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

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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

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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

(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

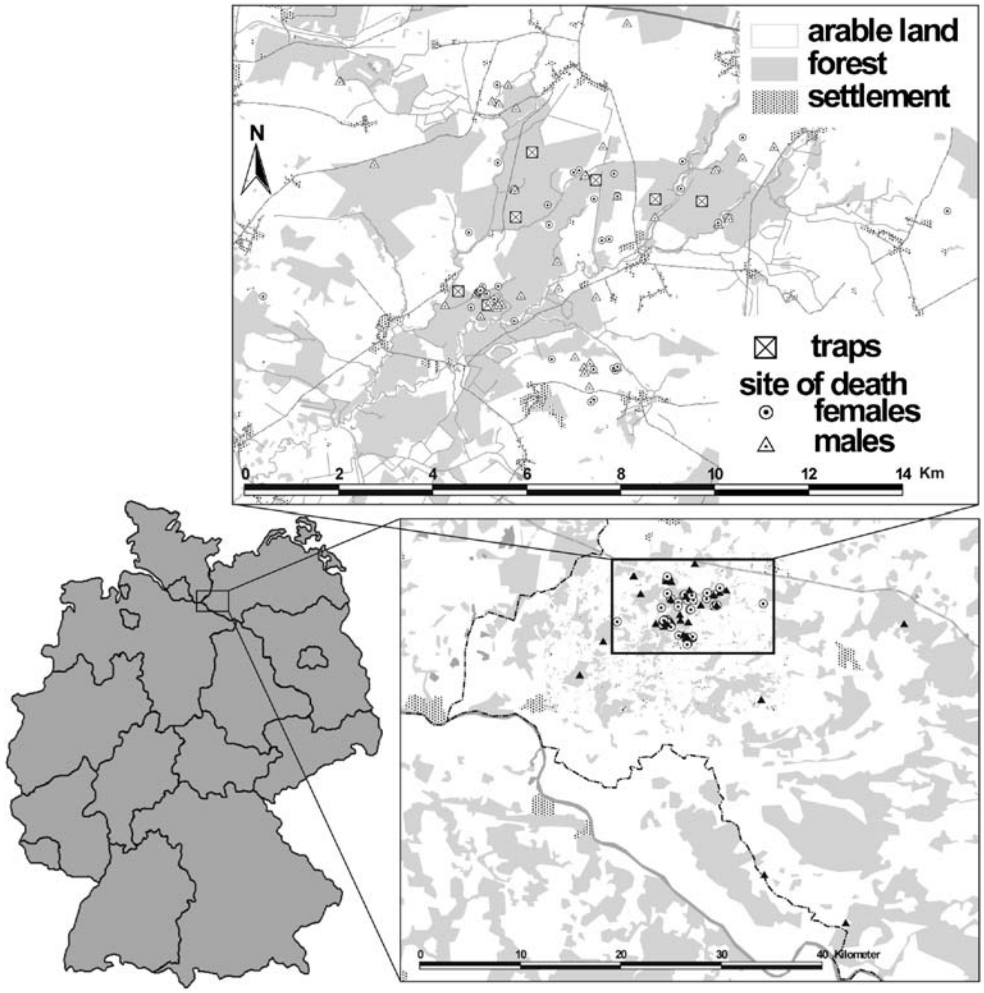

Fig. 1 Location of study area inside Germany, distribution of traps and sites of death of marked wild boar of different sexes

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,

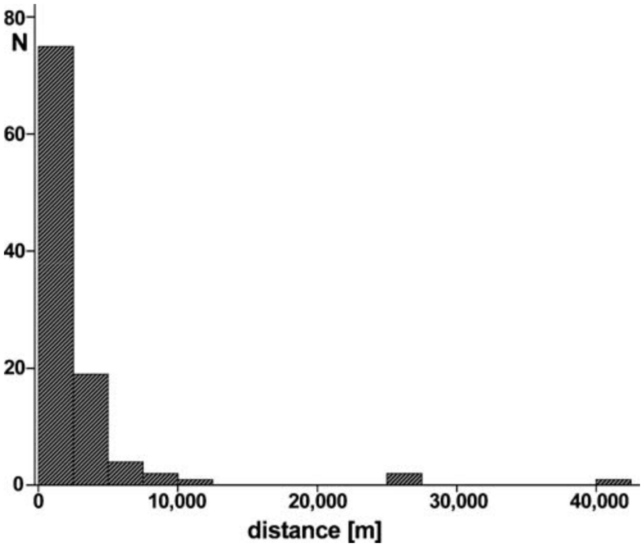

Fig. 2 Number of marked animals within distance-categories (metres) between capture site and site of death (N=104)

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\leq$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;

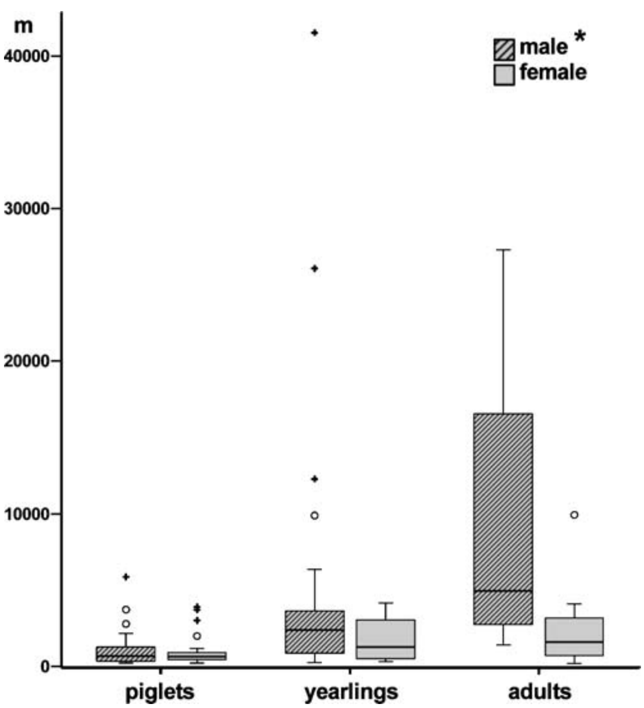

Fig. 3 Distances (metres) between capture site and site of death of marked wild boar of different sex and age class, piglets: male N=24, female N=22; yearlings: male N=26, female N=17; adult: male N=4, female N=11. Box and Whisker plots show median (*horizontal line within box*), 25% and 75% percentiles (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).

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