARD et al. 1991). As food of high energetic content is preferred (e.g. BRIEDERMANN 1990, GERARD et al. 1991, SCHLEY & ROPER 2003), the cultivation structure of attractive crops influences the seasonal foraging site choice and spectrum of ingested food (BRIEDERMANN 1990, GERARD et al. 1991, HERRERO et al. 2006, SCHLEY et al. 2008). Larger seasonal home ranges during summer might result from larger shift of field use home ranges (II, III, COUSSE et al. 1994, MASSEI et al. 1997a) in commuters and field sows. Additionally, the utilisation of agricultural crop fields is depending on temperature and other weather conditions. Wild boar used fields less during dry and hot summers (2003, 2006, III). In agricultural regions with a lower contingent of forest a higher proportion of commuters and field sows might be assumed, even during other seasons (see GERARD et al. 1991, HERRERO et al. 2006).

Wild boar of different age and sex have different requirements (DARDAILLON 1989, SPITZ 1992, COUSSE et al. 1994, MASSEI et al. 1997b). Hence, differing space use patterns are not astonishing. Female yearlings showed a tendency for stronger shifts and larger home ranges than adult sows, especially in summer (II, III), when many wild boar leave the forest and stay for a long time within fields, often causing damages (LABUDZKI & WLAZELKO 1991, GEISSER & REYER 2004, SANTOS et al. 2004, CELLINA 2008, SCHLEY et al. 2008). However, differing behaviour patterns (home ranges sizes, within-group distances during divisions; I, II) do not only reflect different age classes and sexes, but also individuality and variability (see LOTT 1989). This is shown by the high standard deviation of space use data and reflects individual preferences (GERARD et al. 1991). Although some individuals and families have similar space use behaviour over several years, the three behavioural types and combinations of these reflect variability (II, III, GERARD et al. 1992, BOITANI et al. 1994, BAUBET et al. 1998), especially as other individuals change their space use patterns from year to year (III).

Site loyalty, small scale and low dispersal are shown by high proportions of piglets and yearlings shot at nearby distances, staying with their group. With our results we also demonstrated a high philopatry with a male biased but low dispersal rate (V, STUBBE et al. 1989, BRIEDERMANN 1990, TRUVÉ 2004). The more spacious movement patterns of yearlings indicate dispersal in the second year of life. These animals seem to explore their habitat, in summer they are mainly commuters (III, DARDAILLON 1989, SPITZ 1992, COUSSE et al. 1994). Nevertheless, the observed yearlings were able to roam independently, as they did not lead piglets. Non leading yearlings were never classified as forest sows.

Dispersal starts at the age of sexual maturity (at least at 11-16 months, ANDRZEJEWSKI & JEZIERSKI 1978, MEYNHARDT 1990, TRUVÉ & LEMEL 2003). Typically, wild boar populations do not disperse very far and fast (HAMPTON et al. 2004b, COWLED et al. 2006a). However, sometimes fast dispersal and migrations seems to occur (MARKOV et al. 2004, FERREIRA et al. 2009). Female dispersal or migration is rare and spatially limited (MEYNHARDT 1990, TRUVÉ

& LEMEL 2003, TRUVÉ 2004) as most females stay inside their natal home range, often within their mothers group (STUBBE et al. 1989, BRIEDERMANN 1990, NAKATANI & ONO 1995, TRU-VÉ 2004, KAMINSKI et al. 2005). Our data deliver some hints for female dispersal. Such, yearling groups behave predominantly as commuters. Female yearlings seem to be exploring their habitat (III). Additionally, females show a stronger shift of their annual home range centre from the second to the third year of life (II). All animals which were shot outside their mothers home range were older than 17 months, 25 % of these were females (V).

Dispersal is the most important regulatory factor of wild boar populations in Central Europe apart from hunting. The short distances and low dispersal rates, corresponding to literature (V), might also result from the sound nutritional conditions in consequence of frequent mast years, agricultural crops and baiting sites (II-IV), enabling high densities of big game populations (e.g. BOUTIN 1990, CALEY 1997, MASSEI et al. 1997a).

Effect of hunting and other factors (I-IV)

Hunting was often proposed as a main cause for temporary changes in space use, activity and group structure (BOITANI et al. 1994, MAILLARD & FOURNIER 1995, BAUBET et al. 1998, MAILLARD 1998, CALENGE et al. 2002, SODEIKAT & POHLMEYER 2002, 2003, 2007). Seasonal home ranges were described to vary stronger under hunting pressure (MAILLARD & FOURNIER 1995, BAUBET et al. 1998), although many other factors are also decisive (BOITANI et al. 1994).

In most studies wild boar are described as more nocturnal than diurnal (BRIEDERMANN 1971, MCILROY 1989, BOITANI et al. 1992, BOITANI et al. 1994, LEMEL et al. 2003) and small scaled under sound nutritional conditions (SINGER et al. 1981, BOITANI et al. 1994, MASSEI et al. 1997a), even without hunting. The main part of the bi- or polyphasic activity rhythm is used for foraging (BRIEDERMANN 1971, CUARTAS & BRAZA 1990, RUSSO et al. 1997, CAHILL et al. 2003). Although wild boar show a high intraspecific variability in activity and space use, influenced by numerous factors (BRIEDERMANN 1990, CUARTAS & BRAZA 1990, BOITANI et al. 1994, COUSSE et al. 1995, MASSEI et al. 1997a), in popular belief wild boar are more or less diurnal with small scaled movements when undisturbed (MEYNHARDT 1989a, 1990, HENNIG 1998). Accordingly, they are said to become exclusively nocturnal and spacious when hunted (BRIEDERMANN 1971, BEUERLE 1975, HENNIG 1998).

Contrary to literature, little direct influences of hunting on wild boar behaviour were observed in this study (I-IV). Some authors found similar seasonal activity patterns (BRIEDERMANN 1971, CUGNASSE 1987, RUSSO et al. 1997). Activity cycles seem to depend mainly on age and sex (MCILROY 1989, CUARTAS & BRAZA 1990, COUSSE et al. 1994, COUSSE et al. 1995, JANEAU et al. 1995), weather conditions (CALEY 1997, DEXTER 1998, LEMEL et al. 2003) as well as energetic requirements of female wild boar and nutritional conditions (GUNDLACH 1968, BRIEDERMANN 1971, SINGER et al. 1981, CALEY 1997, MASSEI et al. 1997a). The results reflect an interaction between habitat types and season (IV), as availability of food, shelter, and other resources change seasonally within different habitats (MERIGGI & SACCHI

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1992a, b, ROSELL et al. 2004). A reduced activity in cold and frosty winter months (BRIED-ERMANN 1971) saves energy during sparse nutritional conditions (GUNDLACH 1968, MASSEI et al. 1997a) and as winter nights are long, there is no need for permanent or additional (diurnal) activity. During summer female wild boar have increased energy requirements due to nursing, and piglets have a permanent need for food (IV). Thus, the activity cycles are polyphasic (instead biphasic) during farrowing (GERARD & CAMPAN 1988, RUSSO et al. 1997), and the diurnal activity increases (BRIEDERMANN 1971, COUSSE et al. 1995).

Wild boar were preferential nocturnal, independent of hunting pressure (IV, CALEY 1997, RUSSO et al. 1997), as were captivity reared piglets, which retained this pattern after release (BOITANI et al. 1992). However, a higher diurnal activity farther from human structures (normal human activity) was observed (IV, see also MERIGGI & SACCHI 1992b).

According to literature data only battues with high beating pressure and many dogs, partly caused temporary shift or increase of home ranges (MAILLARD & FOURNIER 1995, SODEIKAT & POHLMEYER 2002, 2003, 2007). However, in France home range shifts occurred only after repeated disturbances (MAILLARD & FOURNIER 1995). Also a direct contact was assumed as the main impact on changing behaviour (SINGER et al. 1981, DEXTER 1996, Sodeikat pers. comm., pers. obs.).

In our study, on average, drive hunts did not increase size or change location of home ranges compared to unhunted groups, even not within different age classes. Hunted wild boar showed slight small scaled escape movements only seldom and returned within one week at the latest. Also the overlaps of neighbouring home ranges did not change after drive hunts (IV). Although different hunting methods seem to have an influence on home range size variations (IV, BOITANI et al. 1994, MAILLARD & FOURNIER 1995, DEXTER 1996, BAUBET et al. 1998, CALENGE et al. 2002, SODEIKAT & POHLMEYER 2002), there might be other external and intrinsic interactive factors triggering the seasonality of spatial utilisation patterns of different age classes (II-IV), such as weather, habitat, availability of food, and water resources, vegetation cover, sibling of piglets, nutritional needs, population density (BOITANI et al. 1994, MASSEI et al. 1997a), and intraspecific variability (LOTT 1989). Especially when resources are sparse, activity is higher and home ranges are larger (MASSEI et al. 1997a).

From our results and from literature three anti-predator strategies could be postulated, showing again the flexibility of this species (BAUBET et al. 1998). Wild boar either stay in well known good habitat, shift into secure areas (smaller home range size), or temporary enlarge their home range to avoid predators or hunting (BAUBET et al.1998, TOULON pers. comm.). These patterns especially occurred in summer (III), when piglets are small and need protection. However, hunting pressure is less during summer, thus, these patterns might reflect a combination of anti-predator strategies and different foraging strategies to avoid competition

The hunting methods influenced wild boar behaviour only in moderate intensities. This might be due to comparatively low hunting pressure and a higher impact of other factors (II-IV). In particular the sound nutritional conditions (BOITANI et al. 1994, MASSEI et al. 1997a, TOÏGO et al. 2008) might be responsible for similar seasonal home ranges. The influence of hunting methods and hunting pressure on behavioural patterns is difficult to assess, compared to all

other seasonal intrinsic and extrinsic impacts and influencing biases (II-IV, see also BRIEDERMANN 1971, ANDRZEJEWSKI & JEZIERSKI 1978, BOITANI et al. 1994, MAILLARD & FOURNIER 1995, MASSEI et al. 1997a, LEMEL et al. 2003).

Efficiency of hunting (IV, V)

Although methods like culling, fencing or vaccination (immunocontraceptive and antiviral) are effective (HONE & ATKINSON 1983, DEXTER 1996, KADEN et al. 2000, COWLED et al. 2006b, KILLIAN et al. 2006, TWIGG et al. 2006), hunting is the most important wild boar management tool (MAILLARD 1998, KADEN 1999, KADEN et al. 2000, GEISSER & REYER 2004). Other methods may not be sustainable without additional hunting (MCILLROY & SAILLARD 1989, KADEN et al. 2000, GEISSER & REYER 2004, 2005).

The wild boar in this study had a low natural mortality of 5.6 % (V). The sustainable harvest rate was not exhausted. The sex ratio was slightly male biased (V). The age structure of the hunting bag differed from the structure of the population. Especially the proportions of shot piglets were to small with a mortality rate of 53 % (KEULING & STIER 2009). Single hunt at bait was the main reason for wild boar shootings. A high proportion was also shot within agricultural fields. Additionally, drive hunts can add a high proportion to the total hunting bag (IV, V). The sex ratio of shot piglets equalled the sex ratio of living piglets (V, FRUZINSKI & LABUDZKI 2002), thus in this age class no sex biased hunting occurred.

All over Europe hunting rates seem to be lower than reproduction of wild boar (V, CSANYI 1995, PERIS et al. 2005, TOÏGO et al. 2008), based on an underestimation of population densities and reproductive rates (GENOV et al. 1994). This is reflected in increasing hunting bags in our study area (I-V) and all over Europe.

Different hunting methods vary in their efficiency within different states of Europe (BRIEDERMANN 1977, HERRERO et al. 1995, ELLIGER et al. 2001, LIEBL et al. 2005). In Germany as well as many central and east European countries hunting from hides is the dominant hunting method (IV, V, BRIEDERMANN 1977, ELLIGER et al. 2001, LIEBL et al. 2005). In the USA shooting at baits is a very efficient management tool to reduce white tailed deer *Odocoileus virginianus* in urban areas (DOERR et al. 2001). Drive hunts contribute to the annual hunting bags in regional different amounts (V, BRIEDERMANN 1977, HERRERO et al. 1995, MAILLARD & FOURNIER 1995, SODEIKAT & POHLMEYER 2002, 2007). E.g. the "monterias" (small repeatedly battues) amount to 90 % of the annual hunting bags in western and southern countries (HERRERO et al. 1995, MAILLARD & FOURNIER 1995).

Concluding discussion

Wild boar biology

In our study area, wild boar roam quite small scaled and site loyal all year round, independent from sex and age, based on permanent optimal conditions and low hunting pressure (II-IV, Massei et al. 1997a, Toïgo et al. 2008). However, the very social wild boar shows a high flexibility and individuality of behaviour patterns depending on several external and intrinsic factors (e.g. Boitani et al. 1994, Baubet et al. 1998, Santos et al. 2004). This flexibility is obvious e.g. in high variation of social grouping, spatial usage, and activity and allows for optimal exploitation of resources whilst avoiding intra-familial competition. Variations of group structure, divisions, space use, and activity cycles seem to be rather induced by seasonal changes (see also Boitani et al. 1994, D'Andrea et al. 1995) than by hunting.

Some authors showed low dispersal rates (Stubbe et al. 1989, Briedermann 1990, Truvé 2004) in wild boar populations. Most of the animals stayed near to their site of birth. Whilst adults showed high site fidelity, philopatry (II-V), and high reproduction up to 280 % (Gethöffer et al. 2007, Cellina 2008), only some subadults dispersed (see also Stubbe et al. 1989). The high reproductive success is based on an early sexual maturity and large litters, compared to other ungulates (Kaminski et al. 2005). Females emigrated in lower proportions and covered smaller distances when dispersing than males (Stubbe et al. 1989, Briedermann 1990, Truvé 2004), which prospect new areas first (Truvé 2004).

These patterns are typical for a pioneer species. However, actual pioneer species are strongly specialised to colonise specific habitats. Nevertheless, some characteristic features of a pioneer species occur in wild boar: As mentioned before, reproduction is high and dispersal is male biased. Dardaillon (1989) compared the high dietary diversity of wild boar with pioneer species.

The wide plasticity enables the omnivore wild boar to customize easily to various environments, to colonize new habitats (Genov 1981a, Acevedo et al. 2006) and enlarge the species distribution, like its extension of area since 1950s (Genov 1981b, a) by reacting to changing environmental conditions and optimal foraging, exploiting all available food resources at the best (Genov 1981b, a, Santos et al. 2004). Although mainly described as forest or forest edge species in near natural habitats (e.g. Genov 1981a, Briedermann 1990, Leaper et al. 1999, Fernández et al. 2006, Fonseca 2008), they are able to use arable land optimal (II, III, Dardaillon 1987, Schley & Roper 2003, Geisser & Reyer 2004, Herrero et al. 2006) and do not have the need for large forests (Gerard et al. 1991, Herrero et al. 2006) as long as food, shelter and water are available (Massei et al. 1996, Massei et al. 1997b, a, Baubet et al. 1998, Sodeikat & Pohlmeyer 2007).

I assume the effect of hunting on wild boar behaviour as negligible under moderate hunting pressure and optimal equably distributed nutritional conditions. Thus, no eminent surplus dis-

persal or infection risks, caused by reactions on hunting, seem to be existent. However, wild boar, somehow, react on disturbances, especially hunting. The observed activity and space use patterns seem to be influenced by nutritional needs as well as avoidance of hunting (III, IV). This is particularly obvious in summer, when all three space use patterns occur (III). Wild boar groups are closer associated than other ungulates, nevertheless, divisions are a common behavioural pattern, which has not been described before (I). Thus, wild boar are able to vary the group structure and might be able to regroup (IACOLINA et al. 2009). All these different patterns display different cultures or "intraspecific variability of social systems" (LOTT 1989), where piglets learn behavioural patterns from their mother (I-IV).

Management considerations

Wild boar population management is necessary to counteract the economic problems. A reduction of high populations seems to be inevitable, especially to stop infection chains and to reduce crop damages. A reproduction control sensu stricto might only be done by immuno-contraceptive vaccination (KILLIAN et al. 2006). As the nutritional conditions are already very high in the agricultural environments, stopping supplemental feeding might have less impact on reproduction (GETHÖFFER et al. 2007, CELLINA 2008). Thus, to control reproduction a regulation of the reproductive animals is necessary. Nowadays all age classes of females are highly reproductive, thus mainly piglets and females, yearlings as well as adults, have to be shot (BIEBER & RUF 2005, SODEIKAT et al. 2005b, GETHÖFFER et al. 2007, CELLINA 2008, SERVANTY 2008).

Predation, natural mortality and road mortality have only small impact on wild boar populations, whereas the environment, especially nutrition or hunting, is mainly decisive (V, OKARMA et al. 1995, KANZAKI & PERZANOWSKI 1997, PERIS et al. 2005, NORES et al. 2008, TOÏGO et al. 2008). Mammal populations without predation are strongly dependent on environment and food (SAETHER 1997). Optimal nutritional conditions within agricultural formed environments increase reproduction and population, supported by supplemental feeding (ANDRZEJEWSKI & JEZIERSKI 1978, BOUTIN 1990, MASSEI et al. 1997b, SAETHER 1997, BIEBER & RUF 2005, GEISSER & REYER 2005, GETHÖFFER et al. 2007, CELLINA 2008). Population dynamics of wild boar reflected fluctuations in availability of food, especially oak mast (CAHILL & LLIMONA 2004, MAILLARD & FOURNIER 2004).

The reduction of wild boar populations in woodland during winter is a precondition for regulation and prevention of damages in agricultural fields (III, MEYNHARDT 1989b, HAPP 2002, LIEBL et al. 2005), as well as hunting small piglets early and intense inside agricultural fields in summer (BRIEDERMANN 1977, MEYNHARDT 1991, MAZZONI DELLA STELLA et al. 1995, HENNIG 1998).

In summer 80 % of wild boar groups live predominantly within fields, causing high damages (III, see also GERARD et al. 1991, CAHILL et al. 2003). To avoid crop damages, this proportion of animals, which produce damage, has to be decreased. This should be done mainly by decreasing population or by shooting field sows, commuters, and last but not least by shooting

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piglets, to avoid them to learn these space use patterns (II, III). Besides, mothers of shot piglets might learn and stay in the forest for the future (III, MEYNHARDT 1990).

Supplemental feeding and fencing were already assumed as damage prevention tools to be only efficient at an initial phase, if at all (PASLAWSKI 1975, HONE & ATKINSON 1983, MAILLARD 1998, GEISSER & REYER 2004). After some years the effect will disappear as a result of population increase and habituation. Nevertheless, several studies showed the efficiency of supplemental feeding, afar from crop fields at risk, as a non lethal damage control tool within several species (e.g. ANDRZEJEWSKI & JEZIERSKI 1978, ZIEGLTRUM 2004, FATTEBERT et al. 2005). However, most authors suppose supplemental feeding to be counterproductive in wild boar, as it promotes the already high reproduction, and thus, often does not prevent damages (II, BOUTIN 1990, GEISSER & REYER 2004, BIEBER & RUF 2005, CELLINA 2008). By all means, for halting the population increase or even a population reduction supplemental feeding of wild boar should be reconsidered, if not restricted (BIEBER & RUF 2005, GEISSER & REYER 2005). Nevertheless, hunting at baiting stations with only small amounts of offered food is highly effective (V, BRIEDERMANN 1977, DOERR et al. 2001, ELLIGER et al. 2001, LIEBL et al. 2005).

Hunting management is the most important tool for disease and damage control (MAILLARD 1998, KADEN 1999, GEISSER & REYER 2004). As hunting traditions, demography, landscape, habitat structure and nutritional conditions influence hunting efficiency (BRIEDERMANN 1990, CSANYI 1995, HERRERO et al. 1995, FERNÁNDEZ-LLARIO et al. 2003, ACEVEDO et al. 2005, UEDA & KANZAKI 2005, ACEVEDO et al. 2006, MASSOLO & MAZZONI DELLA STELLA 2006, TSACHALIDIS & HADJISTERKOTIS 2008), hunting techniques have to be adapted to the local conditions (HEBEISEN 2007). Hunting may be conducted as effective management tool for regulating or even reducing population densities and thus, may reduce the risk of spreading epidemics. However, using effective methods intensified will also increase hunting pressure, and thus, might increase spacious behaviour (e.g. MAILLARD & FOURNIER 1995, BAUBET et al. 1998, CALENGE et al. 2002).

Higher numbers of yearlings might increase the risk of infections and damages, they behave more spacious than family groups (I, II, III, V). It is of big importance, to shoot more piglets at an early age (GENOV et al. 1994, BIEBER & RUF 2005) to prevent them from becoming pubescent. This is particularly true, as the total mortality of piglets is much lower than a regulation of the reproduction would necessitate. However, reduction or regulation of a population is easier by shooting augmented yearling and adult females (GENOV et al. 1994, BIEBER & RUF 2005, SERVANTY 2008).

Culling methods like shooting from helicopters, trapping, poisoning, etc. (e.g. MCILLROY & SAILLARD 1989, DEBERNADI et al. 1995, MCILROY 1995, DEXTER 1996, COWLED et al. 2006b, TWIGG et al. 2006) and immunocontraceptive vaccination (KILLIAN et al. 2006) are highly effective; nevertheless, they do not totally replace traditional hunting (HAMPTON et al. 2004a). Traditional hunting may be conducted to control the remaining low density populations (HAMPTON et al. 2004a), to produce venison and at least for recreation. However, a combination of culling and traditional hunting may enhance effectiveness in reducing popula-

tions, especially in densely populated urban or spacious rural areas (DEBERNADI et al. 1995, MCILROY 1995).

As all hunting methods cause similar and negligible disturbances, efficiency should get top priority. The combination of different hunting methods is necessary for reduction (LIEBL et al. 2005). Comprehensive and simultaneous drive hunts with dogs within several hunting grounds on large areas may be highly effective and only short term disturbing (MEYNHARDT 1991, MARSAN et al. 1995, CALENGE et al. 2002, HAPP 2002, LIEBL et al. 2005, SODEIKAT & POHLMEYER 2007), when well prepared by using logs of every hunter from previous hunts (HAPP 2002, WÖLFEL 2003, BÖHM 2004). While planning drive hunts, needs and habitat preferences of wild boar should be considered. For bedding sites wild boar prefer sheltering natural habitats, like woodlands and often also scrubs and heathlands with heterogeneous distribution (CARGNELUTTI et al. 1990, GERARD et al. 1991, FONSECA 1997, CAHILL et al. 2003). Wild boar have closer associations than most other ungulates, but not as close as often described (I, GABOR et al. 1999, BRÜN & KEULING 2008, IACOLINA et al. 2009). The role of the alpha sow is still unanswered. As long as we don not clearly know the actual role of the alpha sow within the groups and reproductive processes an accidental destruction of the social structure of wild boar family groups should be avoided (I, EISENBARTH & OPHOVEN 2002). Thus, on drive hunts only piglets and yearlings should be hunted.

For sustainable management, or even reduction of a population, at least the net population increase has to be harvested. Hence, hunting has to be intensified, particularly to increase the proportion of harvested piglets. As most hunts are held at weekends (recreational hunting) and in winter (depending on reproductive cycle) (BRIEDERMANN 1977, HERRERO et al. 1995), additional hunts during week might be a possibility to increase the hunting bags.

To increase harvest rates for regulating populations, shooting higher proportions of female wild boar has already been stated by BRIEDERMANN et al. (1986). These authors also recommended higher hunting pressure as well as changes in economy and psychology of hunters. However, nothing happened until today. Thus, hunters have to be stimulated (hunting as leisure activity, UEDA & KANZAKI 2005) and "…wildlife managers should consider hunter willingness to harvest piglets and females…" (TOÏGO et al. 2008). Sexual and age class population data have to be reliable, not to destabilise social structures and the dominance hierarchy by biased shooting of age and sex (e.g. by trophy hunt: MILNER-GULLAND et al. 2004, MILNER et al. 2007).

Well organised drive hunts might contribute basically to the annual hunting bag (BRIEDERMANN 1977, MAILLARD & FOURNIER 1995, SODEIKAT & POHLMEYER 2002, 2007). Intensifying comprehensive drive hunts and small battues especially for wild boar (deer should be mainly shot on another different hunt) will increase the proportion of this method at annual hunting bags (CSANYI 1995, CALENGE et al. 2002, BÖHM 2004, LIEBL et al. 2005). Only a cooperation of hunters can raise hunting efficiency and, thus, prevent officially ordered culling.

References

Acevedo P, Vicente J, Villanua D, Alzada V, Pérez E, Gortazar C (2005) Effects of the landscape structure on wild boar (*Sus scrofa* L., 1758) abundance and hunting effectiveness in Atlantic Spain. in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.**259-260**

Acevedo P, Escudero MA, Munoz R, Gortázar C (2006) Factors affecting wild boar abundance across an environmental gradient in Spain. Acta Theriol 51:**327-336**

Acevedo P, Vicente J, Höfle Ú, Cassinello J, Ruiz-Fons F, Gortazar C (2007) Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. Epidemiol Infect 135:**519-527**

Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH (1992) Density dependent changes in the behaviour of female kin in red deer. J Anim Ecol 61:**131-137**

Andrzejewski R, Jezierski W (1978) Management of a Wild Boar population and its effects on commercial land. Acta Theriol 23:**309-339**

Baber DW, Coblentz BE (1986) Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J Mammal 67:**512-525**

Barrett RH, Spitz F (Eds.) (1991) Biology of suidae. - Biologie des suidés. I.R.G.M., Toulouse

Baubet E, Brandt S, Touzeau C (1998) Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus scrofa*). Analyses préliminaires. Gibier Faune Sauvage 15:**655-658**

Beuerle W (1975) Freilanduntersuchungen zum Kampf- und Sexualverhalten des Europäischen Wildschweines (*Sus scrofa* L.). Z Tierpsychol 39:**211-258**

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J Appl Ecol 42:**1203-1213**

Böhm E (2004) Drückjagd auf Sauen. Neumann-Neudamm, Melsungen

Boitani L, Mattei L, Morini P, Zagarese B (1992) Experimental release of captivity reared wild boar (*Sus scrofa*). in: "Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse,.**413-417**

Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild boar in Tuscany, Italy. J Mammal 75:**600-612**

Bon R, Campan R, Dardaillon M, Demeautis G, Gonzales G, Teillaud P (1986) Comparative study of the seasonal variations of the social structures in three french ungulates. Wiss Zeitschr Humboldt-Universität Berlin Math.-Nat. R. 3:**254-258**

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can J Zool 68:**203-220**

Bratton SP (1975) The effect of the European wild boar (*Sus scrofa*) on Gray Beech Forest in the Great Smokey Mountains. Ecology 56:**1356-1366**

Brauer A, Lange E, Kaden V (2006) Oral immunisation of wild boar against classical swine fever: uptake studies of new baits and investigations on the stability of lyophilised C-strain vaccine. Eur J Wildl Res 52:**271–276** doi:10.1007/s10344-006-0048-0

Briedermann L (1971) Ermittlungen zur Aktivitätsperiodik des Mitteleuropäischen Wildschweines (*Sus scrofa* L.). Zool Garten 40:**302-327**

Briedermann L (1977) Jagdmethoden beim Schwarzwild und ihre Effektivität. Beitr Jagd- u Wildforschung 10:**139-152**

Briedermann L, Dittrich G, Goretzki J, Stubbe C, Horstmann H-D, Schreiber R, Klier E, Siefke A, Mehlitz S (1986) Entwicklung der Schalenwildbestände in der DDR und Möglichkeiten der Bestandsregulierung. Beitr Jagd- u Wildforschung 14:**16-32**

Briedermann L (1990) Schwarzwild. Neumann-Neudamm, Melsungen. 2nd edition.

Brün J, Keuling O (2008) Socio-spatial behaviour and genetics of wild boar in North-Eastern Germany. in: Abstracts of the 7th International Symposium on Wild Boar (*Sus scrofa*) and Sub-order Suiformes.**14**

Cahill S, Llimona F, Gràcia J (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. Wildl Biol 9 Suppl:**3-13**

Cahill S, Llimona F (2004) Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**37-52**

Calenge C, Maillard D, Vassant J, Brandt S (2002) Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game Wildl Sci 19:**281-301**

Caley P (1997) Movement, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. Wildl Res 24:**77-87**

Caley P, Hone J (2004) Disease transmission between and within species, and the implications for disease control. J Appl Ecol 41:**94-104**

Cargnelutti B, Gerard JF, Spitz F, Valet G, Sardin T (1990) Occupation par le sanglier (*Sus scrofa*) des habitats dùn agro-écosystème modifiè lors de la mècanisation de l'agriculture. Gibier Faune Sauvage 7:**53-66**

Cargnelutti B, Spitz F, Valet G (1992) Analysis of dispersion of Wild Boar (*Sus scrofa*) in Southern France. in: "Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse.**423-425**

Cellina S (2008) Effects of supplemental feeding on the body condition and reproductive state of wild

boar *Sus scrofa* in Luxembourg. PhD, University of Sussex

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can J Zool 72:**1691-1694**

Cousse S, Janeau G, Spitz F, Cargnelutti B (1995) Temporal ontogeny in the wild boar (*Sus scrofa* L.): a systemic point of view. IBEX J Mt Ecol 3:**122-125**

Cowled BD, Lapidge SJ, Hampton JO, Spencer PBS (2006a) A cautionary finding for applied pest management: measuring the demographic and genetic effects of pest control in a highly persecuted feral pig population. J Wildl Manage 70:**1690–1697**

Cowled BD, Lapidge SJ, Smith M, Linton Staples L (2006b) Attractiveness of a novel omnivore bait, PIGOUT®, to feral pigs (*Sus scrofa*) and assessment of risks of bait uptake by non-target species. Wildl Res 33:**651-660**

Crook JH, Ellis JE, Goss-Custard JD (1976) Mammalian social sytems: Structure and function. Anim Behav 24:**261-274**

Csanyi S (1995) Wild boar population dynamics and management in Hungary. IBEX J Mt Ecol 3:**222-225**

Cuartas P, Braza F (1990) Reparto temporal de actividades del jabali (*Sus scrofa*) en Doñana (SO Spain). Acta Vert 17:**91-102**

Cugnasse JM, P. Teillaud & R. Bon (1987) Résultats préliminaires sur l'activité diurne et sur la structure des groupes de sangliers (*Sus scrofa*L.) dans les monts de l'Epinouse. Gibier Faune Sauvage 4:**267-277**

D'Andrea L, Durio P, Perrone A, Pirone S (1995) Preliminary data of the wild boar (*Sus scrofa*) space use in mountain environment. IBEX J Mt Ecol 3:**117-121**

Dardaillon M (1987) Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (Southern France). Acta Theriol 32:**389-401**

Dardaillon M, Beugnon G (1987) The influence of some environmental characteristics on the movements of wild boar *Sus scrofa*. Biol Behav 12:**82-92**

Dardaillon M (1988) Wild boar social groupings and their seasonal changes in Chamargue, southeastern France. Z Säugetierkunde 53:**22-30**

Dardaillon M (1989) Age-class influence on feeding choices of free-ranging wild boars (*Sus scrofa*). Can J Zool 67:**2792-2796**

Debernadi P, Patriarca E, Sabidussi R (1995) Wild boar (*Sus scrofa*) control in regional park "La Mandria" (Piedmont, NW Italy). IBEX J Mt Ecol 3:**237-240**

Dexter N (1996) The effects of an intensive shooting exercise from a helicopter on the behaviour of surviving feral pigs. Wildl Res 23:**435-441**

Dexter N (1998) The influence of pasture distribution and temperature on habitat selection by feral pigs in a semi-arid environment. Wildl Res 25:**547-559**

Dexter N (1999) The influence of pasture distribution, temperature and sex on home-range size of feral pigs in a semi-arid environment. Wildl Res 26:**755-762**

Dexter N (2003) Stochastic models of foot and mouth disease in feral pigs in the Australian semi-arid rangelands. J Appl Ecol 40:**293-306**

Dinter U (1991) Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten unter besonderer Berücksichtigung menschlicher Störungen. Dissertation, Ludwig-Maximilian-Universität München

Dobrowolska A, Melosik M (2008) Bullet-derived lead in tissues of the wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*). Eur J Wildl Res 54:**231–235** DOI 10.1007/s10344-007-0134-y

Doerr ML, McAninch JB, Wiggers EP (2001) Comparison of four methods to reduce white-tailed deer abundance in an urban community. Wildl Soc Bullet 29:**1105-1113**

Eisenbarth E, Ophoven E (2002) Bewegungsjagd auf Schalenwild. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Elliger A, Linderoth P, Pegel M, Seitler S (2001) Ergebnisse einer landesweiten Befragung zur Schwarzwildbewirtschaftung. WFS-Mitteilungen:**5-7**

Fattebert J, Fischer C, Hebeisen C, Baubet E (2005) Efficiency of supplemental feeding and fencing to diminish wild boar (*Sus scrofa*) damages to agricultural crop in the basin of Geneva, Switzerland. in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.**325**

Fernández-Llario P, Carranza J, Hidalgo de Trucios SJ (1996) Social organisation of the wild boar (*Sus scrofa*) in Doñana National Park. Misc Zool 19:**9-18**

Fernández-Llario P, Mateos-Quesada P, Silverio S, Santos P (2003) Habitat effects and shooting techniques on two wild boar (*Sus scrofa*) populations in Spain and Portugal. Z Jagdwiss 49:**120-129**

Fernández N, Kramer-Schadt S, Thulke H-H (2006) Viability and risk assessment in species restoration: planning reintroductions for the wild boar, a potential disease reservoir. Ecol Soc 11:**6** [online] URL:http://www.ecologyandsociety.org/vol11/iss1/art6/

Ferreira E, Souto L, Soares AMVM, Fonseca C (2006) Genetic structure of the wild boar (*Sus scrofa* L.) population in Portugal. Wildl Biol Pract 2:**17-25** DOI: 10.2461/wbp.2006.2.4

Ferreira E, Souto L, Soares AMVM, Fonseca C (2009) Genetic structure of the wild boar population in Portugal: Evidence of a recent bottleneck. Mamm Biol 74:**263-273** doi:10.1016/j.mambio.2008.05.009

Fischer C, Gourdin H, Obermann M (2004) Spatial behaviour of the wild boar in Geneva, Switzerland: testing methods and first results. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**149-155**

Fonseca C (1997) Influence of landscape and environmental factors upon harvest rate and habitat selection of wild boar in Central Portugal. J Wildl Res 2:**296-302**

Fonseca C (2008) Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. Eur J Wildl Res 54:**361–366** DOI 10.1007/s10344-007-0144-9

Fruzinski B, Labudzki L (2002) Management of wild boar in Poland. Z Jagdwiss 48 Suppl:**201-207**

Gabor TM, Hellgren EC, Van Den Busche RA, Silvy NJ (1999) Demography, sociospatial behaviour and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. J Zool Lond 247:**311-322**

Geisser H, Reyer H-U (2004) Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J Wildl Manage 68:**939-946**

Geisser H, Reyer H-U (2005) The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). J Zool Lond 267:**89-96** doi:10.1017/S095283690500734X

Geist V (1971) Mountain sheep. A study in behaviour and evolution. Univ. of Chicago Press, Chicago, London

Genov P (1981a) Significance of natural biocenoses and agrocenoses as the source of food for wild boar (*Sus scrofa* L.). Ekol Pol 29:**117-136**

Genov P (1981b) Die Verbreitung des Schwarzwildes (*Sus scrofa* L.) in Eurasien und seine Anpassung an die Nahrungsverhältnisse. Z Jagdwiss 27:**221-231**

Genov PW, Massei G, Kostova W (1994) Die Nutzung des Wildschweins (*Sus scrofa*) in Europa in Theorie und Praxis. Z Jagdwiss 40:**263-267**

Gerard JF, Campan R (1988) Variabilité éco-ethologique chez le sanglier europeén: comparision des travaux francaise. Cahiers d'Ethologie Appliquee 8:**63-130**

Gerard JF, Cargnelutti B, Spitz F, Valet G, Sardin T (1991) Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriol 36:**119-129**

Gerard JF, Cargnelutti B, Spitz F (1992) Relation entre anisotropie de l'occupation de l'espace et dispersion: un example chez le sanglier du sud-ouest de la France. Mammalia 56:**177-187**

Gethöffer F, Sodeikat G, Pohlmeyer K (2007) Reproductive parameters of wild boar (*Sus scrofa*) in three different parts of Germany. Eur J Wildl Res 53:**287-297** DOI 10.1007/s10344-007-0097-z

Gómez JM, Garcia D, Zamora R (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. For Ecol Manage 180:**125-134**

Gortázar C, Ferroglio E, Höfle U, Frölich K, Vicente J (2007) Diseases shared between wildlife and livestock: a European perspective. Eur J Wildl Res 53:**241-256** DOI 10.1007/s10344-007-0098-y

Goulding M (2003) Wild boar in Britain. Whittet Books Ltd, Suffolk

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:**1140-1162**

Groot Bruinderink GWTA, Hazebroek E (1996) Wild boar (*Sus scrofa scrofa*L.) rooting and forest regeneration on podzolic soils in the Netherlands. For Ecol Manage 88:**71-80**

Gundlach H (1968) Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik beim Europäischen Wildschwein (*Sus scrofa* L.). Z Tierpsychol 25:**955-995**

Hampton J, Pluske JR, Spencer PBS (2004a) A preliminary genetic study of the social biology of feral pigs in south-western Australia and the implications for management. Wildl Res 31:**375-381**

Hampton JO, Spencer PBS, Alpers DL, Twigg LE, Woolnough AP, Doust J, Higgs T, Pluske JR (2004b) Molecular techniques, wildlife management and the importance of genetic population structure and dispersal: a case study with feral pigs. J Appl Ecol 41:**735-743**

Happ N (2002) Hege und Bejagung des Schwarzwildes. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Hebeisen C (2007) Population size, density and dynamics, and social organization of wild boar (*Sus scrofa*) in the Basin of Geneva PhD, Université de Neuchâtel

Hennig R (1998) Schwarzwild. BLV Verlagsgesellschaft mbH, München, Wien, Zürich. 5. Aufl. edition.

Herrero J, García-Serrano A, García-Gonzáles R (1995) Wild boar (*Sus scrofa* L.) hunting in southwestern Pyrenees (Spain): preliminary data. IBEX J Mt Ecol 3:**228-229**

Herrero J, García-Serrano A, Couto S, Ortuño VM, García-González R (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur J Wildl Res 52:**245-250** DOI 10.1007/s10344-006-0045-3

Higashi M, Yamamura N (1993) What determines animal group size? Insider-outsider conflict and its resolution. Am Nat 142:**553-563**

Hone J, Atkinson B (1983) Evaluation of fencing to control Feral Pig movement. Austr Wildl Res 10:**499-505**

Iacolina L, Scandura M, Bongi P, Appollonio M (2009) Nonkin associations in wild boar social units. J Mammal 90:**666–674**

Ickes K, Dewalt SJ, Thomas SC (2003) Resprouting of woody saplings following stem snap by wild pigs in a Malaysian rain forest. J Ecol 91:**222-233**

Janeau G, Spitz F (1984) L'espace chez le sanglier (*Sus scrofa* L.) occupation et mode d'utilisation. Gibier Faune Sauvage 1:**73-89**

Janeau G, Cargnelutti B, Cousse S, Hewison M, Spitz F (1995) Daily movement pattern variations in wild boar (*Sus scrofa* L.). IBEX J Mt Ecol 3:**98-101**

Kaden V (1999) Bekämpfung der Klassischen Schweinepest beim Schwarzwild. Z Jagdwiss 45:**45-59**

Kaden V, Lange E, Fischer U, Strebelow G (2000) Oral immunisation of wild boar against classical swine fever: evaluation of the first field study in Germany. Vet Microbiol 73:**239-252**

Kaminski G, Brandt S, Baubet E, Baudoin C (2005) Life-history patterns in female wild boars (*Sus scrofa*): mother-daughter postweaning associations. Can J Zool 83:**474-480**

Kanzaki N, Perzanowski K (1997) The potential role of wolf predation in regulating wild boar population in Bieszczady, Poland. Wildl Conserv Japan 2:**205-212**

Kaplan D (2005) The enigma of the establishment of *Quercus ithaburensis* park forest in Northern Israel: co-evolution of wild boar and men? Wildl Biol Pract 1:**95-107** DOI: 10.2461/wbp.2005.1.12

Kern B, Depner KR, Letz W, Rott M, Thalheim S, Nitschke B, Plagemann R, Liess B (1999) Incidence of classical swine fewer (CSF) in wild boar in a densely populated area indicating CSF virus persistence as a mechanism for virus perpetuation. J Vet Med B 46:**63-67**

Keuling O, Stier N (2009) Schwarzwild - Untersuchungen zu Raum- und Habitatnutzung des Schwarzwildes (*Sus scrofa* L. 1758) in Südwest-Mecklenburg unter besonderer Berücksichtigung des Bejagungseinflusses und der Rolle älterer Stücke in den Rotten. Professur für Forstzoologie der TU Dresden, Tharandt. NWM-Verlag

Killian G, Miller L, Rhyan J, Doten H (2006) Immunocontraception of Florida feral swine with a single-dose GnRH vaccine. Am J Reprod Immunol 55:**378-384**

Klös HG, Frädrich H (Eds.) (1991) Sitzungsberichte der Tagung über Wildschweine und Pekaris im Zoo Berlin (12.-15. Juli 1990). Volume 147 Frädrich-Jubiläumsband Band 18. Bongo- Beiträge zur Tiergärtnerei, Berlin

Kramer-Schadt S, Fernández N, Thulke H-H (2007) Potential ecological and epidemiological factors affecting the persistence of classical swine fever in wild boar *Sus scrofa* populations. Mammal Rev 37:**1-20**

Kurz JC, Marchinton RL (1972) Radiotelemetry studies of feral hogs in South Carolina. J Wildl Manage 26:**1240-1248**

Labudzki L, Wlazelko M (1991) Saisonale Dynamik der vom Schwarzwild im Feldanbau verursachten Schäden im Forschungsgebiet Zielonka. Z Jagdwiss 37:**250-257**

Lazo A (1994) Social segregation and the maintenance of social stability in feral cattle population. Anim Behav 48:**1133-1141**

Le Pendu Y, Briedermann L, Gerard JF, Maublanc ML (1995) Inter-individual associations and social structure of a mouflon population (*Ovis orientalis musimon*). Behav Process 34:**67-80**

Leaper R, Massei G, Gorman ML, Aspinall R (1999) The feasibility of reintroducing Wild Boar (*Sus scrofa*) to Scotland. Mammal Rev 29:**239-259**

Lemel J, Truvé J, Söderberg B (2003) Variation in ranging and activity behaviour of European wild boar *Sus scrofa* in Sweden. Wildl Biol 9 Suppl:**29-36**

Liebl T, Elliger A, Linderoth P (2005) Aufwand und Erfolg der Schwarzwildjagd in einem stadtnahen Gebiet. WFS-Mitteilungen:**1-5**

Lott DF (1989) Intraspecific variation in the social system of wild vertebrates. Behaviour 88:**266-325**

Maillard D, Fournier P (1995) Effect of shooting with hounds on home range size of Wild Boar (*Sus scrofa* L.) groups in Mediterranean habitat. IBEX J Mt Ecol 3:**102-107**

Maillard D (1998) Approche du fonctionnement de la population de sanglier (*sus scrofa* L.) de la Réserve Naturelle de Roque-Haute à partir des résultats scientifiques obtenus sur l'espèce en milieu méditerranéen. ecologie mediterranea 24:**223-234**

Maillard D, Fournier P (2004) Timing and synchrony of births in the wild boar (*Sus scrofa* Linnaeus, 1758) in a Mediterranean habitat: the effect of food availability. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**67-74**

Markov NI, Neifel'd ND, Estaf'ev AA (2004) Ecological aspects of dispersal of the wild boar, *Sus scrofa* L., 1758, in the northeast of European Russia. Russ J Ecol 35:**131-134**

Marsan A, Spanò S, Tognoni C (1995) Management attempts of wild boar (*Sus scrofa* L.): First results and outstanding researches in Northern Apennines (Italy). IBEX J Mt Ecol 3:**219-221**

Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of Wild Boar in a Mediterranean coastal area. Acta Theriol 41:**307-320**

Massei G, Genov PV, Staines B, Gorman ML (1997a) Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean costal area. J Zool Lond 242:**411-423**

Massei G, Genov PV, Staines B, Gorman ML (1997b) Mortality of wild boar, *Sus scrofa*, in a Meditteranean area in relation to age and sex. J Zool Lond 242:**394-400**

Massei G, Genov PV (2004) The environmental impact of wild boar. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**135-145**

Massei G, Cowan DP, Coats J, Gladwell F, Lane JE, Miller LA (2008) Effect of the GnRH vaccine GonaCon on the fertility, physiology and behaviour of wild boar. Wildl Res 35:**540–547**

Massolo A, Mazzoni della Stella R (2006) Population structure variations of wild boar *Sus scrofa* in central Italy. Ital J Zool 73:**137 - 144** DOI: 10.1080/11250000600727717

Mazzoni della Stella R, Calvoi F, Burrini L (1995) The wild boar management in a province of Central Italy. IBEX J Mt Ecol 3:**213-216**

McIllroy JC, Saillard RJ (1989) The effect of hunting with dogs on the numbers and movements of feral pigs, *Sus scrofa*, and the subsequent success of poisoning exercises in Namadgi National Park, A.C.T. Wildl Res 16:**353-363**

McIlroy JC (1989) Aspects of the ecology of feral pigs (*Sus scrofa*) in the Murchison area; New Zealand. New Zeal J Ecol 12:**11-22**

McIlroy JC (1995) New techniques for an old problem - Recent advances in Feral Pig control in Australia. IBEX J Mt Ecol 3:**241-244**

Meriggi A, Sacchi O (1992a) Factors affecting damage by wild boars to cereal fields in Northern Italy. in: "Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse.**439-441**

Meriggi A, Sacchi O (1992b) Habitat selection by wild boars in Northern Appenines (N-Italy). in:

"Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse.**435-438**

Meynhardt H (1989a) Schwarzwild-Bibliothek 3: Hege und Bejagung. Neumann-Neudamm, Melsungen

Meynhardt H (1989b) Schwarzwild-Bibliothek 2: Das Revier. Neumann-Neudamm, Melsungen

Meynhardt H (1990) Schwarzwild-Report. Neumann Verlag, Leipzig, Radebeul. 8th edition.

Meynhardt H (1991) Schwarzwild-Bibliothek 4: Wildversorgung, Trophäen und Schadensverhütung. Neumann-Neudamm, Melsungen

Milner-Gulland EJ, Coulson T, Clutton-Brock TH (2004) Sex differences and data quality as determinants of income from hunting red deer *Cervus elaphus*. Wildl Biol 10:**187-201**

Milner JM, Nilsen EB, Andreassen HP (2007) Demographic side effects of selective hunting in ungulates and carnivores. Conservation Biology 21:**36-47**

Nakatani J, Ono Y (1995) Grouping pattern of Japanese wild boar (*Sus scrofa leucomystax*). IBEX J Mt Ecol 3:**128-129**

Nores C, Llaneza L, Álvares MA (2008) Wild boar (*Sus scrofa*) mortality by hunting and wolf (*Canis lupus*) predation. An example in Northern Spain. Wildl Biol 14:**online first**

Okarma H, Jedrzejewska B, Jedrzejewski W, Krasinski ZA, Milkowski L (1995) The roles of predation, snow cower, acorn crop and man related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. Acta Theriol 40:**197-217**

Paslawski (1975) Versuche zur Verminderung von Feldschäden durch Fütterung. Beitr Jagd- u Wildforschung 9:**188-194**

Peris S, Baquedano R, Sánchez A, Pescador M (2005) Mortalidad del jabalí (sus scrofa) en carreteras de la provincia de Salamanca (NO de España): ¿Influencia de su comportamiento social? Galemys 17:**13-23**

Pruitt WO (1960) Behaviour of the barren-ground caribou. Biol pap Univ Alaska 3:**1-44**

Putman RJ, Staines BW (2004) Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. Mammal Rev 34:**285-306**

Reinhardt V, Reinhardt A (1981) Cohesive relationships in a cattle herd (*Bos indicus*). Behaviour 77:**121-151**

Rosell C, Navàs F, Romero S, de Dalmases I (2004) Activity patterns and social organization of wild boar (*Sus scrofa*, L.) in a wetland environment: preliminary data on the effects of shooting individuals. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**157-166**

Russo L, Massei G, Genov PV (1997) Daily home range and activity of wild boar in a Mediterranean area free from hunting. Ethol Ecol & Evol 9:**287-294**

Saether BE (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. TREE 12:**143-149**

Sáez-Royuela C, Telleria JL (1986) The increased population of the Wild Boar (*Sus scrofa* L.) in Europe. Mammal Rev 16:**97-101**

Santos P, Mexia-de-Almeida L, Petrucci-Fonseca F (2004) Habitat selection by wild boar *Sus scrofa*, L. in Alentejo, Portugal. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**167-184**

Schley L, Roper TJ (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. Mammal Rev 33:**43-56**

Schley L, Dufrêne M, Krier A, Frantz AC (2008) Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. Eur J Wildl Res 54:**589–599** DOI 10.1007/s10344-008-0183-x

Schmidt M, Sommer K, Kriebitzsch W-U, Ellenberg H, von Oheimb G (2004) Dispersal of vascular plants by game in northern Germany. Part I: Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Eur J Forest Res 123:**167-176** DOI 10.1007/s10342-004-0029-3

Schwede G, Hendrichs H, McShea W (1993) Social and spatial organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. Anim Behav 45:**1007-1017**

Servanty S (2008) Dynamique d´une population chassée de sanglier (*Sus scrofa scrofa*) en milieu forestier. PhD, Univerité Claude Bernard Lyon

Singer FJ, Otto DK, Tipton AR, Hable CP (1981) Home ranges, movements and habitat use of European wild boar in Tennessee. J Wildl Manage 45:**343-353**

Sodeikat G, Pohlmeyer K (2002) Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). Z Jagdwiss 48 Suppl:**161-166**

Sodeikat G, Pohlmeyer K (2003) Escape movements of family groups of wild boar *Sus scrofa* influenced by drive hunts in Lower Saxony, Germany. Wildl Biol 9 Suppl:**43-49**

Sodeikat G, Pohlmeyer K (2004) Escape Movements of wild boar piglets (*Sus scrofa*, L.) after trapping, marking and releasing. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:**185-193**

Sodeikat G, Papendiek J, Pohlmeyer K (2005a) Wild boars´ (*Sus scrofa*) resting site ranges, preferences and variability concerning drive hunts in mixed forest stands in Lower Saxony, Germany. in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.**485-487**

Sodeikat G, Papendiek J, Richter O, Söndgerath D, Pohlmeyer K (2005b) Modelling population dynamics of wild boar (*Sus scrofa*) in Lower Saxony, Germany. in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.**488-489**

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar fam-

ily groups (*Sus scrofa* L.). Wildl Biol Pract 3:**28-38** DOI:10.2461/wbp.2007.3.4

Somers MJ, Rasa AE, Penzhorn BL (1995) Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. Acta Theriol 40:**257-281**

Spencer PBS, Lapidge SJ, Hampton J, Pluske JR (2005) The sociogenetic structure of a controlled feral pig population. Wildl Res 32:**297-304**

Spitz F (1989) Mortalité et dispersion chez le sanglier (Sus scrofa) de Camargue. Gibier Faune Sauvage 6:27–42. Gibier Faune Sauvage 6:**27-42**

Spitz F (1992) General model of the spatial and social organisation of Wild Boars (*Sus scrofa* L.). in: "Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse,.

Stubbe C, Mehlitz S, Peukert R, Goretzki J, Stubbe W, Meynhardt H (1989) Lebensraumnutzung und Populationsumsatz des Schwarzwildes in der DDR - Ergebnisse der Wildmarkierung. Beitr Jagd- u Wildforschung 16:**212-231**

Toïgo C, Servanty S, Gaillard JM, Brandt S, Baubet E (2008) Disentangling natural fom hunting mortality in an intensively hunted wild boar population. J Wildl Manage 72:**1532–1539** DOI: 10.2193/2007-378

Truvé J, Lemel J (2003) Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. Wildl Biol 9 Suppl:**51-57**

Truvé J (2004) Pigs in space: movement, dispersal and geographic expansion of wild boar (Sus scrofa) in Sweden. Dissertation, University of Göteborg

Tsachalidis EP, Hadjisterkotis E (2008) Wild boar hunting and socioeconomic trends in Northern Greece, 1993–2002. Eur J Wildl Res 54:**643-649** DOI 10.1007/s10344-008-0190-y

Tsarev SA (1991) Cyclic variations of the social structure in wild boar groups (*Sus scrofa*). Zool Zh 70:**97-109 (in Russian)**

Twigg LE, Lowe T, Everett M, Martin G (2006) Feral pigs in north-western Australia: population recovery after 1080 baiting and further control. Wildl Res 33:**417-425**

Ueda G, Kanzaki N (2005) Wild boar hunters profile in Shimane Prefecture, western Japan. Wildl Biol Pract 1:**146-151** DOI: 10.2461/wbp.2005.1.17

Welander J (2000) Spatial and temporal dynamics of wild boar (*Sus scrofa*) rooting in a mosaic landscape. J Zool Lond 252:**263-271**

Wildauer L, Reimoser F (2007) Wild boar (*Sus scrofa*) management - what can we learn from history? in: XXVIIIth International Union of Game Biologists Congress.**p. 42**

Wilke K, Pohlmeyer K, Lotthammer K-H (2000) Konzentration von Blei und Cadmium beim Schalenwild in autobahnnahen Revieren im Raum Gudow, Schleswig-Holstein. Z Jagdwiss 46:**31-44**

Wölfel H (Ed.) (2003) Bewegungsjagden. Leopold Stocker Verlag, Graz-Stuttgart

Ziegltrum GJ (2004) Efficacy of black bear supplemental feeding to reduce conifer damage in western Washington. J Wildl Manage 68:**470-474**

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Dziękuję!   **Thanks!**

Appendix

List of papers

I   Keuling O, Ihde J, Stier N, Roth M (in prep.) Temporary divisions of wild boar groups *Sus scrofa* L. and within-group relationships. manuscript

II   Keuling O, Stier N, Roth M (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur J Wildl Res 54:403-412

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I

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Temporary divisions of wild boar groups
***Sus scrofa* L. and within-group**
relationships

(manuscript)

Temporary divisions of wild boar groups *Sus scrofa* L. and within-group relationships

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Abstract

Wild boar *Sus scrofa* L. live in maternal family groups with strong kin-associations, while the males are solitary. This is unlike most other social ungulates that live in loose kin-based female groups, some of which are associated with males. According to literature data, wild boar groups are fairly stable and divide only temporarily after being hunted or for reproductive purposes. In our study, which was carried out in the south-western part of Mecklenburg-Western Pomerania (north-eastern Germany), we surveyed 16 wild boar groups of two or more radio tagged females ($N = 43$ individuals) by radio telemetry. Groups generally stayed together; however, members of family groups regularly separated for a period of time (13.9 % division of all localisations). Wild boar family groups showed highly flexible behaviour. Yearling groups, already separated from the maternal group, seldom split (2.4 % division). Family groups tended to be more stable in summer with an increase in the proportion of division throughout the winter until spring. Differing associations within groups seemed to be familial relationships, reflecting kinships and "friendships". We classified four types of divisions: short-term local division, short-term extensive division, long-term extensive division, and final division. Temporary and final divisions appear to be common behavioural patterns of wild boar family groups to avoid intra-familial concurrence.

Keywords: *Sus scrofa*; radiotelemetry; group divisions; seasonality; social structure

Introduction

Social groups in animals are believed to be beneficial for foraging efficiency, collective vigilance, protection of offspring, reduction of predation and territorial defence, but may also lead to intraspecific competition on resources and to higher risk of infections and, if closely related, of inbreeding (Jarman 1974, Alcock 1993, Fernández-Llario et al. 1996, Krebs and Davies 1997, Gabor et al. 1999, Krause and Ruxton 2002). Although most vertebrate species show constraints in their flexibility of social systems, intraspecific variations in social systems are common in wild vertebrates, dependant primarily on population density or the habitats carrying capacity (Lott 1989). Flexibility of social systems allows for potentially beneficial new opportunities, but is restricted by costs (Lott 1989).

The maximum group size in mammals (and especially ungulates) is influenced by food availability, and the minimum group size by predation risk (Jarman 1974, Krause and Ruxton 2002). Changing food availability and other factors may result in different social organisations in ungulate species (Geist 1974). Therefore, optimal

group sizes are determined by the predation risk and food availability on-site. Variable groups may better react on varying environmental conditions. Large groups give better predation avoidance, resources may be exploited best during short term but very rich conditions like herds of ungulates in African savannahs (Jarman 1974). Close relatedness allows for conservation of own genes and personal fitness, however, higher degrees of inbreeding might occur. Groups with loose kinship are more or less unions for purpose, nevertheless with less risk of inbreeding.

In polygynous ungulates dispersal is male biased and social groups are usually formed of closely related philopatric females (Greenwood 1980, Kaminski et al. 2005). Territoriality in ungulates is an exclusive attribute of males (Owen-Smith 1977 in Schwede et al. 1993), thus female ungulates do not aggregate for optimising territorial defence. Seasonal changes in group size and composition depend on reproductive behavioural patterns in ungulates, and separation for parturition is common in females (Pruitt 1960, Geist 1971, Reinhardt and Reinhardt 1981, Bon et al. 1986, Briedermann 1990, Klös and Frädrich 1991, Albon et al. 1992, Schwede et al. 1993, Lazo 1994, Le Pendu et al. 1995, Somers et al. 1995). Relationships in female groups have been described as kin-based but loose in Cervidae (Pruitt 1960, Albon et al. 1992, Schwede et al. 1993), Tayassuidae and some Suidae (Barrett and Spitz 1991, Klös and Frädrich 1991), and sometimes open but very gregarious in most Bovidae (Geist 1971, Jarman 1974, Tulloch 1978, Reinhardt and Reinhardt 1981, Hillman 1987, Festa-Bianchet 1991, Lazo 1994). In ruminants mother-daughter bonds last one year, in other ungulates sometimes up to sexual maturity (Reinhardt and Reinhardt 1981, Lazo 1994) and this pattern occurs in most long lived k-selected animals. Contrary to the former in most Suidae female groups individuals are

closely related. All species of the genus *Sus* and the warthogs (*Phacochoerus aethiopicus*, *P. africanus*) live in maternal family groups, while males tend to be solitary once sexually mature (Briedermann 1990, Barrett and Spitz 1991, Klös and Frädrich 1991, Tsarev 1991, Somers et al. 1995). Other Suidae live monogamously or in kin family groups including males, whilst the peccaries (Tayassuidae) live in mixed groups of variable size (Barrett and Spitz 1991, Klös and Frädrich 1991).

The wild boar *Sus scrofa* is a social species with a strong postweaning association between mothers and daughters lasting several years, although fluctuations may occur throughout the year (Kaminski et al. 2005). Thus, the social organisation is matrilineal with overlapping generations of females (Kaminski et al. 2005). Many authors described several types of groups (Dardaillon 1988, Braza and Álvares 1989, Tsarev 1991, Boitani et al. 1994, Nakatani and Ono 1995, Fernández-Llario et al. 1996, Gabor et al. 1999, Rosell et al. 2004) and most authors defined all kinds of family groups as sounders, whereas Gabor et al. (1999) only defined aggregations (Tsarev 1991) or multifamily groups (Dardaillon 1988) as sounders. Female wild boar were described as philopatric, whilst natal dispersal occurs mainly in males (Briedermann 1990, Truvé and Lemel 2003) comparable to other ungulates (Greenwood 1980). What allows wild boar groups to live in small kin groups under high predation or hunting pressure and not to live in large gregarious groups like other ungulates of similar size?

Some authors have described the structure of groups and populations of wild boar using hunting statistics (Boitani et al. 1995, Durio et al. 1995, Moretti 1995, Gabor et al. 1999, Fernández-Llario and Mateos-Quesada 2003, Cahill and Llimona 2004),

live-capture (Andrzejewski and Jezierski 1978, Stubbe et al. 1989) and direct observations (Braza and Álvares 1989, Gabor et al. 1999, Sweitzer et al. 2000, Rosell et al. 2004). Thus the demography of wild boar is relatively well known. However, a key purpose in the study of mammalian societies is to understand the way species characteristics and environmental parameters may affect the relations between individuals and hence social organization (Crook et al. 1976). Long-term data on density, age and sex structure, and ecological parameters enhance wildlife management. The concept of a leading sow, guiding a group and determining its activity, is still widespread and has important influence in the species' management. The shooting of such individuals is thought to have a major disrupting impact on the coordination of spatial activity, and hence on the distribution of crop damages, dispersal of disease and at least for hunting. Knowledge of social organisation and grouping mechanisms may help with the understanding of high reproduction and damage rates, and thus improve hunting effectiveness. To understand the mechanisms shaping group structures, telemetric studies have been carried out to detect temporary separations or final group divisions.

In previous telemetric studies divisions seldom occurred, however, often only one individual was observed that represented its group, or the localisations resulted from long term observations with long intervals between bearings. Although the data of some previous studies (Dardaillon 1988, Braza and Álvares 1989, Tsarev 1991, Boitani et al. 1994, Nakatani and Ono 1995, Fernández-Llario et al. 1996, Rosell et al. 2004) suggest splitting, only Gabor et al. (1999) mentioned regular temporary divisions. So far, only reproductive patterns (Dardaillon 1988, Briedermann 1990, Boitani et al. 1994, Rosell et al. 2004) or hunting (Sodeikat and

Pohlmeyer 2003) were suggested to induce divisions. Within the descriptions of social structure, group divisions have been described only preliminary and sketchily (Cousse et al. 1994, Gabor et al. 1999, Hebeisen et al. 2005, Ihde et al. 2005, Keuling et al. 2005).

In feral pigs in New Zealand, McIlroy (1989) observed piglet and subadult groups, ranging without females, which might have been temporary divisions. So far, in the literature there is no evidence for different group types to originate from temporary group division. Only Gabor et al. (1999) described the sounder as a meta-group (surplus group, hyper-group) in feral pigs, which might consist of several divided but closely related subgroups. The sounder is a stable fission-fusion society with an exchange of members. Within the family groups (groups of closed type) all animals are closely related (Briedermann 1990, Tsarev 1991). Sounders (sensu Gabor et al. 1999) and aggregations do segregate whereas other groups are thought to be stable, except for seasonal changes, and seasonal differences due to reproduction and mortality (Dardaillon 1988, Gerard and Campan 1988, Briedermann 1990, Meynhardt 1990, Boitani et al. 1994, Rosell et al. 2004).

In our study we wanted to determine if family groups are stable or if sounders are a fission-fusion society. With radiotelemetric observation of several individuals within the groups we assessed structuring in wild boar groups. The results presented below suggest, that the cohesion of social groups of wild boar is indeed high. Contrary to the notion that these groups do not separate we present evidence that splitting of groups is common. This result implies that wild boar may benefit from maintaining group structure but may use strategies that are otherwise typical for less gregarious ungulates.

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 of the study area was formed by the Vistula glaciation and rises from 20 m up to 100 m above sea level. Agriculture and forestry combined with low human settlement were the main features of the study area. About 20,000 ha consisted of 40 % agricultural fields, 34 % forest stands, 23 % meadows and pastures (including fallow land) and 3 % housing estates. The centre part of the study area comprised about 2,400 ha of unfragmented forest growing on a flat outwash plain, which enabled precise radiotelemetry triangulations. The forest contained 57 % pine (*Pinus sylvestris, P. 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, Q. petrea, Q. rubra*: 6 %), beech (*Fagus sylvatica*: 6 %), alder (*Alnus glutinosa, A. viridis*: 7 %), birch (*Betula pendula*: 7 %). During the observation period there was abundant acorn mast in the years 2002, 2003 and 2005 and beechnuts (2004). The average annual rainfall amounts to 680 mm and the mean annual temperature is 8.2° C. The mean annual harvest of the wild boar in the study area was 3.6 individuals per 100 ha during the observation period.

Methods

Radiotelemetry
The data from 43 female wild boar out of 16 different groups with at least two or more radio-tagged individuals per group were recorded from 18th November 2002 to 28th April 2006. Within the groups only some females were radio tagged, but not all group members. We captured wild boar and fitted them with ear-tag-transmitters. The transmitters had a beep-ratio of 20 beeps per minute to last up to three years (mean observation period 363 days) and ranged up to 3 km (Keuling et al. 2008a).

For wild boar localisation we took one diurnal location about four times a week and one to five nocturnal locations about twice a week, thus, we got a mean of 381 localisations per year and animal (Keuling et al. 2008a). We assumed an absolute minimum time interval of two hours between localisations as sufficiently independent (Keuling et al. 2008a).

Only acceptable localisations, performed as multiple triangulations with at least three bearings per localisation to eliminate reflected signal errors taken with car mounted (to minimise disturbances) 4-element-YAGI-antennas using TRX-1000S receivers (Wildlife Materials Inc., USA), were taken as positioning of a particular wild boar (Keuling et al. 2008a). In our study, the telemetry error was at median 60 m between assumed and real transmitter location (Keuling et al. 2008a). We mapped all localisations and recorded additional information like activity, date and time as well as bonus notes like sightings, group size and structure or presence of other groups nearby. We noted whether groups were divided (distance between simultaneous localisations of animals of more than 50 m) as well as the distance between observed group members. As different durations and distances of divisions were observed, a classification of division types needed to be established. For this purpose we searched by triangulation for six wild boar groups one hour before sunset by triangulation. We then took directional bearings every 15 minutes until final resting after sunrise and estimated the distance between observer and animal by the power of the signal during 45 nights from November 2003 until March 2004.

We corrected any distance error by triangulations every two hours.

We transcribed the wild boar localisations with a Calcomp® SummaSketchIII digitising tableau to Esri® ArcView 3.2 using the Movement 2.0 extension (Hooge and Eichenlaub 2001). As we recommended defined observation periods in previous publications, we used seasons defined as biological time-units of equal length like in Keuling et al. (2008a, 2009b). We calculated the mean percentages of divisions and the mean distances between group members for every group and season.

We observed three groups with more than two radio-tagged animals (group 10, $N = 3$ radio tagged animals; group 11, $N = 3$; group 1, $N = 7$) to examine relationships between group members. An Index of social affinity (S) between pairs of group members (Lazo 1994) was estimated for all possible pairings within these groups,

$$S = N_{A,B} / N_{group}$$

where $N_{A,B}$ is the number of combined locations of individuals A and B. As all animals have been observed during every session, N_{group} is the minimum number of observations of one individual of the couple.

Subdivision into group types

We classified two categories of groups: 1) adult family groups (AFG) of at least one adult sow leading piglets younger than 12 months, sometimes also with yearlings; 2) yearling groups (YG) consisting of yearlings between 12 (when already divided, starting with nine month) and 24 months of age, not leading piglets and ranging without adults. To determine to which group type the groups actually belonged, we inspected the group structure by direct visual observation regularly at least every two months. However, the exact number of group members was unknown for most of the groups.

Statistics

We used Mann-Whitney U test for comparison of the two group types. For performance of the Mann-Whitney U test we averaged seasonal percentages and distances of divisions from same animal in consecutive years as total appearance of divisions. Unless otherwise noted, all values are presented as mean ±SD. We used Kruskal-Wallis H test to test for differences in frequency and distance of divisions between different family groups and between different yearling groups. As the datasets possessed dissimilar bases of paired and independent data, we could not test for differences in occurrences of divisions in consecutive years and seasons. All tests analysed with SPSS 12.0 were two-tailed with level of significance of $p \leq 0.05$.

Results

Frequency of divisions

In 12.3 % of all independent localisations ($N = 4094$) the observed members of wild boar groups divided. In only 23 cases (4.6 % of divisions) a division occurred after a disturbance (recreational mushroom picking, capture, hunting). However, a direct influence of disturbance was observed only one time during a battue; in all other cases the division occurred only some hours after a disturbance was observed. The different observed groups showed similar proportions of divisions in consecutive years (2003: 7.7 %, 2004: 17.7 %, 2005: 10.0 %).

We found no significant seasonal differences in occurrence of divisions between the groups within the same age class (Kruskal-Wallis H test: yearling groups: $\chi^2 = 8.230$, $df = 8$, $p = 0.411$, family groups: $\chi^2 = 9.123$, $df = 7$, $p = 0.244$) but between the age classes: in family groups divisions were more
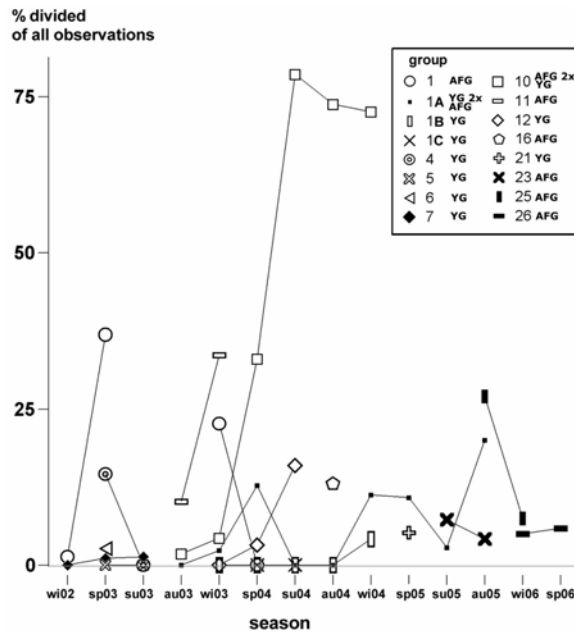
5

Fig. 1: Individual progression of seasonal frequencies of divisions in different sounders AFG = adult family group, YG = yearling group, seasonal frequencies of divisions of one group are connected by lines for better clarity

common than in yearling groups (yearling groups: 2.44 ±4.63 %, $N = 20$, family groups: 13.87 ±12.47 %, $N = 18$; Mann-Whitney U test: $Z = -4.114$, $p \leq 0.001$, $N = 38$). An individual progression of divisions was discernible (Fig. 1). The yearlings of group G10 showed a totally different behaviour and did divide with 64.47 ±21.14 % ($N = 4$) and thus were excluded from analyses. Although not testable, family groups tended to be more stable in summer with an increasing division probability towards winter and spring, whilst yearling groups seemed to remain stable all the year round (Fig. 2).

We found no difference in seasonal distances between group members during division in yearling groups (862.6 ±658.4 m, $N = 8$; Kruskal-Wallis H test yearling groups: $\chi^2 = 6.667$, $df = 6$, $p = 0.353$), but in adult family groups (811.9 ±557.9 m, $N = 18$, Kruskal-Wallis H test adult groups: $\chi^2 = 14.140$, $df = 7$, $p = 0.049$). Nevertheless, there was no difference between the two age classes (Mann-Whitney U test: $Z = -0.056$, $p =$

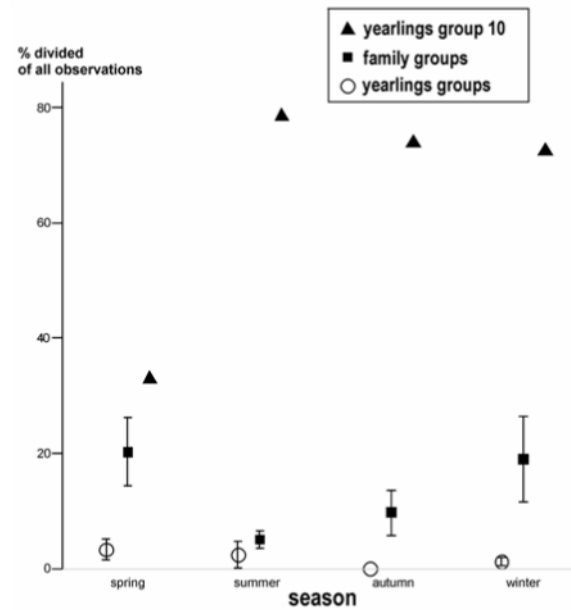0.956, $N = 26$). Also the yearlings of group G10 had a similar mean distance of 941.5 ±132.1 m ($N = 4$).

Fig. 2: Mean seasonal frequencies (±SE) of division within wild boar family and yearling groups

Observations on within-group relationships Some animals within one sounder were closer associated than others but nearly every possible constellation did occur (Tab. 1). Those associations are represented as proportions of constellations. In Figure 3, these occurrences of associations are presented for group G1 by different width of connecting bars. Two main subgroups were obvious: The piglets F75 and F77 were closely associated to the adult female F2. The piglets F76, F81 and F82 were associated very closely jointly, piglet F80 seemed to be closer associated to this group than to the adult female. After the alpha sow (F1, lost transmitter) had been shot, first one part of the group (group G1b: F76, F81, F82; Tab. 1) divided finally. When sow F2 was giving birth, the other yearlings left the group, too (G1c Tab. 1, Fig. 3). After this final division, the subgroups themselves did not divide for one year (Fig. 1, groups G1b and G1c).

Table 1: Occurrence of different subgroup constellations within three wild boar groups and the social affinity (*S*) between group members in row "subgroup I". Numbers in subgroups indicate individuals.

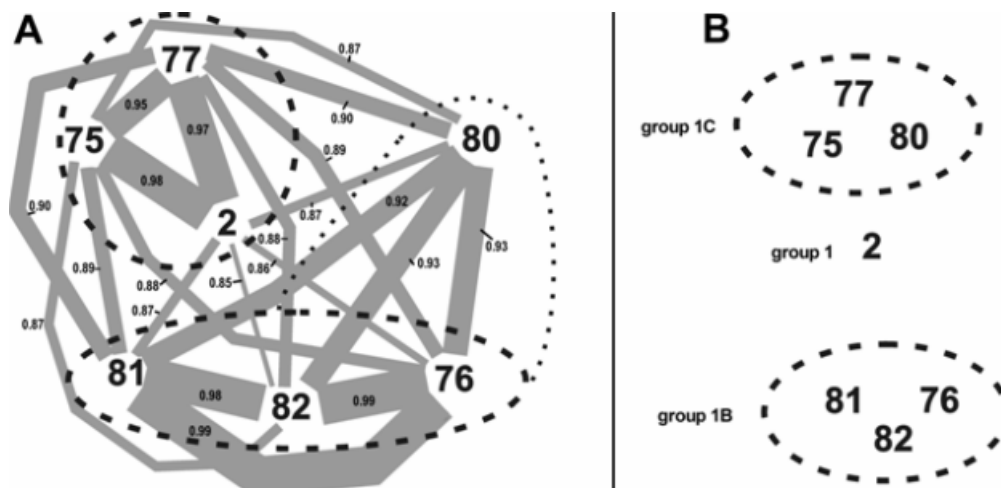| group	subgroups I	subgroups II	III	occurance n	occurance %	*S*
	2, 75	76, 77, 80, 81, 82		3	2.94	
	2, 75, 77	76, 80, 81, 82		5	4.90	
	2, 75, 77, 80	76, 81, 82		3	2.94	see
	2, 75, 77, 81	76, 80, 82		1	0.98	Fig. 3
	2, 75, 76, 77, 81, 82	80		2	1.96	
G1	2, 75, 76, 77, 81	80	82	1	0.98	
	2, 77	75, 76, 80, 81, 82		1	0.98	
	2, 77, 80	75, 76, 81, 82		1	0.98	
	all			85	83.33	
				Σ 102		
		after final division				
	2, 75, 77, 80	76, 81, 82 (G1b)				
	2	76, 81, 82 (G1b)	77, 80 (G1c)			
		(75 dead)				
	59	60	61	8	2.48	
	60, 61	59		23	7.12	0.49
G10	59, 60	61		9	2.79	0.44
	59, 61	60		149	46.13	0.88
	all			134	41.49	
				Σ 323		
	69, 72	63		7	1.83	0.79
G11	63, 69	72		77	20.10	0.97
	63, 72	69		3	0.78	0.78
	all			296	77.28	
				Σ 383		

Fig. 3: A) Associations between group members of group G1; numbers represent ID of radio-tagged animals, the width of connecting bars shows the degree of association, thin lines represent more divisions between group members, small numbers show index of social affinity (*S*); B) New groups after final division (for further details see text and table 1)
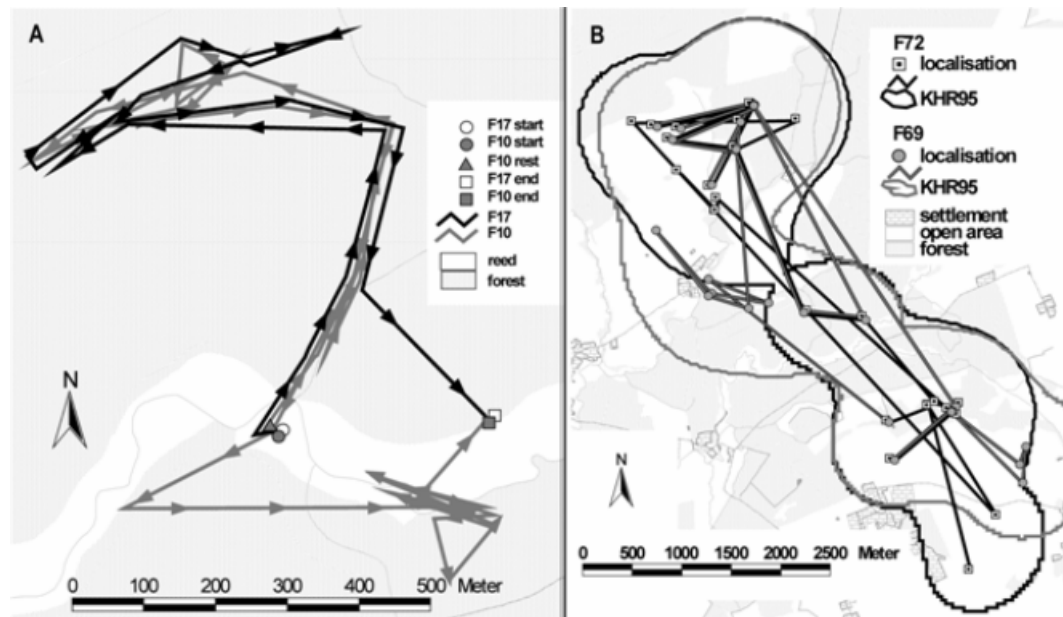
7

Fig. 4: Examples for types of divisions, A) local and short term extensive divisions: group G1a nocturnal movement Nov 26/27 2003, the both adult sows leave the shared diurnal resting site within the reed together, at the feeding site they divide (short-term local division), and wander back conjointly, the alpha sow F17 betakes herself at the edge of the reed, whilst sow F10 rests at the previous resting site, after one hour she starts again (short term extensive division) and joins the rest of the group in the early morning inside the resting site. B) long term extensive divisions of group G11 in April/May 2004, the group roams several days separated and collective respectively, every dot is one diurnal or nocturnal localisation, although separated very often the home ranges are quite similar in size and location. KHR95 = kernel home range 95%

Types of division

We classified four types of divisions:

I) short-term local division: within one night or during diurnal resting, less than 200 m (within-group distance). This type was hard to detect by telemetry, and had to be confirmed by visual observations or "homing in" (Fig. 4A)

II) short-term extensive division: longer lasting division within one night, more than 200 m distance among group members (group really separated) (Fig. 4A)

III) long-term extensive division: more than 200 m distance among group members (Fig. 4B)

  a) collective starting point, division during night, separated at end or vice versa

  b) separated resting sites but partial common movement during night

  c) separated resting sites and no meeting for one or more nights up to several weeks

IV) final division: division of a wild boar family group without reunion (perhaps irregular meetings), e.g. after death of alpha sow

Local divisions did only occur in 1.0 % of all independent localisations, but in 11.11 % of the continuous observed nights. Short term extensive divisions occurred in 0.7 % of the independent cases, long term extensive divisions were most frequent with 10.4 %. In 0.1 % of all bearings, when wild boar were separated, we could not define the type of division.

We observed some final divisions: in summer 2003 two female yearlings (group G1a) finally separated from group G1 by unknown reason, in January 2004 group G1b left group G1 after the death of the alpha sow, three month later group G1c separated, too, at parturition of the remaining adult female (F2, group G1). In group G10 a final division also occurred,

but was not observed by telemetry, as only one transmitter remained. This female (F59, group G10) was later on observed only by herself. Previously, we reported the observation of seven groups of female yearlings during one year without any reunion with a family group (Keuling et al. 2008a), thus final divisions or even eradications of the rest of the group by hunters must have happened.

Discussion

Frequency of divisions

As a direct influence of disturbance was rarely observed and divisions did not differ within the age classes, group fluctuations, occurrence of sub-groups and divisions seem to be a common behavioural pattern, which may possibly help avoiding intra-family concurrence. Also in previous publications few impact of hunting on space use and activity was observed (Sodeikat and Pohlmeyer 2002, 2003, 2007, Keuling et al. 2008b), even after capturing wild boar groups reunited very soon (Sodeikat and Pohlmeyer 2004). We assume the frequencies of divisions to be somewhat higher than observed, as we did not monitor every single individual of a group. Therefore, group divisions in unobserved animals will have gone undetected, as the individual dyads showed individual social affinities. Since adult groups show higher division frequencies and individual behaviour is obvious (Fig. 1), it is not surprising that some adults divided with higher distances than others did. These findings also correspond to literature data, where wild boar groups showed individual spatial usage (e.g. Boitani et al. 1994, Baubet et al. 1998, Keuling et al. 2008a, 2009b). Yearling groups are already divided from maternal groups, they are less experienced, closely kin-related and do not lead piglets, thus less division might occur inside the yearling

groups. In group G10 a special case appeared: the yearlings did not totally divide from maternal sounder. Thus, they remained within a very large group, where temporary divisions seem to occur more frequently. This total sounder might have been on the verge of final segregation or perhaps the only observed sounder in the meaning of Gabor et al. (1999). Thus, not the meta-group or sounder (sensu Gabor et al. 1999) seems to be a fission-fusion society, but the family groups are societies of this kind.

Although wild boar groups divide regularly, the home ranges and core areas of group members are of similar size and location, thus, one individual can be used to represent spatial utilisation for the whole group (mean overlap of kernel home range (KHR95) within groups: 93 %, mean distance between home range centres of different group members: 39 m, see also Keuling et al. 2008a and Fig. 4B).

In summer groups divided least. This result corresponds to literature data, although none of the authors mentioned divisions: Briedermann (1990) described higher proportions of small (separated yearlings) and very big groups (family groups with piglets) in summer, Fernández-Llario et al. (1996) observed biggest group sizes in early summer. Briedermann (1990) and Fernández-Llario et al. (1996) also observed smaller groups in remaining seasons. Most single specimen and small groups occurred in spring (Briedermann 1990), when adult females separate for parturition. In summer the small piglets are mother dependent, most family groups stayed all together in fields (Keuling et al. 2008a, 2009b), while small yearling groups were already divided. In autumn and winter piglets become more independent, and juveniles showed slightly differing movement patterns than their mothers (Cousse et al. 1994). During winter food

resources decreased. An increase of divisions by female adults may therefore be a strategy to reduce direct feeding competition by searching food for themselves and their piglets. Although we detected few direct influences of hunting and other disturbances on the frequency of group divisions, a potential influence of increasing hunting pressure in winter can not be totally excluded.

Seasonal changes in division probability may depend on reproduction (Dardaillon 1988, Gerard and Campan 1988, Briedermann 1990, Meynhardt 1990, Tsarev 1991, Boitani et al. 1994, Rosell et al. 2004). Fernández-Llario et al. (1996) described the social organisation as "…highly dynamic and closely related to the biological cycle of the species." Group size and structure tended to change seasonally (Nakatani and Ono 1995, Rosell et al. 2004): in spring more yearling groups occur, when yearlings range separated from family groups, whilst adult females giving birth come together afterwards. The highest group size is reached in autumn, when families reunite after division. Mixed groups only occur in mating season.

Observations on within-group relationships
Associations within groups seem to be kinship based, as the first part of the group G1 finally divided directly after the death of the alpha sow. Apparently, this sow had been the mother of the closely associated group G1b. On the other hand the relationship of female F80 is not quite clear, being closer associated to group G1b but dividing with group G1c (see Fig. 3B). Groups G10 and G11 also showed diverse associations between group members: one pair was closely associated but the other couples showed lower indices of social affinity (*S*). Perhaps the different dyads were siblings and cousins. Thus, associations within the piglets of one sounder may reflect kinships and

"friendships", similar observations were done in Zebu *Bos indicus*, where personal relationships and personally favoured partners (even non-related) occurred (Reinhardt and Reinhardt 1981).

Types of divisions
Because of telemetry error local divisions are difficult to detect and, thus, might be underestimated. During permanent observations small scale separations are easier to detect, and in our study local divisions occurred in several permanent observed nights but were observed only rarely during single independent localisations.

Temporary long-lasting separation of yearling females (especially in spring and summer) seems to be a normal pattern, as Dardaillon (1988), Nakatani and Ono (1995) and Rosell et al. (2004) reported. But as we could definitely observe three events of final divisions, originating four new subgroups - not to mention undetected final divisions, when yearlings ranged alone without reunion to family groups (Keuling et al. 2008a) - we assume final divisions of yearling females also to be common. This corresponds to Kaminski et al. (2005), who observed 21 % of yearlings leaving their family groups. When a group has a high ratio of yearlings per adult female, they segregate more often and form new family groups with their siblings; when yearlings left, all or none did (Kaminski et al. 2005). Animal groups are said to dissolve when the group size increases above carrying capacity (Higashi and Yamamura 1993). In wild boar, final divisions have been described for big group sizes due to lack of food, hierarchic conflicts and injury, illness or death of at least one group member (Briedermann 1990, Meynhardt 1990). Only few females disperse within short distances (Truvé and Lemel 2003, Truvé 2004). After temporary

divisions (e.g. for parturition) wild boar reunite by olfactory and acoustic communication (Meynhardt 1989). We also assume active searching as well as accidental meetings at resting and feeding sites and other well known social places (baiting stations, wallows) as recovery mechanisms.

Wild boar have closer associations than most other ungulates, but not as close as often described. Altmann (1989), who observed wild boar groups in captivity forming family groups within a sounder, described these groups as close social, but not rigid, associations.

Cousse et al. (1994) characterised piglets as closely associated to their mother and siblings and as attached to the postnatal home range (high site fidelity). However, postweaning piglets sometimes showed different movement patterns than adults with segregations occurring especially during resting periods. The increasing degree in juvenile independence of their mother led to short-time divisions from her to explore the habitat. But these authors observed merely two groups in spring and summer of one single year, thus, assumptions must not be generalised. Cousse et al. (1994) did not mention any home range size. Piglets were more often outside postnatal range than inside, which means the piglets leave or enlarge their home range from spring (postnatal range) to summer, as Keuling et al. (2008a, 2009b) also observed.

Generalisations can only be seen as exemplarily models, which only show the mean behaviour within a big range of flexible eco-ethological patterns. Divisions seem to be a common behavioural pattern within family groups resulting only seldom from disturbances. Although very social, wild boar show a high behavioural flexibility (Keuling et al. 2008a, 2009b) that allows for optimal exploitation of resources whilst avoiding intra-familial competition.

Wild boar groups are adapted to their conditions quite optimal. With a high synchronous reproduction they are able to form big groups to minimise predation risk (Krause and Ruxton 2002). On the other hand large groups are easier to detect (Krause and Ruxton 2002). Thus, such a close kin species looses population fitness and individual fitness (r-strategy) by being attacked more often. The behavioural flexibility enables optimal resource exploitation without being gregarious. Wild boar exceed most other ungulates, as their group behaviour resembles that of social carnivores (Krause and Ruxton 2002). Additionally, wild boar represent r-strategists with the group behaviour of K-strategists (kin family groups).

Divisions of wild boar groups and the flexibility in this system may be very important for population management, particularly conducted by hunting. Since it is often very difficult to detect the alpha-sow, adult sows should only be shot on single hunting activities to prevent the destruction of social constructs. A higher number of small groups may disperse, especially in summer and cause greater damage to cereal crops. A higher number of yearling groups may also increase the risk of infection rates by slightly increased dispersal rates (Keuling et al. 2008a, Keuling et al. 2009a).

References

Albon SD, Staines HJ, Guinness FE, Clutton-Brock TH (1992) Density dependent changes in the behaviour of female kin in red deer. J Anim Ecol 61:131-137

Alcock J (1993) Animal Behaviour - An Evolutionary Approach. 5th ed. Sinauer Associates, Inc., Sunderland, Massachusetts

Altmann D (1989) Sozialverhalten und Revierverteidigung in Beziehung zur Tageszeit beim Wildschwein *Sus scrofa* L. Beitr Jagd- u Wildforschung 16:202-211

Andrzejewski R, Jezierski W (1978) Management of a Wild Boar population and its effects on commercial land. Acta Theriol 23:309-339

Barrett RH, Spitz F (eds) (1991) Biology of suidae. - Biologie des suidés. I.R.G.M., Toulouse

Baubet E, Brandt S, Touzeau C (1998) Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus scrofa*). Analyses préliminaires. Gibier Faune Sauvage 15:655-658

Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild boar in Tuscany, Italy. J Mammal 75:600-612

Boitani L, Trapanese P, Mattei L, Nonis D (1995) Demography of a wild boar (*Sus scrofa,*L.) population in Tuscany, Italy. Gibier Faune Sauvage 12:109-132

Bon R, Campan R, Dardaillon M, Demeautis G, Gonzales G, Teillaud P (1986) Comparative study of the seasonal variations of the social structures in three french ungulates. Wiss Zeitschr Humboldt-Universität Berlin Math.-Nat. R. 3:254-258

Braza F, Álvares F (1989) Utilisation de l´habitat et organisation sociale du sanglier (*Sus scrofa* L.) à Doñana (Sud-Ouest de l´Espagne). Can J Zool 67:2047-2051

Briedermann L (1990) Schwarzwild. 2nd ed. Neumann-Neudamm, Melsungen

Cahill S, Llimona F (2004) Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:37-52

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can J Zool 72:1691-1694

Crook JH, Ellis JE, Goss-Custard JD (1976) Mammalian social sytems: Structure and function. Anim Behav 24:261-274

Dardaillon M (1988) Wild boar social groupings and their seasonal changes in Chamargue, southeastern France. Z Säugetierkunde 53:22-30

Durio P, Gallo Orsi U, Macchi E, Perrone A (1995) Structure and monthly birth distribution of a wild boar population living in mountainous environment. IBEX J Mt Ecol 3:202-203

Fernández-Llario P, Carranza J, Hidalgo de Trucios SJ (1996) Social organisation of the wild boar (*Sus scrofa*) in Doñana National Park. Misc Zool 19:9-18

Fernández-Llario P, Mateos-Quesada P (2003) Population structure of the wild boar (*Sus scrofa*) in two Mediterranean habitats in the western Iberian Peninsula. Folia Zool 52:143-148

Festa-Bianchet M (1991) The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim Behav 42:71-82

Gabor TM, Hellgren EC, Van Den Busche RA, Silvy NJ (1999) Demography, sociospatial behaviour and genetics of feral pigs (*Sus scrofa*) in a semi-arid environment. J Zool Lond 247:311-322

Geist V (1971) Mountain sheep. A study in behaviour and evolution. Univ. of Chicago Press, Chicago, London

Geist V (1974) On the relationship of social evolution and ecology in ungulates. Am Zool 14:205-220

Gerard JF, Campan R (1988) Variabilité éco-ethologique chez le sanglier europeén: comparision des travaux francaise. Cahiers d'Ethologie Appliquee 8:63-130

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140-1162

Hebeisen C, Fischer C, Baubet E (2005) Social organization and group stability of wild boar (*Sus scrofa*) in the basin of Geneva. in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.352-353

Higashi M, Yamamura N (1993) What determines animal group size? Insider-outsider conflict and its resolution. Am Nat 142:553-563

Hillman JC (1987) Group size and association patterns of the common eland (*Tragelaphus oryx*) J Zool Lond 213:641-663

Hooge PN, Eichenlaub B (2001) Movement 2.0, Alaska Biological Science Center, US Geological Survey, Ancorage, AK, USA

Ihde J, Keuling O, Stier N, Roth M (2005) Nocturnal movements of wild boar (*Sus scrofa*) groups with respect to group divisions. Mamm Biol Suppl 70:19

Jarman PJ (1974) The social organization of antelope in relation to their ecology. Behaviour 48:215-267

Kaminski G, Brandt S, Baubet E, Baudoin C (2005) Life-history patterns in female wild boars (*Sus*

scrofa): mother-daughter postweaning associations. Can J Zool 83:474-480

Keuling O, Ihde J, Stier N, Roth M (2005) How stable are wild boar groups *Sus scrofa* L.? in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.131-132

Keuling O, Stier N, Roth M (2008a) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur J Wildl Res 54:403-412 doi:10.1007/s10344-007-0157-4

Keuling O, Stier N, Roth M (2008b) How does hunting influence activity and space use in wild boar *Sus scrofa*. Eur J Wildl Res 54:729-737 DOI 10.1007/s10344-008-0204-9

Keuling O, Lauterbach K, Stier N, Roth M (2009a) Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany. Eur J Wildl Res:online first DOI 10.1007/s10344-009-0296-x

Keuling O, Stier N, Roth M (2009b) Commuting, shifting or remaining? Different spatial usage patterns of wild boar *Sus scrofa* L. in forest and field crops during summer. Mamm Biol 74:145-152 doi:10.1016/j.mambio.2008.05.007

Klös HG, Frädrich H (eds) (1991) Sitzungsberichte der Tagung über Wildschweine und Pekaris im Zoo Berlin (12.-15. Juli 1990). Volume 147 Frädrich-Jubiläumsband Band 18. Bongo- Beiträge zur Tiergärtnerei, Berlin

Krause J, Ruxton GD (2002) Living in Groups. Oxford University Press, Oxford New York

Krebs JR, Davies NB (eds) (1997) Behavioural ecology: an evolutionary approach. 4th ed. Blackwell Publishing, Oxford

Lazo A (1994) Social segregation and the maintenance of social stability in feral cattle population. Anim Behav 48:1133-1141

Le Pendu Y, Briedermann L, Gerard JF, Maublanc ML (1995) Inter-individual associations and social structure of a mouflon population (*Ovis orientalis musimon*). Behav Process 34:67-80

Lott DF (1989) Intraspecific variation in the social system of wild vertebrates. Behaviour 88:266-325

McIlroy JC (1989) Aspects of the ecology of feral pigs *(Sus scrofa)* in the Murchison area; New Zealand. New Zeal J Ecol 12:11-22

Meynhardt H (1989) Schwarzwild-Bibliothek 1: Biologie und Verhalten. Neumann-Neudamm, Melsungen

Meynhardt H (1990) Schwarzwild-Report. 8th ed. Neumann Verlag, Leipzig, Radebeul

Moretti M (1995) Birth distribution, structure and dynamics of a hunted mountain population of wild boars (*Sus scrofa* L.), Ticino, Switzerland. IBEX J Mt Ecol 3:192-196

Nakatani J, Ono Y (1995) Grouping pattern of Japanese wild boar (*Sus scrofa leucomystax*). IBEX J Mt Ecol 3:128-129

Pruitt WO (1960) Behaviour of the barren-ground caribou. Biol pap Univ Alaska 3:1-44

Reinhardt V, Reinhardt A (1981) Cohesive relationships in a cattle herd (*Bos indicus*). Behaviour 77:121-151

Rosell C, Navàs F, Romero S, de Dalmases I (2004) Activity patterns and social organization of wild boar (*Sus scrofa*, L.) in a wetland environment: preliminary data on the effects of shooting individuals. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:157-166

Schwede G, Hendrichs H, McShea W (1993) Social and spatial organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. Anim Behav 45:1007-1017

Sodeikat G, Pohlmeyer K (2002) Temporary home range modifications of wild boar family groups (*Sus scrofa* L.) caused by drive hunts in Lower Saxony (Germany). Z Jagdwiss 48 Suppl:161-166

Sodeikat G, Pohlmeyer K (2003) Escape movements of family groups of wild boar *Sus scrofa* influenced by drive hunts in Lower Saxony, Germany. Wildl Biol 9 Suppl:43-49

Sodeikat G, Pohlmeyer K (2004) Escape Movements of wild boar piglets (*Sus scrofa*, L.) after trapping, marking and releasing. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue:185-193

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar family groups (*Sus scrofa* L.). Wildl Biol Pract 3:28-38 DOI:10.2461/wbp.2007.3.4

Somers MJ, Rasa AE, Penzhorn BL (1995) Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. Acta Theriol 40:257-281

Stubbe C, Mehlitz S, Peukert R, Goretzki J, Stubbe W, Meynhardt H (1989) Lebensraumnutzung und Populationsumsatz des Schwarzwildes in der DDR - Ergebnisse der Wildmarkierung. Beitr Jagd- u Wildforschung 16:212-231

Sweitzer RA, Van-Vuren D, Gardner IA, Boyce WM, Waithman JD (2000) Estimating sizes of wild pig populations in the north and central coast regions of California. J Wildl Manage 64:531-543

Truvé J, Lemel J (2003) Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. Wildl Biol 9 Suppl:51-57

Truvé J (2004) Pigs in space: movement, dispersal and geographic expansion of wild boar (Sus scrofa) in Sweden. Dissertation, University of Göteborg

Tsarev SA (1991) Cyclic variations of the social structure in wild boar groups (*Sus scrofa*). Zool Zh 70:97-109 (in Russian)

Tulloch DG (1978) The water buffalo, *Bubalis bubalis*, in Australia: grouping and home range. Austr Wildl Res 5:327-354

II

Keuling O, Stier N, Roth M (2008)

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

Eur J Wildl Res 54:403-412

ORIGINAL PAPER

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

Oliver Keuling · Norman Stier · Mechthild Roth

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

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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

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 (northeastern 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/km^2) 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 petrea*, *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 $N=14$, fife 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	N total	N 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:

a) minimum convex polygons (MCP) to describe the maximum used space (100% of localisations),
b) kernel home ranges 95% core weighted (KHR95) to describe the home range (Burt 1943),
c) 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
d) 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 ± 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: χ^2=0.315, p=0.854; KHR95: χ^2=0.983, p=0.612; CA: χ^2=0.315, p=0.854; RS: χ^2=0.281, p=0.869).
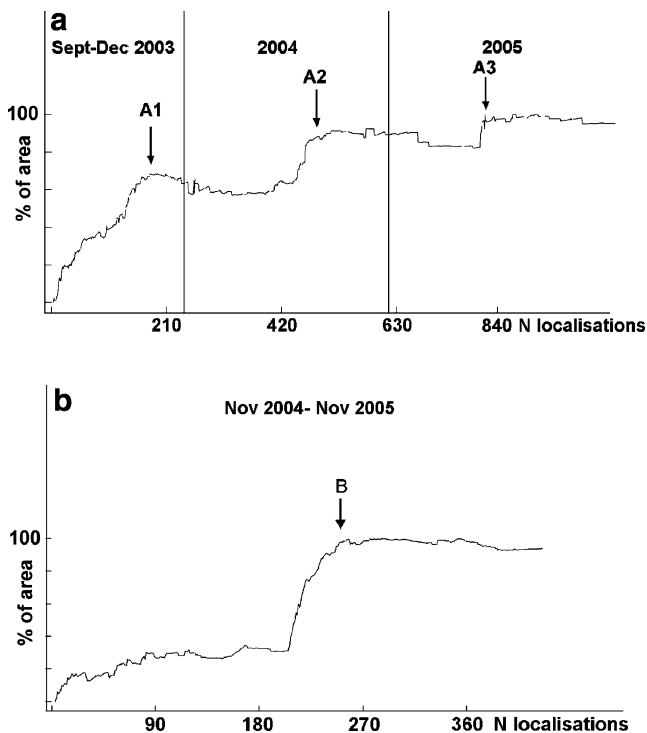
Fig. 1 Two examples for stepwise increasing home range size depending on number of localisations (incremental area analysis for kernel home ranges 95% core weighted): **a** animal *A* total home range (*arrows A1–3* indicate stable annual home ranges 2003, 2004 and 2005), *vertical lines* indicate turns 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 ($1,184.9\pm647.2$ha, $N=7$) 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 $5,254.7\pm1,644.1$ m, $N=7$, family groups $4,550.2\pm1014.6$ m, $N=9$, Mann–Whitney U test: $Z=-0.74$, $p=0.458$). The mean annual KHR95 amounted to $53.0\pm12.5\%$ of MCP, the mean core area represented $76.9\pm7.0\%$ of localisations and was $21.6\pm7.5\%$ of MCP as well as $42.4\pm14.9\%$ 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 $57.9\%\pm18.3$ of MCP, $70.9\pm11.9\%$ of the locations described the mean seasonal core area. The CA was $21.3\pm11.6\%$ of MCP and $35.9\pm16.0\%$ 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 ($1,030.9\pm285.2$ 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).
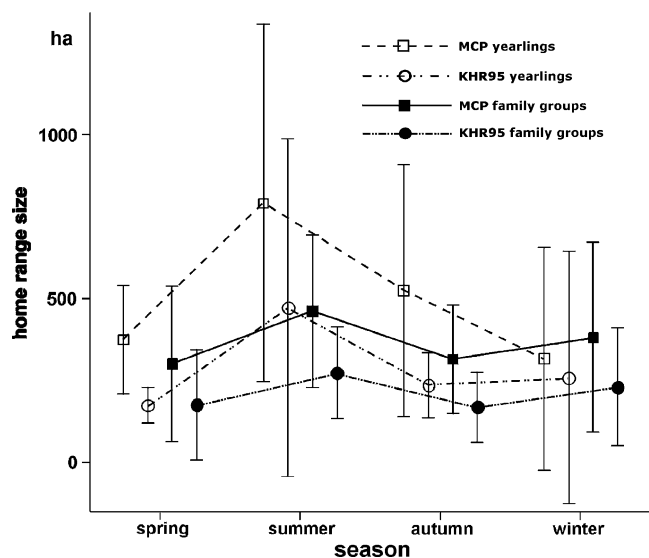

Fig. 2 Mean seasonal home range size$\pm$SD of 24 female yearling and adult wild boar during four seasons (*MCP* Minimum convex polygon, *KHR95* kernel home range 95%, yearlings: spring $N=12$, summer $N=10$, autumn $N=8$, winter $N=7$; family groups: spring $N=14$, summer $N=14$, autumn $N=11$, winter $N=10$)
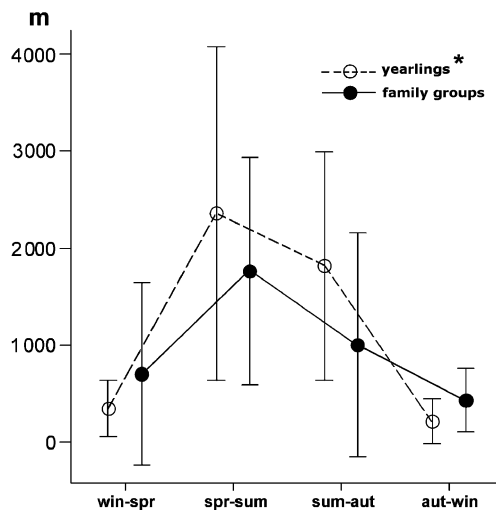
Fig. 3 Mean shifting±SD of seasonal home range centres of yearling and adult female wild boar (yearlings: winter–spring *N*=3, spring–summer *N*=11, summer–autumn *N*=8, autumn–winter *N*=7; family groups: winter–spring *N*=11, spring–summer *N*=12, summer–autumn *N*=9, autumn–winter *N*=7), *Friedman 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*: χ^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*=0934, *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±1,146.4 m, *N*=7) and autumn (1147.4± 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±56.1	51.1±28.0	−1.072	0.284	2,682.1±1,198.4	3,042.9±870.1	−1.449	0.147
Summer	14/10	128.3±98.7	158.7±145.1	−0.282	0.778	3,800.5±1,056.5	5,304.1±2,752.5	−1.018	0.309
Autumn	11/8	61.3±43.3	72.5±36.6	−0.735	0.462	2,555.0±710.6	3,597.8±1,217.9	−1.785	0.074
Winter	10/7	82.4±96.1	115.0±183.5	−0.0	1.0	3,137.8±1,246.3	2,893.6±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 unhunted G
			395		Jan–Apr
		7 G	255		May–Aug
			6,625		Sep–Dec hunted G
			4,510		Jan–Apr
Singer et al. 1981	Great Smoky Mountains, USA	4 YF	345		Summer
			265		Winter with mast
			1,395		Winter without mast
Baubet 1998	French Alps	23 7	1,100		Summer
			415		Winter
Maillard and Fournier 1995	Hérault, S-France	9	1,390		Summer
			5,140		Hunt
Baubet et al. 1998	French Alps	6	1,225		Summer
			1,540		Hunt
Calenge et al. 2002	Haute Marne, NE-France	18		530	Summer
				1,350	Hunt
Calenge et al. 2002	Hérault, S-France	9		380	Summer
				1,380	Hunt
Mauget 1980	Chizé, W-France	7 F	240–425		2–6 months
Gerard and Campan 1988	div. France	3 F	400, 547, 1,600		2, 2, 5 months
Dinter 1991	urban forest Berlin, Germany	8 F	175		2–5 months Apr–Sep
Gerard et al. 1992	Toulouse, S-France	1 adF	400		2 months
Keuling et al. 2001	N-Germany	5 F	470		1–5 months Jun–Nov
Sodeikat and Pohlmeyer 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 local-isations) 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 supple-mental feeding, as wild boar prefer food of natural and agricultural origin (Briedermann 1976, Genov 1981; Baber and Coblentz 1986; Gerard et al. 1991). In addition, sup-plemental food contributes to the increase of wild boar popu-lation, 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 re-flected 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 Pohlmeyer 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.

References

Baber DW, Coblentz BE (1986) Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J Mammal 67:512–525

Baubet E (1998) Biologie du sanglier en montagne: biodémographie, occupation de l'espace et régime alimentaire. Dissertation, L'Université Claude Bernard Lyon

Baubet E, Brandt S, Touzeau C (1998) Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus scrofa*). Analyses préliminaires. Gibier Faune Sauvage 15:655–658

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J Appl Ecol 42:1203–1213

Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild boar in Tuscany, Italy. J Mammal 75:600–612

Bratton SP (1975) The effect of the European wild boar (*Sus scrofa*) on Gray beech forest in the Great Smokey Mountains. Ecology 56:1356–1366

Brauer A, Lange E, Kaden V (2006) Oral immunisation of wild boar against classical swine fever: uptake studies of new baits and investigations on the stability of lyophilised C-strain vaccine. Eur J Wildl Res 52:271–276

Briedermann L (1976) Ergebnisse einer Inhaltsanalyse von 665 Wildschweinmägen. Zool Garten 46:157–185

Briedermann L (1990) Schwarzwild, 2nd edn. Neumann-Neudamm, Melsungen

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352

Calenge C, Maillard D, Vassant J, Brandt S (2002) Summer and hunting season home ranges of wild boar (Sus scrofa) in two habitats in France. Game Wildl Sci 19:281–301

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can J Zool 72:1691–1694

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

de Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. J Anim Ecol 68:221–234

Dinter U (1991) Das Raum-Zeitverhalten von Schwarzwild im Grunewald in den Sommermonaten unter besonderer Berücksichtigung menschlicher Störungen. Dissertation, Ludwig-Maximilian-Universität München

Fernández-Llario P, Maetos-Quesada P (1998) Body size and reproductive parameters in the wild boar Sus scrofa. Acta Theriol 43:439–444

Fischer C, Gourdin H, Obermann M (2004) Spatial behaviour of the wild boar in Geneva, Switzerland: testing methods and first results. in: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys 16(Special Issue):149–156

Gaillard J-M, Brandt S, Jullien J-M (1993) Body weight effect on reproduction of young Wild Boar females: a comparative analysis. Folia Zool 42:204–212

Garrott RA, White GC, Bartmann RM, Weybright DL (1986) Reflected signal bias in biotelemetry triangulation systems. J Wildl Manage 50:747–752

Genov P (1981) Significance of natural biocenoses and agrocenoses as the source of food for wild boar (*Sus scrofa* L.). Ekologia Polska 29:117–136

Gerard JF, Campan R (1988) Variabilité éco-ethologique chez le sanglier europeén: comparision des travaux francaise. Cahiers d'Ethologie Appliquee 8:63–130

Gerard JF, Cargnelutti B, Spitz F, Valet G, Sardin T (1991) Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriol 36:119–129

Gerard JF, Cargnelutti B, Spitz F (1992) Relation entre anisotropie de l'occupation de l'espace et dispersion: un exemple chez le sanglier du sud-ouest de la France. Mammalia 56:177–187

Hahn N, Eisfeld D (1998) Diet and habitat use of wild boar (*Sus scrofa*) in SW-Germany. Gibier Faune Sauvage 15:595–606

Hooge PN, Eichenlaub B (2001) Movement 2.0, animal movement extension to ArcView. Alaska Biological Science Center, US Geological Survey, Ancorage, AK, USA

Janeau G, Spitz F (1984) L'espace chez le sanglier (*Sus scrofa* L.) occupation et mode d'utilisation. Gibier Faune Sauvage 1:73–89

Kaden V (1999) Bekämpfung der Klassischen Schweinepest beim Schwarzwild. Z Jagdwiss 45:45–59

Kenward RE, South AB, Walls SS (2003) Ranges 6 v1.2: For the analysis of tracking and location data. 2.041. Anatrack Ltd., Wareham, UK

Keuling O, Sodeikat G, Pohlmeyer K (2001) Habitat use of Wild Boar Sus scrofa L. in an agroecosystem in Lower Saxony (Germany) with special approach to source of food. in: "Wildlife Management in the 21st Century", 25th International Congress of IUGB, 3–7. Sept.:109

Keuling O, Stier N, Roth M (2005) Does hunting affect the spatial utilisation of wild boar Sus scrofa L.? in: XXVIIth Congress of IUGB, 28. Aug.-3. Sept. Extended abstracts.379–380

Labudzki L, Wlazelko M (1991) Saisonale Dynamik der vom Schwarzwild im Feldanbau verursachten Schäden im Forschungsgebiet Zielonka. Z Jagdwiss 37:250–257

Lemel J, Truvé J, Söderberg B (2003) Variation in ranging and activity behaviour of European wild boar Sus scrofa in Sweden. Wildl Biol 9:29–36

Maillard D, Fournier P (1995) Effect of shooting with hounds on home range size of Wild Boar (Sus scrofa L.) groups in Mediterranean habitat. IBEX JME 3:102–107

Massei G, Genov PV, Staines B, Gorman ML (1997) Factors influencing home range and activity of wild boar (Sus scrofa) in a Mediterranean costal area. J Zool 242:411–423

Massei G, Cowan DP, Miller L (2006) Fertility control to manage wild boar: a viable option? in: Sixth international symposium on wild boar (Sus scrofa) and sub-order suiformes. abstracts:45

Mauget R (1980) Home range concept and activity patterns of European wild boar (Sus scrofa L.) as determined by radio tracking. In: Amlaner CJ, McDonald DW (eds) A handbook of biotelemetry and radiotracking. Pergamon, Oxford, pp 725–728

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37:223–249

Otis DL, White GC (1999) Autocorrelation of location estimates and the analysis of radiotracking data. J Wildl Manage 63:1039–1044

Russo L, Massei G, Genov PV (1997) Daily home range and activity of wild boar in a Mediterranean area free from hunting. Ethol Ecol & Evol 9:287–294

Samuel MD, Pierce DJ, Garton EO (1985) Identifying areas of concentrated use within the home range. J Anim Ecol 54:711–719

Santos P, Fernández-Llario P, Fonseca C, Monzón A, Bento P, Soares AMVM, Mateos-Quesada P, Petrucci-Fonseca F (2006) Habitat and reproductive phenology of wild boar (Sus scrofa) in the western Iberian Peninsula. Eur J Wildl Res 52:207–212

Singer FJ, Otto DK, Tipton AR, Hable CP (1981) Home ranges, movements and habitat use of European Wild Boar in Tennessee. J Wildl Manage 45:343–353

Sodeikat G, Pohlmeyer K (2002) Temporary home range modifikations of wild boar family groups (Sus scrofa L.) caused by drive hunts in Lower Saxony (Germany). Z Jagdwiss 48(Suppl): 161–166

Stubbe C, Mehlitz S, Peukert R, Goretzki J, Stubbe W, Meynhardt H (1989) Lebensraumnutzung und Populationsumsatz des Schwarzwildes in der DDR-Ergebnisse der Wildmarkierung. Beitr Jagd- u Wildforschung 16:212–231

Swihart RK, Slade NA (1985) Testing for independence of observations in animal movements. Ecology 66:1176–1184

Swihart RK, Slade NA (1997) On testing for independence of animal movements. J Agr Biol Envir St 2:48–63

Truvé J (2004) Pigs in space: movement, dispersal and geographic expansion of wild boar (Sus scrofa) in Sweden. Dissertation, University of Göteborg

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Zimmerman JW, Powell RA (1995) Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Can J Zool 73:1123–1133

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Keuling O, Stier N, Roth M (2009)

Commuting, shifting or remaining? Wild boar *Sus scrofa* L. space use patterns in summer

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ORIGINAL INVESTIGATION

Commuting, shifting or remaining?
Different spatial utilisation patterns of wild boar *Sus scrofa* L. in forest and field crops during summer

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Abstract

In a radiotelemetry study in North-East Germany, we analysed spatial utilisation of 22 female wild boar (*Sus scrofa*) out of 21 wild boar groups during summer (2003–2006). We compared summer season home ranges (16 May–15 August) with "field home ranges", i.e. periods between first and last appearance within cereal fields. Wild boar appeared inside fields with beginning of grain and rapeseed flowering and vanished usually with harvest. Three types of spatial utilisation patterns were defined: "field sows", who shifted their home range entirely into fields; "commuters", who roamed between forest and fields; and "forest sows", who remained in the forest. Yearlings were predominantly commuters, whilst family groups did not roam but either shifted to fields or stayed in forest.

Field sows had smaller mean field home ranges than total summer home ranges, whereas commuters and forest sows showed no differences. All three groups did not differ significantly in home range size measures but, however, showed different mean shifts from spring to summer home range. The home range sizes of sows of the different spatial patterns were similar, as all resources were permanently available all-over the study area. However, dislocations into outstanding profitable nutritional habitats (e.g. agricultural fields in summer) may enlarge annual home ranges of commuters and field sows.

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Keywords: Sus scrofa; Spatial utilisation pattern; Field crops; Home range; Habitat choice

Introduction

In many parts of Europe rapidly increasing wild boar populations result in severe economical problems. Wild boar can cause enormous damages notably in crop fields and forest ecosystems (Bratton 1975; Singer et al. 1984; Labudzki and Wlazelko 1991; Killian et al. 2006; Sodeikat and Pohlmeyer 2007) and are suspected of

transmitting disease to domestic livestock (Brauer et al. 2006; Killian et al. 2006; Sodeikat and Pohlmeyer 2007).

Radiotelemetry has been frequently used to reveal spatial utilisation patterns of wild boar (e.g. Mauget 1980; Gerard and Campan 1988; Boitani et al. 1994; Massei et al. 1997b; Hahn and Eisfeld 1998; Fischer et al. 2004), but the roles of age, reproductive status, sex and seasonal changes were often neglected. Several studies indicate that changes in wild boar home range size depend on season, food availability and anthropogenic disturbances (Singer et al. 1981; Boitani et al. 1994;

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Maillard and Fournier 1995; Massei et al. 1997b; Baubet et al. 1998; Calenge et al. 2002; Keuling et al. 2007).

As the maximum group size in mammals (and especially ungulates) is influenced by food availability (Jarman 1974), changing food availability may result in different social organisation (Geist 1974), but may also lead to variation in space and habitat use. Concerning spatial use, wild boar display flexible and individual reactions on many factors such as availability of resources (e.g. food, water and shelter), demographic parameters (e.g. density, group size, age and sex ratios) or disturbances (e.g. like recreation, forestry, hunting and predation) (see also Boitani et al. 1994; Keuling et al. 2007). Hence, wild boar react on changing environmental conditions by variation of seasonal home range size and locations within their relatively small scaled and site loyal annual and total home range. In a previous study, summer home ranges of wild boar tended to be larger than in other seasons, though not significant, due to individual spatial utilisation patterns, which were different between groups of yearling and adult females (Keuling et al. 2007). Seasonal dislocations were reported previously only in two other studies in mountainous areas (Singer et al. 1981; D'Andrea et al. 1995) and once in a lowland area without high snow cover (Keuling et al. 2007).

In the present study, we examined spatial utilisation patterns of female wild boar during the maturing period of cereal crops (when wild boar feed on cereals, see Herrero et al. 2006) to address the following questions: do home range size and location of wild boar sows vary during summer? Are these variations related to different types of spatial utilisation pattern? Are there any differences between yearlings and adults?

Study area

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 of the study area is formed by the Vistula glaciation and rises from 20 up to 100 m above sea level. Agriculture and forestry combined with low human settlement are the main features of the area: the study area of about 20,000 ha consists of 40% agricultural fields, 34% forest stands, 23% meadows and pastures (incl. fallow land) with 3% housing estates. The agricultural land was characterised by large fields of a mean size of 20 ha (up to 150 ha maximum). Twenty-three percent of the agricultural fields were rye and Triticale, 15% barley, 15% wheat, 6% oat, 15% rapeseed, 13% maize and 13% other crops. The core part of the study area comprises about 2400 ha unfragmented forest growing on a quite flat

outwash plain, which enables an easy and precise work on radiotelemetry, and surrounding moraines. The forest contains 57% pine (*Pinus sylvestris*, *P. strobus*), 7% spruce (*Picea abies*, *P. omorica*, *P. glauca*, *P. sitchensis*, *P. pungens*) and 7% other coniferous tree species. The most important deciduous trees are oak (*Quercus robur*, *Q. petrea*, *Q. rubra*: 6%), beech (*Fagus sylvatica*: 6%), alder (*Alnus glutinosa*, *A. viridis*: 7%) and birch (*Betula pendula*: 7%). Based on the Atlantic climate the average annual rainfall amounts to 680 mm and the mean annual temperature is 8.2 °C. The mean annual harvest of the wild boar in the study area was 3.6 individuals per 100 ha during the observation period.

During summer the hunting pressure was lower in the study area, as hunt was mainly conducted as single hunt at the edges between fields and forest.

During summer hunting was concentrated at the edge between forest and fields by single hunt, but occurred only occasionally in forest. However, the overall hunting pressure during summer was lower than in winter, when additional single and drive hunts took place in forest.

Material and methods

We captured wild boar during winter in forest in big cage traps of $5 \times 2 \times 2$ 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 maximum lifespan of 3 years (mean lifespan 363 days), reaching up to 3 km. We located all individuals once at daytime about four times a week (diurnal resting places) and one to five times at night at least twice a week (nocturnal activity). To avoid disturbances we performed the localisations by multiple triangulations with car mounted 4-element-YAGI-antennas (self-made) using TRX-1000S receivers (Wildlife Materials Inc., USA). The telemetry error was at median 60 m between assumed and real transmitter location (Keuling et al. 2007). We transcribed the wild boar positionings with a Calcomp® SummaSketchIII digitising tableau to Esri® ArcView 3.2. Telemetry data were analysed with Ranges 6 v1.2 (Kenward et al. 2003). Home range analyses were done as minimum convex polygons (MCP) (Mohr 1947) to describe the maximum used space (100% of localisations), and kernel home ranges 95% core weighted (KHR95) (Worton 1989) with default settings in Ranges6 (cell default = 40) to describe the home range (Burt 1943). We assumed a time interval of at least 2 h between localisations as sufficiently independent to calculate kernel home ranges (Keuling et al. 2007).

To define different types of spatial utilisation patterns we calculated the proportions of localisations within fields and forest during day and night, respectively.

Telemetry data were recorded during spring and summer 2003–2006. The summer season ("summer home range") was defined as the period from 16 May to 15 August (flowering of rapeseed and grain until harvest of grain), when most of the wild boar groups resided inside the fields (Keuling et al. 2007). Spring was defined from February 16 to May 15 (from rooting

on grassland until shift to fields, parturition season), the telemetry data of this season were used solely for analysis of shifting; spring home range sizes are presented by Keuling et al. (2007). Field-use periods of wild boar ("field home range") were defined as the time span between first and last appearance of individuals in cereal fields within the defined summer season. If no first or last day could be detected, because either the field-use period extended over the summer period or fields were not attended at all, the whole summer home range was used for comparison. In this paper, we refer to data from 22 female wild boar out of 21 different groups. We subdivided these groups into two age classes: "yearlings without piglets" and "family groups" (sounders) (Keuling et al. 2007).

We calculated the spatial shift of home ranges by the distance between centres of spring and summer kernel home ranges, based on Ranges6. We analysed differences between summer and field home range sizes with Wilcoxon rank-sum test, and, after describing varying spatial patterns, differences of home range measurements between these different groups of behavioural types with Kruskal–Wallis H-test, including the Nemenyi test for paired comparison between groups. We accomplished the Nemenyi test with Microsoft® Excel and further analyses in SPSS 12.0. All tests were two-tailed with level of significance of $p \leqslant 0.05$.

Results

The earliest day wild boar appeared within fields was 3 May (median 26 May), however, some individuals visited the fields even in other seasons casually. The last observed day in the field was 1 September (median 5 August), although some groups returned to maize fields in late autumn. The last day for one group to finally return to the forest was 19 October, but we did not consider the autumn period in our analyses.

The results revealed differences in spatial utilisation pattern of wild boar sows during summer which resulted in the definition of three behavioural types.

The most common behavioural type with 45% of all observed cases was that of "field sows", which shifted their entire home range for a certain period into the arable land. They stayed most of the time within cereal fields during day and night (Table 1, Fig. 1), moving

back into the forest very seldom, mainly in the beginning or at the end of the period (Fig. 2, group 1c). "Commuters" moved frequently between forest and fields (Fig. 2, group 7), staying in fields during daytime less than 70% but more than 35% during nighttime (Fig. 1). Some of the commuters showed combined types, e.g. remaining for a time and then commuting or shifting; some were commuting and showed partial dislocations (Table 1). Commuters appeared in 35% of the observed cases. Only 20% of wild boar acted as "forest sows", which did hardly visit the fields especially during the day (Table 1, Fig. 1, Fig. 2, group 23). Yearlings were mostly ranging as commuters but never as forest sows, whilst family groups (sounders) were predominantly shifting or remaining (Table 1). Out of the 22 observed animals 7 were observed for more than one summer. Four of them showed different spatial patterns in different years (Table 2).
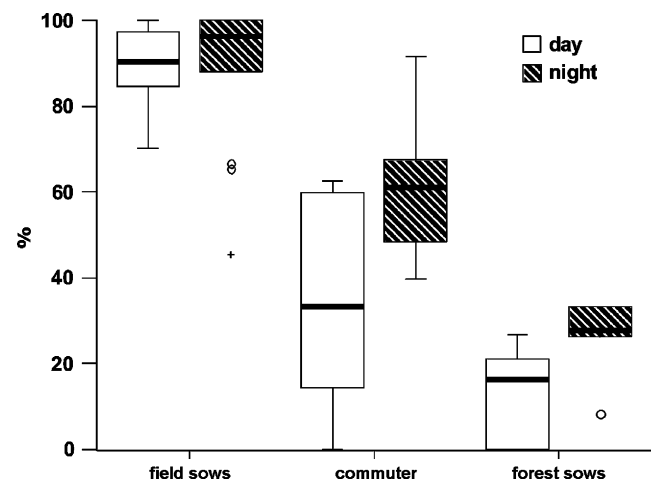

Fig. 1. Percentage of localisations during day and night-time inside cereal fields during the field-use period for wild boar related to different types of spatial patterns. Box and whisker plots show median (horizontal line within box), 25% and 75% percentiles (box) and range (whiskers), circles indicate statistical outliers (observations between 1.5 and 3 interquartile ranges), plus indicates extreme value; field sows $N = 14$, commuters $N = 11$, forest sows $N = 6$.

Table 1. Definition of spatial patterns by wild boar groups during season of maturing of cereal crops (field-use period in summer)

Type	% fi:fo[a] day	% fi:fo[a] night	N family groups	N yearling groups
Field sows	$\geqslant 70$	$\geqslant 65$	11	3
Commuter	< 70	$\geqslant 35$	2	9
Real commuter	< 60	$\geqslant 40$	1	6
Commuter with partial shift	$\geqslant 60–70$	$\geqslant 60$	1	2
Commuter staying lot in forest	< 30	$\geqslant 35–40$	–	1
Forest sows	< 30	< 35	6	–

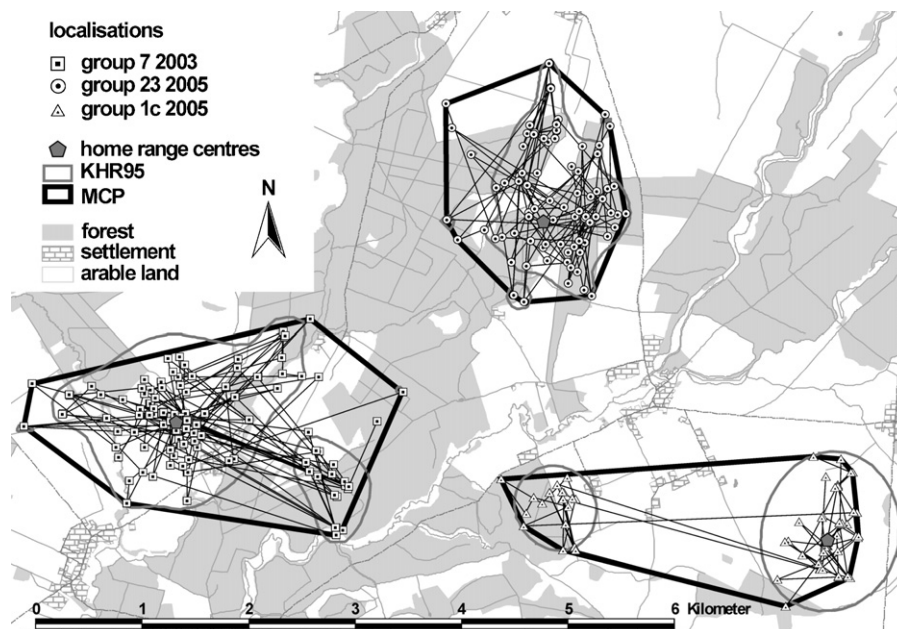[a] % fi:fo = proportion of localisations within field:forest.

Fig. 2. Examples for three wild boar groups with different spatial patterns during field-use period. Group 1c: field sounder, shifted home range core from forest completely to fields and forest edge; group 7: commuter, stayed in forest for resting, shuttled to fields by night; group 23: forest sounder, stayed in forest with only few visits to the fields during night. Lines connect independent consecutive localisations.

Table 2. Individual patterns of spatial utilisation in different years and age at first year

Group	Age	2003	2004	2005	2006
1	A		FI	FI	
1a	Y	C	FI	FI	FO
1b	Y		FI	FI	
1c	Y		C	FI	
4	A	FO			
5	Y	C			
7	Y	C			
9	Y	C			
10(59)	Y		C	FI	
10(155)	A				FO
11	A		C		
12	Y		C		
13	Y		C	C	
14	Y		C		
15	A		FI		
19	Y			FI	
21	Y			FI	
22	A			FI	
23	A			FO	
24	A			C	FO
26	A				FI
28	A				FO

A: adult within family group; Y: yearling; C: commuter; FI: field sounder; FO: forest sounder; numbers in brackets give ID of individual animal.

Field sows had smaller field home ranges than total summer home ranges (Fig. 3; Wilcoxon test, $N = 14$; MCP: $Z = -2.578$, $p = 0.01$; KHR95: $Z = -2589$, $p = 0.01$), whereas in commuters the size was similar (Fig. 3; Wilcoxon test: commuters, $N = 11$; MCP: $Z = -1.095$, $p = 0.273$; KHR95: $Z = -0.338$, $p = 0.735$). Forest sows had no shorter period of field use.

The three types did not differ in home range size (Fig. 3; summer season Kruskal–Wallis H-test, df $= 2$, $N = 31$; MCP: chi$^2 = 5.318$, $p = 0.07$; KHR95: chi$^2 = 3.855$, $p = 0.146$; field-use period Mann–Whitney U-test, $N = 25$; MCP: $Z = -1.478$, $p = 0.139$; KHR95: $Z = -1.916$, $p = 0.055$). Only the shift of home range centre from spring to summer did differ (Kruskal–Wallis df $= 2$, $N = 26$, chi square $= 7.499$, $p = 0.024$). Forest sows tended to smaller shifts of home range centres than both other groups without being significant (Fig. 3; Nemenyi test: chi$^2 = 5.99$, df $= 2$, $N = 26$, $p > 0.05$).

Discussion

Spatial utilisation pattern of wild boar in agroecosytems during summer can be defined as proportions of diurnal and nocturnal presence within arable land and forest. However, in some cases classification was not
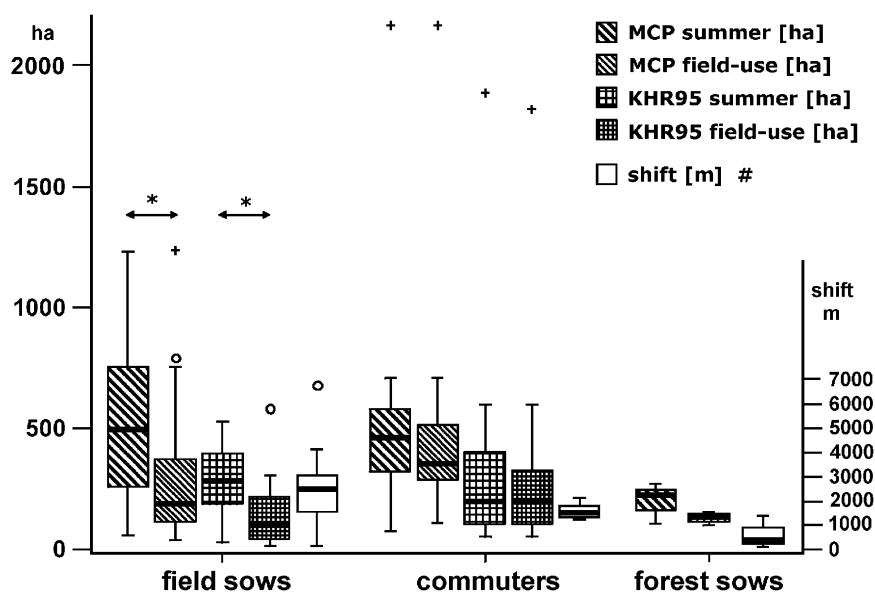
Fig. 3. Home range sizes [ha] and shift [m] of wild boar groups with different spatial utilisation patterns. Box and whisker plots show median (horizontal line within box), 25% and 75% percentiles (box) and range (whiskers), circles indicate statistical outliers (observations between 1.5 and 3 interquartile ranges), plus indicate extreme values. MCP, minimum convex polygon; KHR95, kernel home range 95%; Wilcoxon test: $^*p = 0.01$, Kruskal–Wallis: $^\#p = 0.024$; field sows $N = 14$, commuters $N = 11$, forest sows $N = 6$.

easy, as some of the animals expressed different behaviour during the observed period. These animals appeared mostly as commuters and were treated accordingly, although they switched between remaining, commuting and shifting. These three behavioural types and the combination of them within several individuals reflect the high behavioural flexibility and also individuality of this species (Gerard et al. 1992; Boitani et al. 1994; Baubet et al. 1998; Keuling et al. 2007). Wild boar are mainly described as a predominantly forest or forest edge species, mostly occurring in near-natural habitats (e.g. Genov 1981; Briedermann 1990; Fonseca 2007). Therefore, in habitat suitability studies only forest stands of adequate size (larger than at least 500 ha) were considered (Howells and Edward-Jones 1997; Leaper et al. 1999; Fernández et al. 2006), although Briedermann (1990) already described the use of centres of large fields during summer as periodical home range (field sows). Actually, many authors confirmed the wild boar as a species able to live in more open habitats but, however, requiring forest or bush land for shelter in winter and using fields as available or preferred in summer (e.g. Lescourret and Génard 1985; Dardaillon 1987; Geisser and Reyer 2004; Fonseca 2007; Schley et al. 2008, see overview on nutrition in Schley and Roper 2003). Only Gerard et al. (1991) and Herrero et al. (2006) observed wild boar using cropland in agricultural regions predominantly almost year-round, however, needing some very small forests or scrubs for shelter.

In our study most individuals were classified as "field sows", followed by commuters (using forest edges),

indicating a high usage of fields in summer (Keuling et al. in preparation; see also Gerard et al. 1991; Schley and Roper 2003; Herrero et al. 2006). This might also support the hypothesis that wild boar are able to use areas free of large forests and perhaps to exist in purely agricultural landscapes (see also Gerard et al. 1991; Herrero et al. 2006) containing only small habitats offering shelter during the rest of the year (e.g. small scrub, heath or moor lands or small forests), if hunting pressure is comparatively low. The general sound food and shelter conditions (combined with low hunting pressure during summer) meet the requirements of all wild boar in the forest as well as in the fields, which is supported by only marginal variation in home range size and limited shift of home range centres. In agricultural dominated areas a higher proportion of wild boar might tend to commute or shift into fields under sparse nutritional conditions in the forest (see also Gerard et al. 1991; Herrero et al. 2006), whereas in regions dominated by forest we would assume a higher proportion of forest sows.

Family groups stayed mostly at one site inside fields (best nutrition and even sound shelter) or forest (best shelter with poorer nutrition) probably to avoid being hunted (Baubet et al. 1998; Sodeikat and Pohlmeyer 2007). Small site loyal periodical home range sizes inside fields or forest may result from optimal nutrition as well as from hunting pressure at the edge between forest and fields. Thus, many females either used large fields (mean 20 ha) for shelter and nutrition or stayed inside the forest. Female yearlings were mainly commuting; they

might have been exploring their habitat (searching for best resource and, perhaps mother independent home ranges). It has also been shown that wild boar of different age and sex have different requirements (Dardaillon 1989; Spitz 1992; Cousse et al. 1994; Massei et al. 1997a). Adults select the most secure area to raise their piglets and to find optimal feeding places. So, it is not surprising to find them mostly in forests or inside the fields (at any time of the day). It also underlines that good feeding conditions are found anywhere. Female yearlings have less experience than females; hence, they do not show a high avoidance of being hunted. As none of the observed yearlings led piglets (those leading piglets stayed mainly within the family groups), they were able to roam and explore their habitat, often in groups together with female and male siblings.

Although wild boar behaved similar throughout several years and within one "family" (see Table 2, Groups 1–1c), spatial behaviour in summer seems to be rather dependent on weather and individual preferences. Some adults changed their behaviour in different years (see Table 2, Groups 1a, 24). In extremely dry and hot summers only very few wild boar acted as "field sows" (2003, 2006), compared to summers with higher precipitation and lower temperatures (2004, 2005). However, piglets might learn behavioural patterns from their mother und thus some different "cultures" of spatial utilisation might exist.

In a previous study, female wild boar used seasonal home ranges of similar size with a tendency for larger summer home ranges and increased bidirectional centre shifting to summer home ranges especially in yearlings (Keuling et al. 2007, see also Massei et al. 1997b). These larger summer home ranges might result from the larger shifts in field sows and commuters. The summer home range sizes of field sows were larger than their field home ranges. Also the summer home range sizes of commuters tended to be larger than their field home ranges. The field home ranges of both types were of similar size as all other seasonal home ranges seasons observed by Keuling et al. (2007). As yearlings never belonged to the type of forest sows, their summer home ranges tended to be larger.

As food resources seem to be more or less equably distributed in our study area, the field home range sizes did not differ between different spatial utilisation patterns, however, dislocations may enlarge home ranges of longer periods (e.g. annual home ranges) of commuters and field sows. A shift of the home range centre to the fields in field sows (and also commuters) enlarged annual home ranges for those types (Keuling et al. 2007). Summer home ranges of forest sows ranged at the lower limit of average summer home range sizes (Fig. 3, see also Keuling et al. 2007). The small scaled summer home range sizes of all wild boar groups correspond to various literature data (e.g. Singer et al.

1981; Gerard et al. 1992; Boitani et al. 1994; Maillard and Fournier 1995; Massei et al. 1997b; Baubet et al. 1998; Calenge et al. 2002; Fischer et al. 2004; Keuling et al. 2007). Some authors assumed hunting as the main factor for bigger home ranges during other seasons (Maillard and Fournier 1995; Baubet et al. 1998), which did not occur in our study (Keuling et al. 2007). This might be a sign for only low or at least year-round constant hunting pressure of similar intensity within different habitats in our study area as well as for the sound nutritional conditions.

Wild boar prefer food of high energetic content (Mackin 1970; Schley and Roper 2003; Schley et al. 2008) which may be of natural origin (e.g. acorn mast, Briedermann 1976; Genov 1981; Schley and Roper 2003) or anthropogenic (e.g. crop fields). The latter preference often results in damages in agriculture (Briedermann 1976; Schley and Roper 2003; Geisser and Reyer 2004; Herrero et al. 2006; Schley et al. 2008). Variation in home ranges result from variation in food resources, habitat structure and population density (Calenge et al. 2002). Foraging site choice in summer mainly depends on the cultivation of attractive crops. This is confirmed by larger seasonal shifting of home range centres observed in summer, depending on the spatial location of agricultural crops like rapeseed and wheat (Keuling et al. 2007). Changing food availability influences summer home ranges as most of the animals now forage on agricultural crops (see also Briedermann 1990; Gerard et al. 1991; Keuling et al. 2001; Herrero et al. 2006). Supporting this view, Briedermann (1990) reported that the seasonal spectrum of ingested food strongly reflected the scheme of agricultural crops. However, preferences of different crops occur (e.g. Herrero et al. 2006).

Seasonal dislocations were reported only in two other studies: Singer et al. (1981) detected a shift of home ranges for 20 wild boar of both sexes in Great Smoky Mountains National Park, TN, USA, towards higher elevations in summer with a mean shift of 6 km, however, some animals remained at lower elevations. In contrast, D'Andrea et al. (1995) found wild boar in Italian Alps resting in higher elevation during winter, probably to avoid human disturbances like poaching, in summer they rested near to the lower situated all-year feeding places. Home ranges were smaller, when food abundance was high (Singer et al. 1981; Boitani et al. 1994), whereas Massei et al. (1997b) and Caley (1997) assumed smaller home ranges during poor nutritional conditions. We assume that both strategies occur in wild boar. When nutritional conditions are poor wild boar have to roam searching for food, or especially water in dry seasons (Baber and Coblentz 1986; Caley 1997; Massei et al. 1997b). On the other side they might avoid energy loss, especially in winter when food is sparse but body-fat condition is still good (Singer et al. 1981;

Boitani et al. 1994). In our study seasonal home range sizes did not differ as nutritional conditions can be judged as good year-round (Keuling et al. 2007). The study area consists of richly structured habitats, offering oak and beech mast in forest and hedgerows and high nutritional conditions in the fields. Possible poor conditions are mitigated by supplemental feeding at many baiting stations.

A high individual flexibility in spatial behaviour enables wild boar populations an optimal utilisation of seasonal resources such as food and shelter.

Acknowledgements

References

Baber, D.W., Coblentz, B.E., 1986. Density, home range, habitat use, and reproduction in feral pigs on Santa Catalina Island. J. Mammal. 67, 512–525.

Baubet, E., Brandt, S., Touzeau, C., 1998. Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus scrofa*). Analyses préliminaires. Gibier Faune Sauvage 15, 655–658.

Boitani, L., Mattei, L., Nonis, D., Corsi, F., 1994. Spatial and activity patterns of wild boar in Tuscany, Italy. J. Mammal. 75, 600–612.

Bratton, S.P., 1975. The effect of the European wild boar (*Sus scrofa*) on Gray Beech Forest in the Great Smokey Mountains. Ecology 56, 1356–1366.

Brauer, A., Lange, E., Kaden, V., 2006. Oral immunisation of wild boar against classical swine fever: uptake studies of new baits and investigations on the stability of lyophilised C-strain vaccine. Eur. J. Wildl. Res. 52, 271–276.

Briedermann, L., 1976. Ergebnisse einer Inhaltsanalyse von 665 Wildschweinmägen. Zool. Garten 46, 157–185.

Briedermann, L., 1990. Schwarzwild, second ed. Neumann-Neudamm, Melsungen.

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24, 346–352.

Calenge, C., Maillard, D., Vassant, J., Brandt, S., 2002. Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game Wildl. Sci. 19, 281–301.

Caley, P., 1997. Movement, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. Wildl. Res. 24, 77–87.

Cousse, S., Spitz, F., Hewison, M., Janeau, G., 1994. Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can. J. Zool. 72, 1691–1694.

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

Dardaillon, M., 1987. Seasonal feeding habits of the wild boar in a Mediterranean wetland, the Camargue (Southern France). Acta Theriol. 32, 389–401.

Dardaillon, M., 1989. Age-class influence on feeding choices of free-ranging wild boars (*Sus scrofa*). Can. J. Zool. 67, 2792–2796.

Fernández, N., Kramer-Schadt, S., Thulke, H.-H., 2006. Viability and risk assessment in species restoration: planning reintroductions for the wild boar, a potential disease reservoir. Ecol. Soc. 11, 6 (online) 〈http://www.ecologyandsociety.org/vol11/iss1/art6/〉.

Fischer, C., Gourdin, H., Obermann, M., 2004. Spatial behaviour of the wild boar in Geneva, Switzerland: testing methods and first results. In: Fonseca, C., Herrero, J., Luis, A., Soares, A.M.V.M. (Eds.), Wild Boar Research 2002. A Selection and Edited Papers From the "4th International Wild Boar Symposium". Galemys, 16 Special Issue, pp. 149–155.

Fonseca, C., 2007. Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. Eur. J. Wildl. Res. (online), doi:10.1007/s10344-007-0144-9.

Geisser, H., Reyer, H.-U., 2004. Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. J. Wildl. Manage. 68, 939–946.

Geist, V., 1974. On the relationship of social evolution and ecology in ungulates. Am. Zool. 14, 205–220.

Genov, P., 1981. Significance of natural biocenoses and agrocenoses as the source of food for wild boar (*Sus scrofa* L.). Ekol. Pol. 29, 117–136.

Gerard, J.F., Campan, R., 1988. Variabilité éco-ethologique chez le sanglier europeén: comparision des travaux francaise. Cahiers d'Ethologie Appliquée 8, 63–130.

Gerard, J.F., Cargnelutti, B., Spitz, F., Valet, G., Sardin, T., 1991. Habitat use of wild boar in a French agroecosystem from late winter to early summer. Acta Theriol. 36, 119–129.

Gerard, J.F., Cargnelutti, B., Spitz, F., 1992. Relation entre anisotropie de l'occupation de l'espace et dispersion: un example chez le sanglier du sud-ouest de la France. Mammalia 56, 177–187.

Hahn, N., Eisfeld, D., 1998. Diet and habitat use of wild boar (*Sus scrofa*) in SW-Germany. Gibier Faune Sauvage 15, 595–606.

Herrero, J., García-Serrano, A., Couto, S., Ortuño, V.M., García-González, R., 2006. Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. Eur. J. Wildl. Res. 52, 245–250.

Howells, O., Edward-Jones, E., 1997. A feasibility study of reintroducing wild boar (*Sus scrofa*) to Scotland: are existing woodlands large enough to support minimum viable populations? Biol. Conserv. 81, 77–89.

Jarman, P.J., 1974. The social organization of antelope in relation to their ecology. Behaviour 48, 215–267.

Kenward, R.E., South, A.B., Walls, S.S., 2003. Ranges 6 v1.2: For the Analysis of Tracking and Location Data. Anatrack Ltd., Wareham, UK.

Keuling, O., Sodeikat, G., Pohlmeyer, K., 2001. Habitat use of wild boar *Sus scrofa* L. in an agroecosystem in Lower Saxony (Germany) with special approach to source of food. In: Hadjisterkotis, E. (Ed.), ''Wildlife Management in the 21st Century,'' 25th International Congress of IUGB, 3–7 Septtember, p. 109.

Keuling, O., Stier, N., Roth, M., 2007. Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. Eur. J. Wildl. Res., doi:10.1007/s10344-007-0157-4.

Killian, G., Miller, L., Rhyan, J., Doten, H., 2006. Immunocontraception of Florida feral swine with a single-dose GnRH vaccine. Am. J. Reprod. Immunol. 55, 378–384.

Labudzki, L., Wlazelko, M., 1991. Saisonale Dynamik der vom Schwarzwild im Feldanbau verursachten Schäden im Forschungsgebiet Zielonka. Z. Jagdwiss. 37, 250–257.

Leaper, R., Massei, G., Gorman, M.L., Aspinall, R., 1999. The feasibility of reintroducing Wild Boar (*Sus scrofa*) to Scotland. Mammal Rev. 29, 239–259.

Lescourret, F., Génard, M., 1985. Recherches d'indices d'alimentation et connaissance des milieux exploités par le sanglier (*Sus scrofa scrofa*) en été dan l'Herault. Gibier Faune Sauvage 2, 63–73.

Mackin, R., 1970. Dynamics of damage caused by wild boar to different agricultural crops. Acta Theriol. 15, 447–458.

Maillard, D., Fournier, P., 1995. Effect of shooting with hounds on home range size of Wild Boar (*Sus scrofa* L.) groups in Mediterranean habitat. IBEX J. Mt. Ecol. 3, 102–107.

Massei, G., Genov, P.V., Staines, B., Gorman, M.L., 1997a. Mortality of wild boar, *Sus scrofa*, in a Mediterranean area in relation to age and sex. J. Zool., Lond. 242, 394–400.

Massei, G., Genov, P.V., Staines, B., Gorman, M.L., 1997b. Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean costal area. J. Zool., Lond. 242, 411–423.

Mauget, R., 1980. Home range concept and activity patterns of European wild boar (*Sus scrofa* L.) as determined by radio tracking. In: Amlaner, C.J., McDonald, D.W. (Eds.), A Handbook of Biotelemetry and Radiotracking. Pergamon Press, Oxford, pp. 725–728.

Mohr, C.O., 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37, 223–249.

Schley, L., Roper, T.J., 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. Mammal Rev. 33, 43–56.

Schley, L., Dufrêne, M., Krier, A., Frantz, A.C., 2008. Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. Eur. J. Wildl. Res. (online), doi:10.1007/s10344-008-0183-x.

Singer, F.J., Otto, D.K., Tipton, A.R., Hable, C.P., 1981. Home ranges, movements and habitat use of European wild boar in Tennessee. J. Wildl. Manage. 45, 343–353.

Singer, F.J., Swank, W.T., Clebsh, E.E.C., 1984. The effects of wild pig rooting in a deciduous forest. J. Wildl. Manage. 48, 464–473.

Sodeikat, G., Pohlmeyer, K., 2007. Impact of drive hunts on daytime resting site areas of wild boar family groups (*Sus scrofa* L). Wildl. Biol. Pract. 3, 28–38.

Spitz, F., 1992. General model of the spatial and social organisation of Wild Boars (*Sus scrofa* L.). In: Spitz, F., Janeau, G., Gonzales, G., Aulagnier, S. (Eds.), ''Ongulés/Ungulates 91''. Proc. Intern. Symp., Toulouse.

Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70, 164–168.

IV

Keuling O, Stier N, Roth M (2008)

How does hunting influence activity and space use in wild boar *Sus scrofa*

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How does hunting influence activity and spatial usage in wild boar *Sus scrofa* L.?

Oliver Keuling · Norman Stier · Mechthild Roth

Abstract Increasing wild boar (*Sus scrofa* L.) population densities all over Europe cause severe economic problems. In popular belief, the wild boar is a more or less diurnal species, causing only minor problems when undisturbed, but is assumed to become nocturnal and wide-ranging when opposed to hunting pressure. In our study, we investigated the impact of hunting and several environmental factors on movements, spatial utilisation and activity patterns by radiotelemetry. Activity pattern revealed a mean proportion of diurnal activity of 12% of all localisations with a monthly change. The wild boar showed increased diurnal activity on undisturbed feeding habitats, especially in early summer. Different hunting methods did influence activity and spatial utilisation in terms of activity and smaller home ranges in areas with only single hunt, although this might be biased by seasonal effects. Flight distances increased significantly after single hunt and capture incidents, but still ranged inside the annual home ranges. Battues did not influence the spatial utilisation before and after hunt significantly. In only 14% of the observed cases did wild boar show small scaled escape movements after battues. The overlaps of home ranges did not change after battues.

Keywords Hunting impact · Influencing factors · Battue · Activity pattern · Hunting management

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Introduction

Rapidly increasing wild boar *Sus scrofa* L. densities are regarded to be responsible for severe economical problems in many parts of Europe, as they can cause enormous damages notably in crop fields and forest ecosystems (Bratton 1975; Singer et al. 1984; Labudzki and Wlazelko 1991; Groot Bruinderink and Hazebroek 1996; Killian et al. 2006) and are suspected of transmitting disease to domestic livestock (Killian et al. 2006; Gortázar et al. 2007). Consequently, farmers and animal health authorities claim for a stringent reduction of wild boar populations (Bieber and Ruf 2005; Killian et al. 2006; Sodeikat and Pohlmeyer 2007). To develop an effective and biologically based wild boar management, detailed information about population structure, reproduction and spatial usage is required. This need for knowledge is in particular true for family groups dominated by females who are the main subject of regulatory management measures.

Activity patterns of wild boar were described by many authors (e.g. Briedermann 1971; Gerard and Campan 1988; Cousse et al. 1995; Russo et al. 1997). The activity rhythm is biphasic or polyphasic with a high intraspecific variability; the main part of activity is used for foraging (Briedermann 1990; Cuartas and Braza 1990; Cousse et al. 1995; Cahill et al. 2003); the start of activity is closely correlated to sunset (Gerard and Campan 1988; Cousse et al. 1995; Lemel et al. 2003). Although some authors observed higher nocturnal than diurnal activities in wild boar (Briedermann 1971; McIlroy 1989; Boitani et al. 1992, 1994; Lemel et al. 2003), in popular belief, wild boar are more or less diurnal with small scaled movements when undisturbed (Meynhardt 1989, 1990; Hennig 1998), as this is assumed to be the natural behaviour (Briedermann 1971, 1990). On the other hand, they are supposed to become nocturnal and wide-

ranging under hunting pressure (Briedermann 1971; Beuerle 1975; Hennig 1998).

As wild boar should behave more natural when less disturbed, diurnal activity should increase when wild boar are exposed only to minor, short-term hunting pressure (e.g. only few battues per year, no single hunt). Permanent hunting pressure (single hunt, repeated battues) was assumed as the main factor for larger home ranges in winter/hunting season (Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002). Contrariwise, in some cases, wild boar reacted on hunting with smaller (and sometimes after battues shifted) home ranges in secure places (Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeyer 2002). Battues seem to be less and only short time disturbing than single hunt, but they may cause escape movements or higher overlap of home ranges (Maillard and Fournier 1995; Sodeikat and Pohlmeyer 2007). Higher dispersal may enhance crop damages and provide contact for spreading disease, however, it is still unknown which hunting method has least influence on wild boar movements.

In this study, we investigated the impact of different hunting methods on activity and spatial patterns as well as the influence of seasonal activity cycles and environmental factors on diurnal activity of wild boar. As solitary male wild boar cause less damage in agriculture and are not the reproducing animals of interest for population management, our study focused on female groups as basics for further investigations.

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 was divided into a relatively 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, surrounded by a mosaic of fields, grassland and small forests, comprised 2,400 ha unfragmented forest, which consisted of 71% coniferous tree species, important for shelter (57% pine *Pinus sylvestris*, 7% spruce *Picea* spec. and 7% other). The most important deciduous trees were oak (*Quercus robur, Q. petrea, Q. rubra*, 6%), beech (*Fagus sylvatica*, 6%), alder

(*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). Based on the Atlantic climate, the average annual rainfall amounted to 680 mm and the mean annual temperature was 8.2°C. The density of the wild boar population is unknown. However, the mean annual harvest of wild boar in the whole study area increased continuously from 2.83 individuals per 100 ha in 1999/2000 to 5.13 individuals per 100 ha in 2005/2006. Thus, we assume even higher densities within the forested core area.

As the intensity of hunting (e.g. hunters per 100 ha, attempts per shot wild boar) is rarely stated in other studies, it is difficult to asses the level of hunting pressure. Some authors describe about ten hunters, five beaters and one to five dogs per 100 ha as optimal for conducting drive hunts on ungulate species (Eisenbarth and Ophoven 2002; Happ 2002; Wölfel 2003), which is similar to our study area where battues were conducted with 8.3 hunters, 5.3 beaters and 2.7 dogs per 100 ha driven forest area. Battues were normally conducted once a year on the same area. Where population densities were assumed to be still high, another small battue was arranged. Within battues, 68 man-hours were operated per 100 ha, five wild boar were shot per 100 ha. Thus, 14 man-hours were needed to shoot one wild boar (for comparison, see Elliger et al. 2001, 41 h per wild boar). On these battues also other ungulates, mainly fallow deer *Dama dama* (in higher amounts at the same hunt), were shot. To shoot one sow on single hunt, about six attempts were needed (for comparison, see Liebl et al. 2005, ten attempts for one shot wild boar). Thus, about 24 single hunt attempts on wild boar were conducted per 100 ha and year. These were 72 man-hours per 100 ha (plus another 50 h per 100 ha for shooting other ungulates), which were about 18 man-hours per shot animal (for comparison, see Elliger et al. 2001, 36 h per wild boar). Areas where only single hunt was conducted took 74.5% (66% fields, 8.5% forest) of the analysed areas. On 17% of the study area single hunt and battues were both conducted in forest, on 8.5% of area wild boar were hunted only at battues. Sixty percent of the animals were shot on single hunt from hides at baiting stations, 28% were shot at the edge of fields (hides, stalking) or during harvest (hunters surrounding harvested field), 7% were shot at battues, and in 5%, the hunting method was unknown to us.

Materials and methods

Radiotelemetry

The data presented in this paper were recorded from 18th Nov. 2002 to 25th Nov. 2006. We captured wild boar in big cage

traps of $5 \times 2 \times 2$ 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 maximum lifespan of 3 years (mean lifespan 363 days), reaching up to 3 km. From 152 captured wild boar 68 females of 29 different groups were fitted with ear tag radiotransmitters. Eleven of these groups appeared as yearling groups, 12 as family groups. Another six groups survived from the age of yearling up to family group and thus appear within the data as both. The mean weight of captured piglets during capturing period (September to February) was 32 kg alive ($N=143$, sex ratio 1:0.88), that of adult females (November to May) was 75 kg ($N=8$). The age structure of shot animals was 45% piglets (younger 12 months, $N=47$, sex ratio 1:0.91), 41% yearlings (13–24 months, $N=43$, sex ratio 1:0.65) and 14% adults (older 24 months, $N=14$, sex ratio 1:2.75). The group structure of the observed population is described in Table 1. The peak of parturition was in early April. All observed animals presented in this paper were of good health and body condition at capture, sightings and when shot.

We localised 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. To avoid disturbances, we performed the localisations with car-mounted four-element YAGI antennas (self-made) using TRX-1000S receivers (Wildlife Materials Inc., 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 less than 4 ha, were used to minimise the telemetry error (Zimmerman and Powell 1995), and the centre of the polygon was taken as positioning of a particular wild boar. We mapped all localisations and recorded additional information, e.g. activity, date and time as well as bonus notes, like sightings, group size and structure, disturbances, shooting of a marked group member and the presence of other groups nearby. The telemetry error was at median 60 m between assumed and real transmitter location (Keuling et al. 2008).

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 6 v1.2 (Kenward et al. 2003). Home ranges were calculated for every season (see Keuling et al. 2008) to test the impact of different hunting methods on seasonal home range sizes as kernel home ranges 95% core weighted default settings (KHR95), describing the home range (Burt 1943). We assumed an absolute minimum time interval of 2 h between localisations as sufficiently independent to calculate kernel home ranges (see de Solla et al. 1999;

Keuling et al. 2008). To investigate the direct impact of battues on periodical home ranges 2 weeks before and after battues, respectively, these were estimated as (a) kernel home ranges (KHR95) and as (b) minimum convex polygons (MCP), which describes the maximum used space (100% of localisations). We calculated the spatial shift of home ranges by the distance between centres of temporary kernel home ranges 2 weeks before and 2 weeks after the battues. Diurnal activity was defined as activity (alternating strength of signals) during daytime, i.e. between sunrise and sunset.

Statistics

As wild boar behaved similarly in space utilisation within groups and in different age classes (Keuling et al. 2008), we used the data of only one animal per group as representative for its group and pooled the data of different groups and age classes for the analyses.

We used a binary logistic regression to test the impact of six main categories of factors potentially influencing diurnal activity. For every factor every localisation has been assigned to an area of specified characteristics of each factor. These factors were: (1) month: 1–12 (Jan–Dec); (2) forest–open land; (3) habitat category: dense coniferous forest, open coniferous forest, dense deciduous forest, open deciduous forest, grassland, bearded cereals (barley, rye, triticale), beardless cereals (wheat, oat), reed, rapeseed, maize; (4) structure: open (mown grassland and fields), dense low (rapeseed, maize, reed), dense high (forest with dense understorey, thickets), open low (high grassland, cereals), open high (older forest without understorey); (5) human disturbance (distance to human structures: roads and settlement): (a) <50 m against >50 m, (b) <150 m against larger distances; (6) hunting method: (a) only one to two battues per year, (b) single hunt plus battues, (c) only single hunt all over the year in forest, (d) only single hunt in agricultural fields.

With Kruskal–Wallis H test, we tested the influence of different hunting methods (defined as under regressions,

Table 1 Observed group structure

Type	Percentage	N
Single sow	7.7	3
Yearling groups	30.8	12
One sow with piglets (some temporary with yearlings)	17.9	7
Two sows with piglets (some temporary with yearlings)	25.6	10
Three or more sows with piglets and yearlings	12.8	5
Piglets without sow	5.1	2

factor 6) on seasonal home range size, as post hoc test, we used Nemenyi test. The respective hunting method was assigned to every home range depending on the situation of the home range centre (KHR).

To detect the dimension of "flight distances" of family groups after disturbance (hunting/capture), the difference in distances between daytime resting on the day before and after hunting incident (distance of surviving group members when one marked member of the group was shot during the night by single hunt) and hunting site as well as captures were tested with the Wilcoxon rank-sum test. We compared these groups with the Mann–Whitney U test.

Differences in home range estimates 2 weeks before and after battues were compared with the Wilcoxon rank-sum test. For differences in home range measurements between hunted (battues) wild boar groups and unhunted control groups, we used the Mann–Whitney U test. We examined the differences in overlapping home ranges of neighbouring groups before and after battue (and control) with the Wilcoxon rank-sum test as well as the differences between hunted and control sample with the Mann–Whitney U test, and when not any, one or both groups, respectively, have been hunted with the Kruskal–Wallis H test.

We accomplished the Nemenyi test with Excel and further analyses in SPSS 12.0. Unless otherwise noted, all values are presented as mean±SE. All tests were two-tailed with level of significance of $p \leq 0.05$.

Results

Diurnal and nocturnal activity patterns

In winter, female wild boar (Fig. 1) showed relatively low nocturnal activity (70% of all nocturnal localisations). Corresponding to the short daytime, the resting period
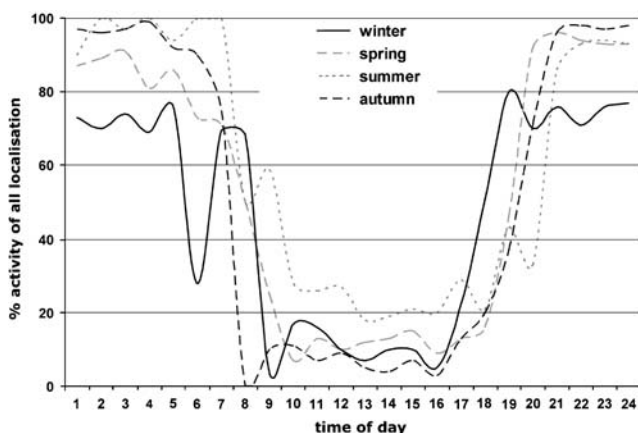

Fig. 2 Seasonal change of diurnal activity throughout the year based on radiotelemetry locations [bar shows percentage of locations with activity of all diurnal (sunrise to sunset) locations]

was also short with a low rate of diurnal activity (about 10% of all diurnal localisations). In spring, the nocturnal activity rose and the resting period increased in length as well depending on longer daytime periods, maintaining the same proportion of diurnal activity. In summer, the nighttime activity achieved nearly 100%, but during the long daytime, the activity was also relatively high (about 25%, Fig. 1). The activity pattern of autumn was similar to that of spring.

The regression analyses showed a seasonal impact on diurnal activity of wild boar groups (diurnal localisations $N=$ 5,138; Table 2, Fig. 2). In May and June, diurnal activity was significantly higher, in October lower than in the other months, with an annual mean diurnal activity of 12.1%. Habitat type also influenced diurnal activity: Higher activity during daytime was recorded in fields of unbearded cereals (wheat and oat) as well as in rapeseed compared to other agricultural habitats and forests (Table 2, Fig. 3). The structure of vegetation did not influence diurnal activity (Table 2), but the distance to human structures did (Table 2).

Fig. 1 Seasonal activity patterns of female wild boar expressed as percentage of telemetry locations (100%=all localisations during hourly time of day, total localisations $N=10,388$)
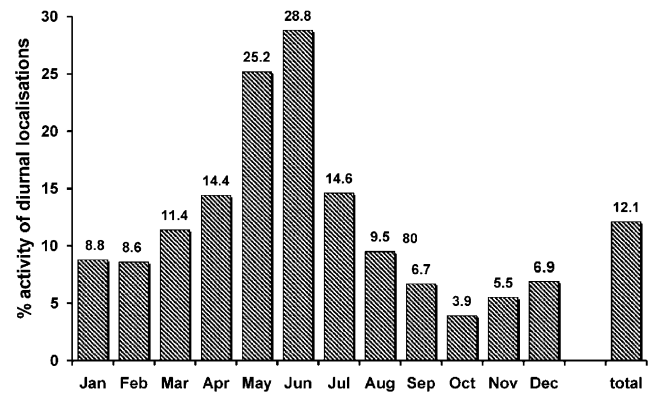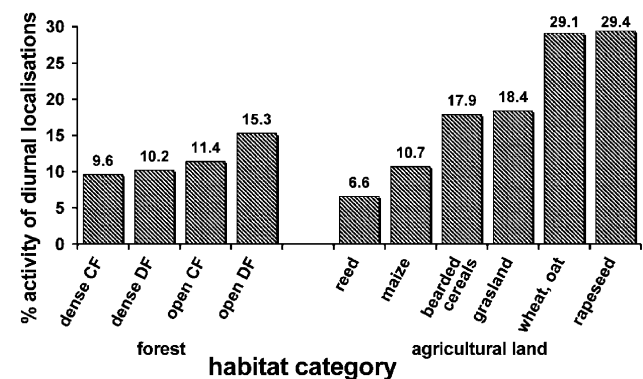

Fig. 3 Diurnal activity of wild boar in different habitat categories based on radiotelemetry locations [bar shows percentage of locations with activity of all diurnal (sunrise to sunset) locations]. *CF* coniferous forest, *DF* deciduous forest

Table 2 Binary logistic regression of seven factors potentially affecting diurnal activity of wild boar

Factor	r_B	±SE	Wald	df	p
Month			173.305	11	≤0.001
Hunting method			41.938	3	≤0.001
Distance, 150	0.302	0.096	9.858	1	0.002
Habitat category			47.100	9	≤0.001
Constant	−1.723	0.084	424.460	1	≤0.001
Distance, 50			2.168	1	0.141
Structure			1.851	4	0.763
Forest/open			0.002	1	0.964

For the model: $\chi^2 = 359.761$, df 16, $p \leq 0.001$, 2LL=3,447.954, Nagelkerkes $R^2 = 0.129$. For description of factors, see text.

Thus, wild boar showed higher diurnal activity at locations farther than 150 m from roads, tracks and buildings. The hunting method also seemed to affect diurnal activity (Table 2): In areas with only one to two battues per year, wild boar were active in 10.6% of all diurnal localizations. In areas with battues and single hunt, they were active in 8.0%. In forest areas with only single hunt, 18.1% of localisations showed activity, and within fields, where also only single hunt was undertaken, wild boar were active in 17.7% of the cases.

Impact of hunting methods on seasonal home ranges

The hunting method modified the size of seasonal home ranges of wild boar groups (KHR95) (Kruskal–Wallis H test: $\chi^2 = 11.654$, df=3, $N=63$, $p=0.009$; Fig. 4). On forested areas with only single hunt, mean home range size was significantly smaller than on fields with single hunt (Nemenyi test: $\chi^2 = 7.81$, df=3, $N=63$, $p \leq 0.05$; no significant difference between the other hunting methods).

Impact of single hunt and capture on location of daytime resting sites

The distance between daytime resting and hunting site (single hunt) of family groups was significantly larger after the hunting incident (1,317.6±178.3 m) than before (747.1±153.7 m; Wilcoxon: $Z=-2.807$, $N=17$, $p=0.005$), similar to distances between daytime resting and catching site before and after recapture (before recapture, 351.1± 61.7 m; after recapture, 800.0±124.2 m; Wilcoxon: $Z=-2.371$, $N=9$, $p=0.018$). For those wild boar which had been captured for the first time, the flight distances were slightly but not significantly larger (1,190.3±146.7 m, $N=31$; Mann–Whitney U test: $Z=-1.006$, $N=40$, $p=0.314$) than those of recaptured ones. Consequently, there was no significant difference in flight distances between hunted and captured wild boar (Mann–Whitney U test: $Z=-1.223$, $N=57$, $p=0.221$).

Impact of battues on wild boar spatial usage

We found no difference in home range size 2 weeks before and after battue in wild boar groups, which had been involved in battues (Fig. 5; Wilcoxon, $N=22$, MCP: $Z=-1.282$, $p=0.200$; KHR95: $Z=-1.640$, $p=0.101$) or in the unhunted control groups in the same time periods (Fig. 5;
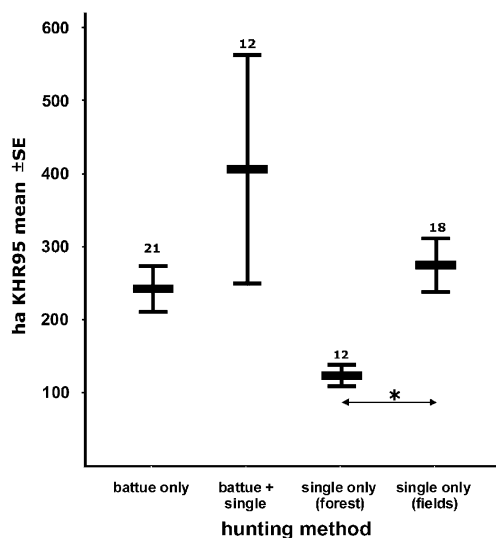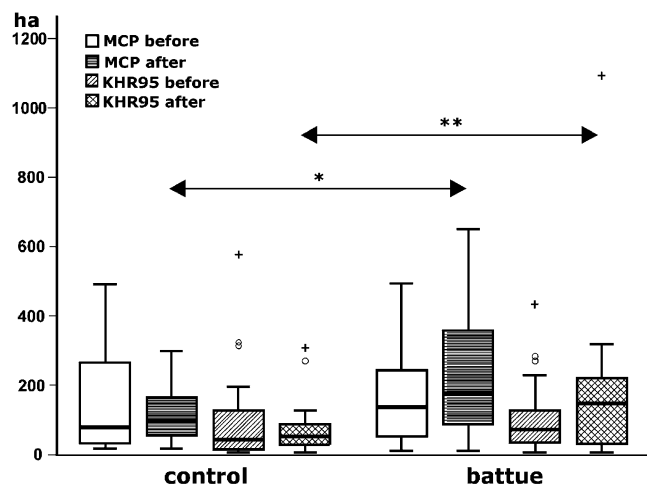

Fig. 4 Home range sizes (mean ha±SE) of wild boar groups located (kernel home range center) on areas managed with different hunting methods; N shown above error bars, *asterisk*: Nemenyi: $p \leq 0.05$

Fig. 5 Home range sizes (MCP and KHR95) of wild boar groups involved in battues ($N=22$) 2 weeks before and after the battue as well as unhunted control groups ($N=20$) during the same time periods. *Box and whisker plots* show median (*horizontal line within box*), 25% and 75% percentiles (*box*) and range (*whiskers*); *circles* indicate statistical outliers (observations between 1.5 and 3 interquartile ranges); *plus sign* indicates extreme values. U test: *$p=0.044$, **$p=0.047$
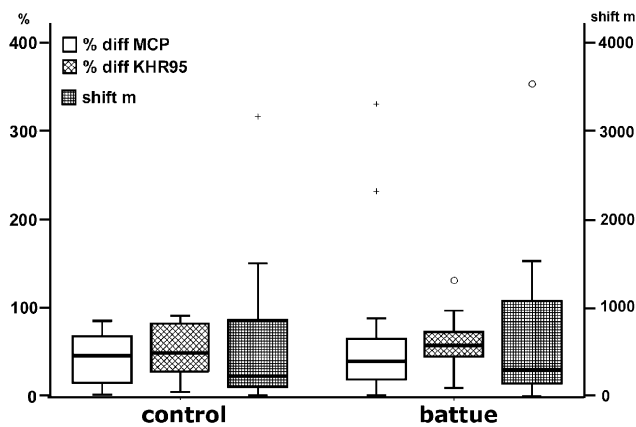
Fig. 6 Changes of home range sizes and locations of wild boar groups located 2 weeks before and after battues ($N=22$) as well as unhunted control groups ($N=20$) during the same time periods. *Box and whisker plots* show median (*horizontal line within box*), 25% and 75% percentiles (*box*) and range (*whiskers*); circles indicate statistical outliers (observations between 1.5 and 3 interquartile ranges); *plus sign* indicate extreme values. *% diff MCP*: percentage of mcp home range changes, *% diff KHR95*: percentage of kernel home range (95%) changes, *shift m*: shifting of khr centres

Wilcoxon, $N=20$, MCP: $Z=-0.149$, $p=0.881$; KHR95: $Z=-0.485$, $p=0.627$). Before battues, home ranges of hunted and unhunted groups were similar in size (Fig. 5; Mann Whitney U test, $N=42$, MCP: $Z=-1.259$, $p=0.208$, KHR95: $Z=-0.579$, $p=0.562$). After hunts, the MCP and KHR95 were different between hunted and unhunted groups (Fig. 5; Mann–Whitney U test, $N=42$, MCP: $Z=-2.015$, $p=0.044$, KHR95: $Z=-1.990$, $p=0.047$). However, the relative changes of MCP and KHR95 home ranges (percental difference in home range sizes before and after battues) and the shift of home range centres did not differ between wild boar involved in battues and the unhunted control group (Fig. 6; Mann–Whitney U test, $N=42$, MCP-diff: $Z=-0.101$, $p=0.920$, KHR95-diff: $Z=-0.730$, $p=0.465$, shift: $Z=-1.007$, $p=0.314$). All these measures did not differ between yearling and family groups (Mann–Whitney U test, $N=42$, MCP difference: $Z=-0.267$, $p=0.790$, KHR difference: $Z=-0.160$, $p=0.873$, shift: $Z=-1.574$, $p=0.115$). Only in three cases (13.6%) did slight escape movements (max. 2.1 km beyond annual home range) for less than 7 days follow a battue. In one of these cases, the group has been observed in the same area in September of the following year without any previous disturbance.

The overlap of kernel home ranges of neighbouring wild boar groups did not change after battues in which at least one of both groups had been involved (Wilcoxon: $Z=-0.604$, $N=21$, $p=0.546$). The same applied to the control groups (not involved in battue) in the corresponding periods of time (Wilcoxon: $Z=-0.357$, $N=10$, $p=0.721$). Thus, the overlap of KHR95 did not differ between control and hunted pairs (Mann–Whitney U test, $N=31$: before: $Z=-0.170$, $p=0.865$;

after: $Z=-0.642$, $p=0.521$). There were also no differences between pairs of wild boar groups (a) that had not been hunted, (b) when one or (c) when both groups had been involved in a battue (overlap before, $11.37\pm3.04\%$; after, $7.01\pm1.58\%$; Kruskal–Wallis H test: $N=31$, $df=2$; before: $\chi^2=3.254$, $p=0.196$; after: $\chi^2=0.550$, $p=0.760$).

Discussion

The various hunting methods seem to influence wild boar behaviour in similar and only moderate intensities. This is particularly true for activity and movement patterns. However, we found some significant effects to be discussed in the following.

Activity

The activity patterns reflected seasonal daytime length and weather conditions as well as energetic requirements of female wild boar. During winter, wild boar do not need to be active persistently in long nights. Especially when frozen soil prevents rooting, it is more efficient to stay at the resting site and use fat deposits than wander around. Reduced activity during cold winter months, also described by Briedermann (1971), saves energy (Gundlach 1968; Massei et al. 1997). Nights are long enough without the need for diurnal activity in winter, spring and autumn. During summer, when piglets are still small, adult females have enhanced energy requirements due to nursing. Thus, they have to forage during the entire short summer nights and also show a higher proportion of diurnal activity. In Italy, females showed polyphasic instead of biphasic activity pattern during farrowing season, with a tendency to increasing diurnal activity in June and July (Russo et al. 1997). Thus, wild boar seem to be most active during periods of short nighttimes (see also Briedermann 1971) with a relatively high proportion of diurnal activity. The large rapeseed and wheat fields, which many wild boar used during summer (Keuling et al. 2008), offered the possibility for undisturbed diurnal activity providing shelter and food (see also Meriggi and Sacchi 1992a, b). Juveniles from 3 to 8 months were mainly diurnal, while adults were nocturnal (Cousse et al. 1995). This might be another reason for higher diurnal activity of female wild boar with piglets during summer. Thus, the results reflect an interaction between habitat types and season, as availability of food, shelter and other resources change seasonally within different habitats.

The higher diurnal activity in fields and forest with only single hunt may be either a reaction on the hunting method or on seasonal influences, which must not be mutually exclusive. Although a tendency towards higher daytime

activity might be caused by nocturnal hunting, we assume other effects like seasonal influences to be more likely. The influence of the hunting method on activity pattern is hardly to assess compared to all other impacts and influencing biases. However, a perturbation by man does exist, as wild boar are more active when farther from human structures and as they prefer cereal fields far from human structures (Meriggi and Sacchi 1992b). This conclusion does not allow any reverse, less permanent hunting pressure which does not cause inevitably higher proportions of diurnal activity, and hence, other factors may be mainly decisive.

Meynhardt (1989) observed a certain diurnal activity in undisturbed areas. In our study area, some diurnal activity was always obvious, although to a lower degree than in other studies (see McIlroy 1989; Boitani et al. 1992, 1994). Other authors observed mainly nocturnal activity and less diurnal activity in areas with low or without hunting pressure (Caley 1997; Russo et al. 1997). Activity cycles seem to depend mainly on age and sex (McIlroy 1989; Cuartas and Braza 1990; Cousse et al. 1994, 1995; Janeau et al. 1995), weather conditions (Caley 1997; Lemel et al. 2003) or food and water resources (Caley 1997; Massei et al. 1997). Cousse et al. (1994) described slightly different spatial patterns of post-weaning piglets and their mothers. Piglets are closely associated with their mother and siblings, their initial movements being very small scaled and bound to the site of birth. The increasing degree of independence of post-weaning piglets leads to temporary separation from their mother while exploring the expanded home range (Cousse et al. 1994; Janeau et al. 1995). Those solo attempts occur mainly during diurnal resting phases, as we could record by video observation (Saebel et al., unpublished data). In the study of McIlroy (1989) in New Zealand, immature feral pigs were more active than adults, and males were more active than females. Feral pigs showed more nocturnal (49%) than diurnal (33%) activity (McIlroy 1989). In addition, Boitani et al. (1992) observed in captivity reared wild boar a significantly higher nocturnal (70%) than diurnal (40%) activity. These proportions of daily activity did not change within 8 weeks after release and were similar to those of free ranging wild boar (Boitani et al. 1994). Briedermann (1971) described diurnal activity for wild boar in captivity and assumed hunting pressure to increase nocturnal activity in free ranging wild boar.

Impact of hunting and other disturbances on wild boar movements

Hunting is often proposed as a main cause for size changes and shifting of home ranges in winter, e.g. the hunting season (Boitani et al. 1994; Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002; Sodeikat and

Pohlmeyer 2002, 2007), although size of core areas remained stable. Maillard and Fournier (1995) estimated seasonal home ranges varying stronger under hunting pressure, but their sample size was small. However, all these authors do not presume any impact of hunting pressure on dispersion of wild boar. Wild boar enlarging their home range during hunting season are more likely to get shot (Baubet et al. 1998). Although hunting seems to have an influence on home range size, there might be other internal and extrinsic factors triggering the seasonality of spatial utilisation patterns such as weather, availability of food and water resources, vegetation cover, sibling of piglets, population density (Boitani et al. 1994; Massei et al. 1997) and intraspecific variability (Lott 1989). Especially when resources are sparse, activity is higher and home ranges are larger (Massei et al. 1997). Therefore, it would be very difficult to prove hunting as the only factor of changing seasonal home range sizes.

In areas with combined hunting methods, home ranges tended to be slightly larger and showed more variation than in other areas, whereas in forested areas with only single hunt, home ranges were significantly smaller. As home range size did not differ significantly between seasons in our study area (Keuling et al. 2008), varying home range sizes may be influenced by different hunting methods (besides many other factors) as assumed in other studies (Boitani et al. 1994; Maillard and Fournier 1995; Dexter 1996; Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeyer 2002). Some authors assumed hunting as the main factor for larger home ranges in winter/hunting season, with animals trying to avoid hunters and searching for secure areas (Maillard and Fournier 1995; Baubet et al. 1998; Calenge et al. 2002), despite observing many animals not changing their home ranges or including dispersing subadults to analyses (e.g. Calenge et al. 2002). To the contrary, in some cases, wild boar reacted on hunting with smaller (sometimes shifted) home ranges in secure places (Baubet et al. 1998; Calenge et al. 2002; Sodeikat and Pohlmeyer 2002). There seem to be two main anti-predator strategies: (a) mainly staying in well-known home range, perhaps reducing space into more secure places and (b) enlarging or shifting home range to avoid predators or hunters respectively (see also Baubet et al. 1998; Sodeikat and Pohlmeyer 2007). We assume other influences like seasonal resources, habitat availability within individual home ranges and intraspecific variability as more important than the hunting method.

Although distances increased after disturbance (single hunt, capture) between disturbed and resting site, all movements remained within the seasonal home range measurements (Keuling et al. 2008). Singer et al. (1981) observed even smaller daily movements after human disturbance. Thus, single hunt and capture for scientific

purposes (see also Sodeikat and Pohlmeyer 2004) apparently do not increase wild boar movements.

According to literature data, battues with high beating pressure and many dogs partly caused temporary shift or increase of home ranges (Maillard and Fournier 1995; Sodeikat and Pohlmeyer 2002, 2003, 2007). However, in France, home range shifts occurred only after repeated disturbances (Maillard and Fournier 1995). In Germany, wild boar returned after 4 to 6 weeks to their previous area; in some cases, home range size even decreased (Sodeikat and Pohlmeyer 2002). Shooting feral pigs from helicopters in Australia as a pest control induced non-significant smaller home ranges after hunting (Dexter 1996). Dexter (1996) assumed that direct contact to humans and dogs by ground battues may displace wild boar, but not shooting from helicopters.

In our study, we could not document a significant impact of hunting on wild boar home range size or location. Being well adapted to human disturbances and hunting (see also Meynhardt 1990), only minor reactions to single hunt and battues could be observed under good nutritional conditions. Most variation in activity or spatial usage patterns seemed to be rather induced by seasonal changes (Boitani et al. 1994; Maillard and Fournier 1995; Massei et al. 1997; Keuling et al. 2008). Therefore, we assume the influence of hunting on increasing animal movements as negligible if hunting pressure is moderate (e.g. only few effective battues per year instead of repeated "monterias"). Hence, hunting may be conducted as management tool for regulating or even reducing population densities and thus may reduce the risk of spreading epidemics.

References

Baubet E, Brandt S, Touzeau C (1998) Effet de la chasse sur les stratégies d'occupation de l'espace des sangliers (*Sus scrofa*). Analyses préliminaires. Gibier Faune Sauvage 15:655–658

Beuerle W (1975) Freilanduntersuchungen zum Kampf- und Sexualverhalten des Europäischen Wildschweines (*Sus scrofa* L.). Z Tierpsychol 39:211–258

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J Appl Ecol 42:1203–1213 doi:10.1111/j.1365-2664.2005.01094.x

Boitani L, Mattei L, Morini P, Zagarese B (1992) Experimental release of captivity reared wild boar (*Sus scrofa*). in: "Ongulés/Ungulates 91". Proceedings of the International Symposium, Toulouse, pp 413–417

Boitani L, Mattei L, Nonis D, Corsi F (1994) Spatial and activity patterns of wild boar in Tuscany, Italy. J Mammal 75:600–612 doi:10.2307/1382507

Bratton SP (1975) The effect of the European wild boar (*Sus scrofa*) on Gray Beech Forest in the Great Smokey Mountains. Ecology 56:1356–1366 doi:10.2307/1934702

Briedermann L (1971) Ermittlungen zur Aktivitätsperiodik des Mitteleuropäischen Wildschweines (*Sus scrofa* L.). Zool Gart 40:302–327

Briedermann L (1990) Schwarzwild. 2nd edn. Neumann-Neudamm, Melsungen

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24:346–352 doi:10.2307/1374834

Cahill S, Llimona F, Gràcia J (2003) Spacing and nocturnal activity of wild boar *Sus scrofa* in a Mediterranean metropolitan park. Wildl Biol 9(Suppl):3–13

Calenge C, Maillard D, Vassant J, Brandt S (2002) Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game Wildl Sci 19:281–301

Caley P (1997) Movement, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. Wildl Res 24:77–87 doi:10.1071/WR94075

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can J Zool 72:1691–1694

Cousse S, Janeau G, Spitz F, Cargnelutti B (1995) Temporal ontogeny in the wild boar (*Sus scrofa* L.): a systemic point of view. IBEX J Mt Ecol 3:122–125

Cuartas P, Braza F (1990) Reparto temporal de actividades del jabalí (*Sus scrofa*) en Doñana (SO Spain). Acta Vert 17:91–102

de Solla SR, Bonduriansky R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. J Anim Ecol 68:221–234 doi:10.1046/j.1365-2656.1999.00279.x

Dexter N (1996) The effects of an intensive shooting exercise from a helicopter on the behaviour of surviving feral pigs. Wildl Res 23:435–441 doi:10.1071/WR9960435

Eisenbarth E, Ophoven E (2002) Bewegungsjagd auf Schalenwild. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Elliger A, Linderoth P, Pegel M, Seitler S (2001) Ergebnisse einer landesweiten Befragung zur Schwarzwildbewirtschaftung. WFS-Mitteilungen, pp 5–7

Garrott RA, White GC, Bartmann RM, Weybright DL (1986) Reflected signal bias in biotelemetry triangulation systems. J Wildl Manage 50:747–752 doi:10.2307/3800995

Gerard JF, Campan R (1988) Variabilité éco-ethologique chez le sanglier europeén: comparision des travaux francaise. Cah Ethologie Appliquee 8:63–130

Gortázar C, Ferroglio E, Höfle U, Frölich K, Vicente J (2007) Diseases shared between wildlife and livestock: a European perspective. Eur J Wildl Res 53:241–256 doi:10.1007/s10344-007-0098-y

Groot Bruinderink GWTA, Hazebroek E (1996) Wild boar (*Sus scrofa scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. For Ecol Manage 88:71–80

Gundlach H (1968) Brutfürsorge, Brutpflege, Verhaltensontogenese und Tagesperiodik beim Europäischen Wildschwein (*Sus scrofa* L.). Z Tierpsychol 25:955–995

Happ N (2002) Hege und Bejagung des Schwarzwildes. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Hennig R (1998) Schwarzwild. 5. Aufl. ed. BLV Verlagsgesellschaft mbH, München

Hooge PN, Eichenlaub B (2001) Movement 2.0. Alaska Biological Science Center, US Geological Survey, Ancorage, AK, USA

Janeau G, Cargnelutti B, Cousse S, Hewison M, Spitz F (1995) Daily movement pattern variations in wild boar (Sus scrofa L.). IBEX J Mt Ecol 3:98–101

Kenward RE, South AB, Walls SS (2003) Ranges 6 v1.2: For the analysis of tracking and location data. Anatrack Ltd., Wareham, UK

Keuling O, Stier N, Roth M (2008) Annual and seasonal space use of different age classes of female wild boar Sus scrofa L. Eur J Wildl Res (in press) doi:10.1007/s10344-007-0157-4

Killian G, Miller L, Rhyan J, Doten H (2006) Immunocontraception of Florida feral swine with a single-dose GnRH vaccine. Am J Reprod Immunol 55:378–384 doi:10.1111/j.1600-0897.2006.00379.x

Labudzki L, Wlazelko M (1991) Saisonale Dynamik der vom Schwarzwild im Feldanbau verursachten Schäden im Forschungsgebiet Zielonka. Z Jagdwiss 37:250–257 doi:10.1007/BF02239730

Lemel J, Truvé J, Söderberg B (2003) Variation in ranging and activity behaviour of European wild boar Sus scrofa in Sweden. Wildl Biol 9(Suppl):29–36

Liebl T, Elliger A, Linderoth P (2005) Aufwand und Erfolg der Schwarzwildjagd in einem stadtnahen Gebiet. WFS-Mitteilungen, pp 1–5

Lott DF (1989) Intraspecific variation in the social system of wild vertebrates. Behaviour 88:266–325 doi:10.1163/156853984X00353

Maillard D, Fournier P (1995) Effect of shooting with hounds on home range size of wild boar (Sus scrofa L.) groups in Mediterranean habitat. IBEX J Mt Ecol 3:102–107

Massei G, Genov PV, Staines B, Gorman ML (1997) Factors influencing home range and activity of wild boar (Sus scrofa) in a Mediterranean costal area. J Zool (Lond) 242:411–423

McIlroy JC (1989) Aspects of the ecology of feral pigs (Sus scrofa) in the Murchison area, New Zealand. N Z J Ecol 12:11–22

Meriggi A, Sacchi O (1992a) Habitat selection by wild boars in Northern Appenines (N-Italy). "Ongulés/Ungulates 91". Proceedings of the International Symposium, Toulouse, pp 435–438

Meriggi A, Sacchi O (1992b) Factors affecting damage by wild boars to cereal fields in Northern Italy. "Ongulés/Ungulates 91". Proceedings of the International Symposium, Toulouse, pp 439–441

Meynhardt H (1989) Schwarzwild-Bibliothek 2: Das Revier. Neumann-Neudamm, Melsungen

Meynhardt H (1990) Schwarzwild-Report. 8th ed. Neumann, Leipzig, Radebeul

Russo L, Massei G, Genov PV (1997) Daily home range and activity of wild boar in a Mediterranean area free from hunting. Ethol Ecol Evol 9:287–294

Singer FJ, Otto DK, Tipton AR, Hable CP (1981) Home ranges, movements and habitat use of European wild boar in Tennessee. J Wildl Manage 45:343–353 doi:10.2307/3807917

Singer FJ, Swank WT, Clebsh EEC (1984) The effects of wild pig rooting in a deciduous forest. J Wildl Manage 48:464–473 doi:10.2307/3801179

Sodeikat G, Pohlmeyer K (2002) Temporary home range modifications of wild boar family groups (Sus scrofa L.) caused by drive hunts in Lower Saxony (Germany). Z Jagdwiss 48(Suppl):161–166 doi:10.1007/BF02192404

Sodeikat G, Pohlmeyer K (2003) Escape movements of family groups of wild boar Sus scrofa influenced by drive hunts in Lower Saxony, Germany. Wildl Biol 9(Suppl):43–49

Sodeikat G, Pohlmeyer K (2004) Escape movements of wild boar piglets (Sus scrofa, L.) after trapping, marking and releasing. Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue, pp 185–193

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar family groups (Sus scrofa L.). Wildl Biol Pract 3:28–38 doi:10.2461/wbp.2007.3.4

Wölfel H (ed) (2003) Bewegungsjagden. Leopold Stocker, Graz-Stuttgart

Zimmerman JW, Powell RA (1995) Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Can J Zool 73:1123–1133

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Keuling O, Lauterbach K, Stier N, Roth M (2009)

Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany

ORIGINAL PAPER

Hunter feedback of individually marked wild boar *Sus scrofa* L.: dispersal and efficiency of hunting in northeastern Germany

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Abstract Increasing wild boar (*Sus scrofa* L.) population densities all over Europe cause severe economic problems. For understanding mechanisms of epidemics, the knowledge of dispersal is required. Thus, we investigated dispersal rates and distances with regard to sex and age of wild boar in southwestern Mecklenburg-Western Pomerania. From 152 marked wild boar, 105 have been registered as dead, of which, 51% were males and 49% females. Forty-five percent were shot as piglets, 41% as yearlings, and 14% as adults. The distance between capture site and site of death ranged between 184 m and 41.5 km. Piglets were shot closer to their capture site (mean distance 1 km) than older animals (mean 4 km), although this difference was only significant for males. In general, males tended to disperse further before being shot (3.8 km) than females (1.6 km). Only 3.8% of all animals were shot at distances larger than 10 km. As most animals (84.6%) were shot inside their natal home range, only a small proportion (15.4%) did actually disperse (shot outside mothers home range), which is 32% of all animals surviving to the age of yearlings. Of those dispersed animals, 25% were females. The low dispersal rate is biased by female philopatry and allows actual dispersal only at very high population densities or in sparsely populated regions. In consideration for the low natural mortality proved by radio-tagged animals, the harvest rate is lower than the net reproduction. We did not detect any sex-biased hunting. The dominating hunting method was single hunt at bait, although drive hunts are highly effective. However, hunting rates on piglets and females were too low for regulating the population.

Keywords *Sus scrofa* · Dispersal · Hunting efficiency · Sex ratio · Philopatry

Introduction

In many parts of Europe, wild boar *Sus scrofa* L. population increase, and dispersal into new areas is accompanied by economic problems (e.g., Labudzki and Wlazelko 1991; Groot Bruinderink and Hazebroek 1996; Gortázar et al. 2007). Consequently, farmers and animal health authorities call for a stringent reduction of wild boar populations (Kaden 1999; Bieber and Ruf 2005; Killian et al. 2006). For understanding mechanisms of epidemics and damages, it is essential to gain knowledge about space use and dispersal functions.

The wild boar is a social species with a strong post-weaning association between mothers and daughters that usually lasts several years, although some fluctuations occur throughout the year, mainly depending on reproduction (Dardaillon 1988; Kaminski et al. 2005). Dispersal in wild boar is male-biased, and social groups are usually formed by closely related philopatric females (Stubbe et al. 1989; Briedermann 1990; Truvé and Lemel 2003; Kaminski et al. 2005) comparable with most polygynous ungulates

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(Greenwood 1980). Piglets stay with their mother within the family groups for about 1 year (Briedermann 1990; Nakatani and Ono 1995). With increasing age, mother-piglet pair bonds loosen (Dardaillon 1988; Cousse et al. 1994; Kaminski et al. 2005; Keuling et al. in preparation), and piglets become more and more independent. Most females stay inside their natal home range and often with their mother (Stubbe et al. 1989; Briedermann 1990; Nakatani and Ono 1995; Truvé 2004; Kaminski et al. 2005); whereas, male yearlings are excluded from their family groups at the age of sexual maturity, which is at 9 to 14 months (Andrzejewski and Jezierski 1978; Meynhardt 1990; Happ 2002; Truvé 2004).

Only few data are available about dispersal in wild boar (Andrzejewski and Jezierski 1978; Stubbe et al. 1989; Markov et al. 2004; Truvé 2004; Jerina et al. 2005). Data indicate low dispersal rates (Stubbe et al. 1989; Briedermann 1990; Truvé 2004), although high dispersal distances can be seen in male wild boar (Andrzejewski and Jezierski 1978; Stubbe et al. 1989). The direction and intensity of dispersal is influenced by several factors, such as population density, landscape structure and habitat quality, and climate (Dardaillon and Beugnon 1987; Spitz 1989; Cargnelutti et al. 1992; Gerard et al. 1992; Gabor et al. 1999).

Besides data on dispersal, feedback from hunters concerning marked shot animals also allows conclusions to be drawn on hunting efficiency. For regulating a population, combined and effective hunting methods have to be conducted to harvest at least the net reproduction (Briedermann 1990; Happ 2002; Keuling et al. 2008b). Some authors describe different models to accomplish regulation of wild boar populations by hunting different proportions of age classes (Bieber and Ruf 2005; Servanty et al. 2005; Sodeikat et al. 2005; Servanty 2008). In common opinion, biased sex and age ratios cause higher reproduction, although food conditions have also been demonstrated as a main cause for higher reproduction (Gethöffer et al. 2007; Cellina 2008).

In this study, we investigate dispersal rates of individually marked female and male wild boar by measuring the distance between capture site and subsequent death site. Furthermore, we use this data to estimate hunting efficiency.

Study area

The centre of the study area (capture area) was located 60 km east of Hamburg in the federal state of Mecklenburg-Western Pomerania (northeastern Germany, 53.28°N, 10.55°E; Fig. 1). The landscape was formed by the Vistula glaciation and rises from 20 up to 100 m above
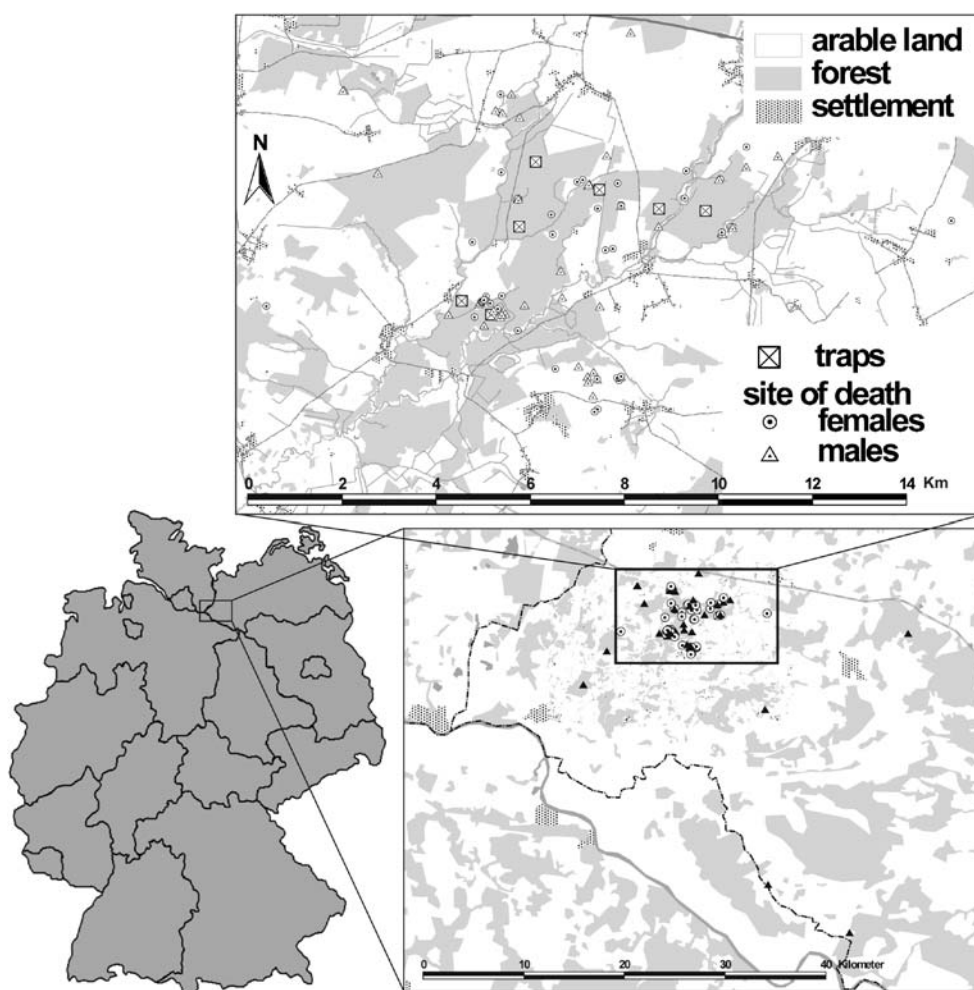
sea level. Agriculture and forestry combined with low human settlement (20 inhabitants/km^2) were the main features of the area: the study area consisted of 40% agricultural land, 34% forest stand, 23% meadows and pastures, with 3% housing estates. The agricultural land was characterised by large fields of a mean size of 20 ha. The forest consisted of 57% pine (*Pinus sylvestris* and *Pinus strobus*), 14% other coniferous tree species, 12% oak *Quercus* sp. and beech *Fagus sylvatica*, as well as 17% other deciduous tree species. During the observation period, there was abundant mast of acorns (2002, 2003, and 2005) and beechnuts (2004). Approximately 1,000 kg supplemental food per 100 ha was offered every year (Keuling et al. 2008a). 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 hunting bag of wild boar in the study area increased continuously from 2.83 individuals per 100 ha in 1999/ 2000 to 5.13 individuals/100 ha in 2005/2006. These hunting bags were comparatively high, as the mean annual hunting bags in Germany amounted to less than two individuals per 100 ha. Additionally, the hunting bags stagnated during the observation period.

Methods

The data presented in this paper were recorded from 18th November 2002 to 15th July 2007. We captured 152 wild boar in big cage traps of 5×2×2 m and fitted them with ear-tags printed with the address and phone number of our institute. Separately, 68 females and 11 males of 30 different groups, i.e., family groups with at least one adult female and with piglets and yearling groups (Keuling et al. 2008a, b), were fitted with ear tag radiotransmitters (Andreas Wagener Telemetrieanlagen, Cologne, Germany).

We localised the radio-tagged wild boar groups once at daytime about four times a week and one to five times at night at least twice a week (Keuling et al. 2008a). We mapped all localisations and transcribed the positionings with a Calcomp® SummaSketchIII digitising tableau to Esri® ArcView 3.2. We calculated home ranges as minimum convex polygons (MCP) with Animal Movement 2.0 extension (Hooge and Eichenlaub 2001) for ArcView. A wild boar was defined as dispersed, when it was shot more than 200 m (due to telemetry error and an additional plus, Keuling et al. 2008a) outside its mothers MCP-home range (mothers home range: home range of animals captured simultaneously or home range of piglets staying with mother until the age of about 12 months, see Briedermann 1990; Nakatani and Ono 1995). We collected date, time, and location of capture and shooting/death of

Fig. 1 Location of study area inside Germany, distribution of traps and sites of death of marked wild boar of different sexes

every marked individual to measure the distance between capture and death site.

We calculated the proportions of sex and age classes (piglets: younger than 12 months, yearlings: 12–23 months, and adults: 24 months or older; age determination by dentition) of shot marked individuals to estimate hunting efficiency, natural mortality, and sex bias of marked and shot wild boar. We observed 54 radio-tagged wild boar until their death. The proportions of mortality causes (shot and reported, shot and not reported, natural death, and traffic) of radio-tagged wild boar were calculated and extrapolated on simply marked animals to calculate potential survival and mortality and, thus, hunting efficiency.

To assess differences in dispersal distances between age classes, we used the Kruskal–Wallis H test with the Nemenyi test and between sexes, the Mann–Whitney U test. We accomplished the Nemenyi test with Excel and further analyses in Statistical Package for the Social Sciences SPSS 15.0. Unless otherwise noted, all values are presented as mean±SE. All tests were two-tailed with level of significance of $p \leq 0.05$.

Results

Dispersal

From 152 (143 piglets) captured and marked wild boar, 105 have been confirmed as dead, with information about date and location of death for most of them (N=104). The distance between capture site and site of death ranged between 0.18 and 41.53 km (Fig. 1), whereby most individuals were shot within 4 km distance to their capture site (87.5%). Between 4 and 10 km distance, 8.7% were shot, and 3.8% were shot at distances larger than 10 km (Fig. 2). However, only 15.4% of the replied animals (11 yearlings and five adults) were shot outside their mother's home range and thus classified as dispersed.

The mean distance between capture site and site of death was lowest within the age class of piglets (1.12±0.18 km). The yearlings were shot at a distance of 3.91±1.11 km, the adults at a distance of 4.35±1.77 km (Fig. 3). There was no difference between these age classes in females (H test: chi^2=4.031, df=2, N=50, p=0.133), but in males, piglets dispersed significantly further than yearlings and adults,
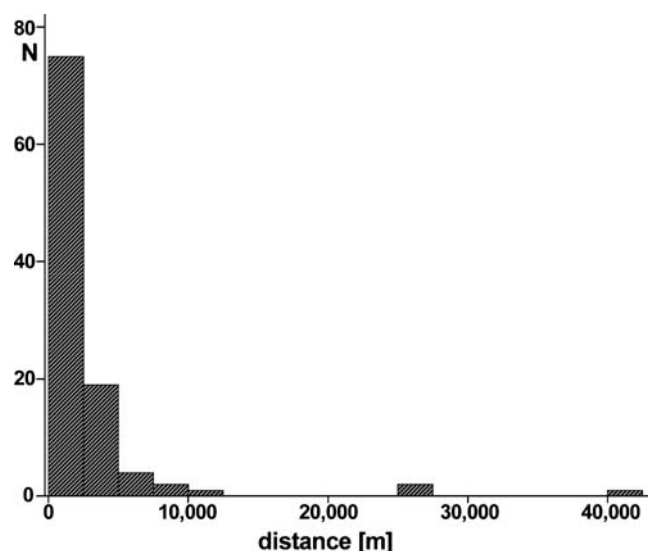
Fig. 2 Number of marked animals within distance-categories (metres) between capture site and site of death (*N*=104)

while there was no difference between the latter (H test: chi^2=14.364, *df*=2, *N*=54, *p*=0.001; Nemenyi test: chi^2=5.99, *df*=3, *N*=63, *p*≤0.05).

Males were shot at a mean distance of 3.80±1.00 km from their capture site and females at 1.59±0.24 km;
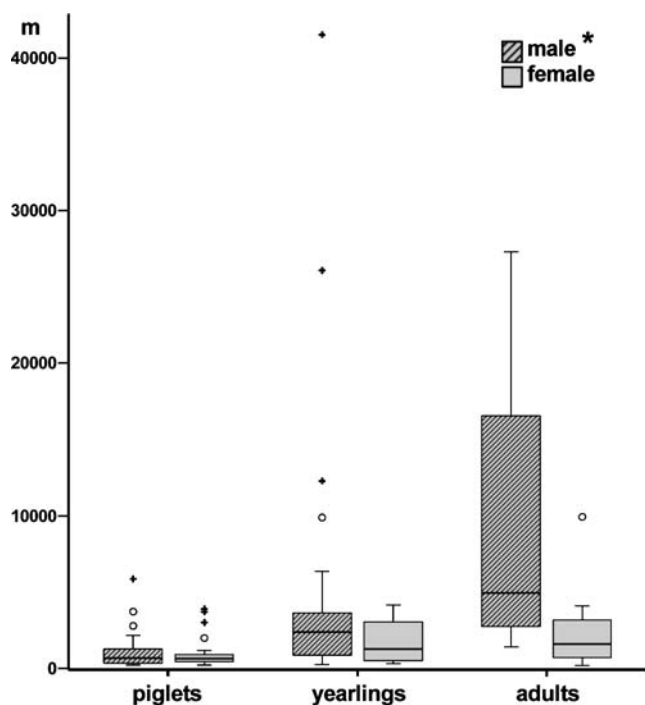

Fig. 3 Distances (metres) between capture site and site of death of marked wild boar of different sex and age class, piglets: male *N*=24, female *N*=22; yearlings: male *N*=26, female *N*=17; adult: male *N*=4, female *N*=11. Box and Whisker plots show median (*horizontal line within box*), 25% and 75% percentiles (box) and range (whiskers), *circles* indicate statistical outliers (observations between 1.5 and 3 interquartile ranges), plus indicate extreme values. *H test *p*=0.001 m

however, this divergence was not significant (Mann–Whitney *U* test: *Z*=−1.379, *N*=104, *p*=0.168). Even within the different age classes, only slight tendencies for bigger dispersal of males occurred at higher ages (Fig. 3; piglets *U* test male–female: *N*=46, *Z*=−0.066, *p*=0.947; yearlings *U* test male–female: *N*=43, *Z*=−1.565, *p*=0.118; adults *U* test male–female: *N*=15, *Z*=−1.697, *p*=0.090). Only when all animals older than 11 months were compared males showed a higher distance (*U* test: *N*=59, *Z*=−2.199, *p*=0.028).

Animals shot inside their natal home range (*N*=88; 84.6%) had a mean distance of 1.35±0.18 km, similar to that of piglets. Only two animals (2.3%) were shot at distances above 4 km inside their natal home range. All animals shot outside their natal home range (*N*=16) were at an age of at least 17 months and moved on average 10.38±2.84 km before being shot. However, 31.3% of them were shot within 4 km.

Only 15.4% of all shot animals actually dispersed (Table 1). However, the proportional dispersal rate increased with the age of the surviving (Table 1). Twenty-five percent of the dispersed animals were females.

Efficiency of hunting

As previously stated, 105 wild boar (54 radio-tagged until their dead and 51 simply ear-tagged or failed/lost radio-transmitter) were reported as dead.

Within all individuals observed by radiotelemetry until their death (*N*=54), four were shot but not announced (7.4%), and five were found dead with help of the transmitters (9.3%, three died of disease, two were shot but unsuccessfully trailed). The natural mortality was very low with 5.6%. Allowing for 16.7% natural, undetected, and not reported mortality, we assume about another undetected 16 dead animals out of 98 simply ear-tagged animals (without or lost/failed transmitter, respectively). Out of these simply marked animals, three were accidentally found until now: one was replied as traffic casualty,

Table 1 Numbers of shot and dispersed animals at different sex and age, all dispersed animals were older than 16 months

	N dispersed		N shot		
	Total	Total	≥11months	≥17months
Male	12	54 (22.2)	36 (33.3)	24 (50.0)
Female	4	50 (8.0)	32 (12.5)	19 (21.1)
Σ	16	104 (15.4)	68 (23.5)	43 (37.2)

Numbers in parenthesis give percentage of dispersed animals in the age class of that column and the sex of that row

one died after unsuccessful trail, and one of unknown reason. This means there are 31 surviving animals (98 marked minus 51 reported minus 16 natural and not reported).

The sex ratio (SR) was 1.13:1 within captured piglets (*N*=143). Within the shot individuals, the SR was nearly the same for piglets, 1.14:1 (*N*=47), but male-biased in yearlings (SR=1.53:1, *N*=43) and female-biased in adults (SR=0.57:1, *N*=11). For all shot animals captured and marked as piglet, the SR was 1.20:1 (*N*=101). Hence, the SR of not reported animals was 0.88:1.

The dominating hunting method was single hunt at bait with 58.5% of all shot animals. Another 23.5% were shot within fields or at harvest, 4.3% on collective hides or at stalking, 7.4% on drive hunts, and in 5.3%, the hunting method was not replied.

Discussion

Dispersal

As piglets stay with their mother within their natal home range for approximately 1 year (Briedermann 1990; Nakatani and Ono 1995), most of the marked piglets, and thus of all studied individuals, were, not unexpectedly, shot within a radius of only few kilometres from their capture site. Piglets showed short distances between capture site and site of death, like also Stubbe et al. (1989) reported, stayed close to their site of birth, and thus showed high site fidelity. Also, intra population dispersal has proved to occur more likely than inter population dispersal in feral pigs (Hampton et al. 2004b; Cowled et al. 2006).

As only a small amount of all marked animals (15.4%) dispersed, all others were either shot before reaching dispersal age or they did not disperse at all. All dispersed animals were older than 16 months, although males seem to be ready to leave their mother at the age of 11 months (Andrzejewski and Jezierski 1978; Truvé and Lemel 2003). However, these males might stay inside their mothers' home range and start dispersing later, actually, at least at 17 months or above (see also Andrzejewski and Jezierski 1978; Truvé and Lemel 2003). From the age of sexual maturity onwards, males were shot at larger mean distances than same-aged females, although some females might also disperse for several reasons (high population density, death of mother, division of group; Keuling et al. in preparation). The age of sexual maturity and starting dispersal corresponds with parturition of new piglets. As not every individual dispersed, a high variability existed. The small number of adult males prohibits statistical significant differences between males and females within this age class, similarly the high number of yearlings shot while still inside their natal home range. Only part of the population surviving the first year really does disperse (half of males and one sixth of females).

Table 2 Overview on literature data of distances between capture and shooting site of marked wild boar

Author	Study area	Mean distance (km)	Maximum distance (km)
Heck 1950	Europe		200
Andrzejewski and Jezierski 1978	PL		♂ >250
Dietrich 1984	Former DDR (D)		♂ 250
Dardaillon and Beugnon 1987; Spitz 1989	Camargue, F	20	68
Stubbe et al. 1989	Former DDR, five game research areas (ne D)	♂ Y 8 ♀ Y 6	
Briedermann 1990		♂ 4.5 ♀ 2.8	
Caley 1997	AUS	♂ 3.2 ♀ 1.8	♂ 22 ♀ 9
Eisfeld and Hahn 1998	D (sw)		♂ 17 ♀ 15
Sodeikat and Pohlmeyer 1999	D (n)	*P* <4.7 Y <10	♂ 23
Truvé 2004	D	♂ 16.6 ♀ 4.5	♂ >50
Jerina et al. 2005	SLO		75
This study	D (ne)	♂ 3.8 ♀ 1.6	♂ 42 ♀ 10

P piglet, *Y* yearling, ♂ male, ♀ female

The dispersal distances correspond to literature data (Table 2). This puts the impression of far dispersal into perspective, as a high proportion of both sexes stayed within their natal area (see also Briedermann 1990; Truvé 2004). Many male yearlings stayed within or near their natal home range and did not leave the core study area. However, as one third of all marked individuals are not replied dead so far and their actual home range is not known, we do not know whether they dispersed or not. Thus, for adults, a higher dispersal rate (especially of males) is quite likely. Numerous marked males are still alive and thus providing no information about potential dispersal so far. As male yearlings are likely to be shot during dispersal, their dispersal distances and rates might be higher under unhunted conditions.

Furthest dispersal distances are reported from long-term studies (Table 2) or from spreading populations (Sweden, Truvé 2004). For comparison of literature data and recent studies, we have to regard if the population is stable or spreading. In our case, the population seems to be more stable than in Sweden.

Female wild boar dispersal occurs seldom; only migrations after environmental changes or the death of the alpha sow have been observed yet (Meynhardt 1990). We did not observe such migrations after final divisions (see also

Keuling et al. in preparation) and only once without knowing the reason, which might have also been just a temporary excursion.

Nutritional conditions and population density influence dispersal of wild boar (Stubbe et al. 1989; Truvé 2004). Apart from hunting, dispersal (natal and dispersal and spontaneous adult dispersal) is the most important regulatory factor of wild boar populations in Central Europe. Short dispersal distances and low dispersal rates might result from sound nutritional conditions (compare Cargnelutti et al. 1992) inside the capture area, caused by frequent mast years, agricultural crops, and baiting sites (Keuling et al. 2008a, b, 2009) which enables higher big game population densities.

Wild boar space use, independent from sex, is quite small-scaled (Keuling et al. 2008a) and site loyal inside our study area. We could prove a high philopatry within wild boar with male-biased low dispersal rates, comparable to other studies (Stubbe et al. 1989; Briedermann 1990; Truvé 2004), as most individuals stayed near to their site of birth. Genetic exchange does result mainly from males (e.g., Hampton et al. 2004a); dispersal does mainly occur at very high population densities or in sparsely populated regions (Cargnelutti et al. 1992; Gabor et al. 1999).

Table 3 Overview on literature data of sex ratios

Foeti	Piglets	Yearlings	Adults	Total	Region	Author
	1.13:1 c 1.14:1	1.53:1	0.57:1	1.20:1	MV, D	This study
1.12:1	1.2:1	1.19:1			n-DDR (D)	Briedermann 1971
0.85:1				1.11:1	DDR (D)	Stubbe and Stubbe 1977
0.8:1	1.14:1 c 1.25:1	1.26:1	0.76:1<2 0.42:1>2		w-PL	Fruzinski and Labudzki 2002
				1.01:1	LUX	Cellina 2008
1.08:1					e-F	Servanty 2008
				0.98:1	s-CH	Moretti 1995
				1.24:1 c	Bologna, I	Fenati et al. 2008
	1.14:1	0.88:1	0.65:1	0.92:1	Piedmont, I	Durio et al. 1995
0.83:1	0.92:1	1.75:1	0.99:1	1.17:1	Tuscany, I	Boitani et al. 1995
				1.19:1	Tuscany, I	Massolo and Mazzoni della Stella 2006
0.83:1					H	Nàhlik and Sándor 2003
	1.75:1	1.12:1	0.42:1	1:1	Pyrenees, E	Herrero et al. 1995
	0.72:1	0.71:1			Barcelona, E	Cahill and Llimona 2004
0.88:1	0.74:1	0.44:1	0.39:1	0.8:1	w-E	Garzon-Heydt 1992
1.1:1				0.81:1	Cáceres, w-E	Fernández-Llario et al. 1999; Fernández-Llario and Mateos-Quesada 2003
				1.6:1	N.T., AUS	Caley and Ottley 1995
				1:1 c	N.S.W, AUS	Saunders 1993

c captured, all other are hunted

Efficiency of hunting

As the SR of the shot piglets equals the SR of captured piglets, there seems to be no sex-biased hunting in this age group. This is due to the missing ability of hunters distinguishing the sex in this age class. Nevertheless, the amount of shot piglets is too low. If these animals have to be shot at a higher age (yearlings), many female yearlings are not allowed to be shot as they lead piglets for the first time. It is of big importance to shoot more piglets at an early age (Genov et al. 1994; Bieber and Ruf 2005) to prevent them from becoming pubescent to reduce population increase. However, Genov et al. (1994) also promoted a higher hunting rate of older females, as this result in a lower productivity of the population. Reduction or regulation of a population is easier by shooting female yearlings and adults (Bieber and Ruf 2005; Servanty 2008). In our case, less female yearlings than needed for regulation were shot like in most other European studies (Table 3).

In our study, the harvest rate is less than the total net reproduction. This is also reflected by the permanently increasing annual hunting bag (see study area). Although some undetected mortality of the still not replied animals might exist (natural mortality and not replied), these cases are sparse. The population will increase further, a fact that Genov et al. (1994) already reported for most European countries. This bias between harvest and reproductive rate is based on an underestimation of population densities and reproduction rates (Genov et al. 1994).

Hunting from hides is the dominating hunting method and is highly effective (see also Briedermann 1977; Elliger et al. 2001; Liebl et al. 2005) as only 18 man-hours are needed per shot wild boar (Keuling et al. 2008b). Also, Doerr et al. (2001) described sharpshooting at bait as the most effective management tool for white-tailed deer *Odocoileus virginianus* in an urban area. Drive hunts are only held during winter (November–January), thus, they contribute only to a small amount to the annual hunting bag. As the main target game species in our study area are fallow deer *Dama dama*, the hunting pressure at the drive hunts in our study area is relatively low (Keuling et al. 2008b) compared to other studies where the hunts are mainly for wild boar, e.g., "monterias" in Spain, battues in France, and other parts of Germany (Herrero et al. 1995; Maillard and Fournier 1995; Sodeikat and Pohlmeyer 2007). The lower pressure by beaters, and especially less dogs, may be one reason for lower hunting bags. However, with 7.4%, the drive hunts (only held in winter in forested areas) contribute considerably to the total hunting bag, while being highly effective with only 14 man-hours per shot wild boar and causing only few and short time disturbances for all species (Keuling et al. 2008b). Intensifying drive hunts and a comprehensive combination of hunting methods might be an effective management tool (Calenge et al. 2002; Liebl et al. 2005).

References

Andrzejewski R, Jezierski W (1978) Management of a wild boar population and its effects on commercial land. Acta Theriol 23:309–339

Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. J Appl Ecol 42:1203–1213

Boitani L, Trapanese P, Mattei L, Nonis D (1995) Demography of a wild boar (*Sus scrofa* L.) population in Tuscany, Italy. Gibier Faune Sauvage 12:109–132

Briedermann L (1971) Zur Reproduktion des Schwarzwildes in der Deutschen Demokratischen Republik. Tag-Ber Akad Landwirtsch-Wiss Berlin 113:169–186

Briedermann L (1977) Jagdmethoden beim Schwarzwild und ihre Effektivität. Beitr zur Jagd- und Wildforschung 10:139–152

Briedermann L (1990) Schwarzwild, 2nd edn. Neumann-Neudamm, Melsungen

Cahill S, Llimona F (2004) Demographics of a wild boar *Sus scrofa* Linnaeus, 1758 population in a metropolitan park in Barcelona. In: Wild Boar Research 2002. A selection and edited papers from the "4th International Wild Boar Symposium". Galemys, 16 Special Issue, pp 37–52

Calenge C, Maillard D, Vassant J, Brandt S (2002) Summer and hunting season home ranges of wild boar (*Sus scrofa*) in two habitats in France. Game Wildl Sci 19:281–301

Caley P (1997) Movement, activity patterns and habitat use of feral pigs (*Sus scrofa*) in a tropical habitat. Wildl Res 24:77–87

Caley P, Ottley B (1995) The effectiveness of hunting dogs for removing feral pigs (*Sus scrofa*). Wildl Res 22:147–154

Cargnelutti B, Spitz F, Valet G (1992) Analysis of dispersion of wild boar (*Sus scrofa*) in Southern France. In: "Ongulés/Ungulates 91". Proc. Intern. Symp. Toulouse, pp 423–425

Cellina S (2008) Effects of supplemental feeding on the body condition and reproductive state of wild boar *Sus scrofa* in Luxembourg. PhD, University of Sussex

Cousse S, Spitz F, Hewison M, Janeau G (1994) Use of space by juveniles in relation to their postnatal range, mother, and siblings: an example in the wild boar, *Sus scrofa* L. Can J Zool 72:1691–1694

Cowled BD, Lapidge SJ, Hampton JO, Spencer PBS (2006) A cautionary finding for applied pest management: measuring the demographic and genetic effects of pest control in a highly persecuted feral pig population. J Wildl Manage 70:1690–1697

Dardaillon M (1988) Wild boar social groupings and their seasonal changes in Chamargue, southeastern France. Z Säugetierkd 53:22–30

Dardaillon M, Beugnon G (1987) The influence of some environmental characteristics on the movements of wild boar Sus scrofa. Biol Behav 12:82–92

Dietrich U (1984) Ergebnisse und Tendenzen der Forschungen am Wildschwein Sus scrofa in den Jahren 1975–1983. Säugetierkdl Mitt 31:223–237

Doerr ML, McAninch JB, Wiggers EP (2001) Comparison of four methods to reduce white-tailed deer abundance in an urban community. Wildl Soc Bull 29:1105–1113

Durio P, Gallo Orsi U, Macchi E, Perrone A (1995) Structure and monthly birth distribution of a wild boar population living in mountainous environment. Ibex J Mt Ecol 3:202–203

Eisfeld D, Hahn N (1998) Raumnutzung und Ernährungsbasis von Schwarzwild. Arbeitsbereich Wildökologie und Jagdwirtschaft, Forstzoologisches Institut Universität Freiburg

Elliger A, Linderoth P, Pegel M, Seitler S (2001) Ergebnisse einer landesweiten Befragung zur Schwarzwildbewirtschaftung. WFS-Mitteilungen, pp 5–7

Fenati M, Monaco A, Guberti V (2008) Efficiency and safety of Xylazine and Tiletamine/Zolazepam to immobilize captured wild boars (Sus scrofa L. 1758): analysis of field results. Eur J Wildl Res 54:269–274. doi:10.1007/s10344-007-0140-0

Fernández-Llario P, Mateos-Quesada P (2003) Population structure of the wild boar (Sus scrofa) in two Mediterranean habitats in the western Iberian Peninsula. Folia Zool 52:143–148

Fernández-Llario P, Carranza J, Mateos-Quesada P (1999) Sex allocation in a polygynous mammal with large litter size: the wild boar. Anim Behav 58:1079–1084

Fruzinski B, Labudzki L (2002) Management of wild boar in Poland. Z Jagdwiss 48(Suppl):201–207

Gabor TM, Hellgren EC, Van Den Busche RA, Silvy NJ (1999) Demography, sociospatial behaviour and genetics of feral pigs (Sus scrofa) in a semi-arid environment. J Zool Lond 247:311–322

Garzon-Heydt P (1992) Study of a population of wild boar Sus scrofa castilianus Thomas, 1912 in Spain, based on hunting data. In: 18th IUGB Congress, pp 489–492

Genov PW, Massei G, Kostova W (1994) Die Nutzung des Wildschweins (Sus scrofa) in Europa in Theorie und Praxis. Z Jagdwiss 40:263–267

Gerard JF, Cargnelutti B, Spitz F (1992) Relation entre anisotropie de l'occupation de l'espace et dispersion: un example chez le sanglier du sud-ouest de la France. Mammalia 56:177–187

Gethöffer F, Sodeikat G, Pohlmeyer K (2007) Reproductive parameters of wild boar (Sus scrofa) in three different parts of Germany. Eur J Wildl Res 53:287–297. doi:10.1007/s10344-007-0097-z

Gortázar C, Ferroglio E, Höfle U, Frölich K, Vicente J (2007) Diseases shared between wildlife and livestock: a European perspective. Eur J Wildl Res 53:241–256. doi:10.1007/s10344-007-0098-y

Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28:1140–1162

Groot Bruinderink GWTA, Hazebroek E (1996) Wild boar (Sus scrofa scrofa L.) rooting and forest regeneration on podzolic soils in the Netherlands. For Ecol Manag 88:71–80

Hampton J, Pluske JR, Spencer PBS (2004a) A preliminary genetic study of the social biology of feral pigs in south-western Australia and the implications for management. Wildl Res 31:375–381

Hampton JO, Spencer PBS, Alpers DL, Twigg LE, Woolnough AP, Doust J, Higgs T, Pluske JR (2004b) Molecular techniques, wildlife management and the importance of genetic population structure and dispersal: a case study with feral pigs. J Appl Ecol 41:735–743

Happ N (2002) Hege und Bejagung des Schwarzwildes. Franckh-Kosmos Verlags-GmbH & Co., Stuttgart

Heck L (1950) Schwarzwild. Bayerischer Landwirtschaftsverlag GmbH, München

Herrero J, García-Serrano A, García-Gonzáles R (1995) Wild boar (Sus scrofa L.) hunting in south-western Pyrenees (Spain): preliminary data. Ibex J Mt Ecol 3:228–229

Hooge PN, Eichenlaub B (2001) Movement 2.0. Alaska Biological Science Center, US Geological Survey, Ancorage, AK, USA

Jerina K, Adamic M, Krze B (2005) Influences of topography and highway as migration barrier on dispersal patterns of wild boar (Sus scrofa) in Slovenia. In: XXVIIth Congress of IUGB, 28 Aug–3 Sept extended abstracts, pp 133–135

Kaden V (1999) Bekämpfung der Klassischen Schweinepest beim Schwarzwild. Z Jagdwiss 45:45–59

Kaminski G, Brandt S, Baubet E, Baudoin C (2005) Life-history patterns in female wild boars (Sus scrofa): mother-daughter postweaning associations. Can J Zool 83:474–480

Keuling O, Stier N, Roth M (2008a) Annual and seasonal space use of different age classes of female wild boar Sus scrofa L. Eur J Wildl Res 54:403–412. doi:10.1007/s10344-007-0157-4

Keuling O, Stier N, Roth M (2008b) How does hunting influence activity and space use in wild boar Sus scrofa. Eur J Wildl Res 54:729–737. doi:10.1007/s10344-008-0204-9

Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? Different spatial usage patterns of wild boar Sus scrofa L. in forest and field crops during summer. Mamm Biol 74:145–152. doi:10.1016/j.mambio.2008.05.007

Killian G, Miller L, Rhyan J, Doten H (2006) Immunocontraception of Florida feral swine with a single-dose GnRH vaccine. Am J Reprod Immunol 55:378–384

Labudzki L, Wlazelko M (1991) Saisonale Dynamik der vom Schwarzwild im Feldanbau verursachten Schäden im Forschungsgebiet Zielonka. Z Jagdwiss 37:250–257

Liebl T, Elliger A, Linderoth P (2005) Aufwand und Erfolg der Schwarzwildjagd in einem stadtnahen Gebiet. WFS-Mitteilungen, pp 1–5

Maillard D, Fournier P (1995) Effect of shooting with hounds on home range size of wild boar (Sus scrofa L.) groups in Mediterranean habitat. Ibex J Mt Ecol 3:102–107

Markov NI, Neifel'd ND, Estaf'ev AA (2004) Ecological aspects of dispersal of the wild boar, Sus scrofa L., 1758, in the northeast of European Russia. Russ J Ecol 35:131–134

Massolo A, Mazzoni della Stella R (2006) Population structure variations of wild boar Sus scrofa in central Italy. Ital J Zool 73:137–144. doi:10.1080/11250000600727717

Meynhardt H (1990) Schwarzwild-Report, 8th edn. Neumann Verlag, Leipzig, Radebeul

Moretti M (1995) Birth distribution, structure and dynamics of a hunted mountain population of wild boars (Sus scrofa L.), Ticino, Switzerland. Ibex J Mt Ecol 3:192–196

Nàhlik A, Sándor G (2003) Birth rate and offspring survival in a free-ranging wild boar Sus scrofa population. Wildlife Biol 9 (Suppl):37–42

Nakatani J, Ono Y (1995) Grouping pattern of Japanese wild boar (Sus scrofa leucomystax). Ibex J Mt Ecol 3:128–129

Saunders G (1993) The demography of Feral pigs (Sus scrofa) in Kosciusko National Park, New South Wales. Wildl Res 20:559–569

Servanty S (2008) Dynamique d'une population chassée de sanglier (Sus scrofa scrofa) en milieu forestier. PhD, Univerité Claude Bernard Lyon

Servanty S, Gaillard J-M, Togo C, Lebreton J-D, Baubet E, Klein F (2005) Population management based on incomplete data: modelling the case of wild boar (Sus scrofa scrofa) in France. In: XXVIIth Congress of IUGB, 28 Aug–3 Sept extended abstracts, pp 256–257

Sodeikat G, Pohlmeyer K (1999) Untersuchungen zum Wanderverhalten des Schwarzwildes in schweinepestgefärdeten Gebieten

im östlichen Niedersachsen, Sachbericht 1998 an das Niedersächsische Ministerium für Ernährung, Landwirtschaft und Forsten. Institut für Wildtierforschung an der Tierärztlichen Hochschule Hannover

Sodeikat G, Pohlmeyer K (2007) Impact of drive hunts on daytime resting site areas of wild boar family groups (Sus scrofa L.). Wildl Biol Pract 3:28–38. doi:10.2461/wbp.2007.3.4

Sodeikat G, Papendiek J, Richter O, Söndgerath D, Pohlmeyer K (2005) Modelling population dynamics of wild boar (Sus scrofa) in Lower Saxony, Germany. In: XXVIIth Congress of IUGB, 28 Aug–3 Sept extended abstracts, pp 488–489

Spitz F (1989) Mortalité et dispersion chez le sanglier (Sus scrofa) de Camargue. Gibier Faune Sauvage 6:27–42. Gibier Faune Sauvage 6:27–42

Stubbe W, Stubbe M (1977) Vergleichende Beiträge zur Reproduktions- und Geburtsbiologie von Wild- und Hausschwein - Sus scrofa L., 1758. Beitr zur Jagd- und Wildforschung 10:153–179

Stubbe C, Mehlitz S, Peukert R, Goretzki J, Stubbe W, Meynhardt H (1989) Lebensraumnutzung und Populationsumsatz des Schwarzwildes in der DDR - Ergebnisse der Wildmarkierung. Beitr zur Jagd- und Wildforschung 16:212–231

Truvé J (2004) Pigs in space: movement, dispersal and geographic expansion of wild boar (Sus scrofa) in Sweden. Dissertation, University of Göteborg

Truvé J, Lemel J (2003) Timing and distance of natal dispersal for wild boar Sus scrofa in Sweden. Wildlife Biol 9 (Suppl):51–57

Errata

Paper II:
Page 2: "elder" should be "alder"
Page 9: "side" should be "site"

Erklärung

Hiermit versichere ich, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe; die aus fremden Quellen direkt oder indirekt übernommenen Gedanken sind als diese kenntlich gemacht worden. Bei der Auswahl und Auswertung des Materials sowie bei der Herstellung des Manuskripts habe ich keine externe Hilfe erhalten

Insbesondere habe ich nicht die Hilfe eines oder mehrerer Promotionsberater in Anspruch genommen. Dritte haben von mir weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit der vorgelegten Dissertation stehen.

Die Arbeit wurde bisher weder im Inland noch im Ausland in gleicher oder ähnlicher Form einer anderen Prüfungsbehörde zum Zwecke der Promotion vorgelegt.

Ich bestätige, dass ich die Promotionsordnung der Fakultät Forst-, Geo- und Hydrowissenschaften der TU Dresden anerkenne.

Dresden, den 17.09.2009

Oliver Keuling

Hinweis / Notice:

Veröffentlichung „Anhang V" / Paper „Appendix V" :

Keuling O, Lauterbach K, Stier N, Roth M (2009) Hunter feedback of
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